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**Interrelationships among families of the order Cypriniformes
(Teleostei)**

Siebert, Darrell J., Ph.D.

City University of New York, 1987

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INTERRELATIONSHIPS AMONG FAMILIES OF THE
ORDER CYPRINIFORMES (TELEOSTEI)

BY

DARRELL J. SIEBERT

A dissertation submitted to the Graduate Faculty
in Biology in partial fulfillment of the
requirement for the degree of Doctor
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ABSTRACT
INTERRELATIONSHIPS AMONG FAMILIES OF THE
ORDER CYPRINIFORMES (TELEOSTEI)

BY

DARRELL J. SIEBERT

Advisor: Dr. Gareth Nelson

A new classification expressing the interrelationships among families of the Cypriniformes is proposed. There are two great groups of cypriniform fishes, the Cobitidoidea, consisting of all non-cyprinid cypriniforms (Gyrinocheilidae, Catostomidae, Cobitididae, and Homalopteridae), and the Cyprinidae.

Cobitidoid monophyly is supported by an anterolateral process of the lateral ethmoid, palatamaxillary elements, interconnection of the preopercular and infraorbital laterosensory canals, and by an infraorbital series with the first infraorbital as the largest element and the second and third infrorbitals greatly reduced.

Within the Cobitidoidea monophyly of a catostomid-cobitidid-homalopterid group is supported by segmentation of the third copula of their basibranchial series into basibranchials 4-6, of which basibranchial 4 is characteristically shaped. Cobitidids and homalopterids together are a monophletic group as shown by their possession of an ossified basibranchial 4, ossified palatamaxillary elements, a transersus ventralis V process

on their ceratobranchial V, and size relationships within their epibranchial series. The Noemacheilinae as now known probably are not monophyletic. Nonetheless all noemacheilines are more closely related to fishes of the Homalopterinae than they are to cobitidids. Ellopostoma is postulated as the sister group of the Homalopterinae (homalopterins and gastromyzontins). Monophyly of the Homalopteridae, including the Noemacheilinae, is supported by a consolidation of their infrapharyngobranchial series, basihyal and basibranchial shape, and a free preopercular laterosensory canal.

Monophyly of the Cyprinidae (including Psilorhynchus) is supported by their capacious subtemporal fossa, ceratobranchial V morphology, the relationship between the infrapharyngobranchial series and the first epibranchial, and a distinctive circumorbital series.

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INTRODUCTION

Recently the interrelationships among the major groups of ostariophysans (gonorhynchiforms, cypriniforms, characiforms, siluroids and gymnotoids; fig. 1) have been examined (Fink and Fink, 1981) and set down in clear fashion open to test. This is an obvious step forward on the path toward an understanding of the systematics of one of the great vertebrate groups. The same sort of improvement of the classifications within the major subgroups of ostariophysans has yet to be achieved, but is the focus of active research. The aim of this work is to contribute to the improvement of the classification of one of those subgroups, the Cypriniformes.

Cypriniforms (sensu Fink and Fink, 1981) make up the largest component of the ostariophysans, the group of fishes that dominate the freshwaters of the world. Of the nearly 6,000 species of ostariophysans over 40% are cypriniforms. Nelson (1984) lists 256 genera and over 2,420 recognized species but the area in which cypriniforms are most diverse, Asia, is the region in which they are most poorly known and the number of species of cypriniforms actually may well exceed 3,000. Of the known species, most (over 2,000) belong to the Cyprinidae, the world's largest, and most widespread freshwater fish family. The remaining species belong to the families Gyrinocheilidae (2 species), Catostomidae (60-70 species),

Cobitididae (about 60 species) and Homalopteridae (about 225 species). They are found widely throughout Africa, Asia, Europe, North America and the islands of Sumatra, Java, Borneo, the Philippines, Taiwan, and Japan. In fresh waters of these regions cypriniforms are often the most abundant of all fishes. They are not naturally found in Australia, Central America south of northern Guatemala or South America. Their absence from South and most of Central America seems conspicuous and has puzzled some zoogeographers. Biogeography is perhaps the most difficult of all the biological disciplines and it is easy to forget that absence from a particular region is not what generally needs an explanation but that inhabitation of an area is the information basic to biogeography.

Cypriniforms are so diverse it is difficult to characterize them as a group. Gill (1905, 1907), writing mainly about the largest subgroup of them, the cyprinids, did as good a job as anyone who has cared to try. Suffice it to say, cypriniforms are diverse of habit. Commonly known in the English-speaking world as carps, barbs, bream, chubs, dace, hillstream fishes, loaches, minnows, shiners and suckers, they range in size from miniature (Roberts, 1986) to very large (to 2m and 45kg in North America, Miller, 1955; to 2.75m in Asia, Sen and Jayaram, 1982). Most species however, are small to moderately sized fishes. Collectively cypriniforms eat nearly

everything, as herbivores they consume diatoms to macrophytes and as carnivores zooplankton to macroinvertebrates and other fishes. They inhabit the span of freshwater habitats, from the chill of mountain streams to the hot aquatic environs of deserts and the tropics, and from swift lotic waters to still lentic ones. Cypriniforms vary in color from the drab and cryptic to strikingly colorful and marked. Economically the loaches and small, colorful southeast Asian minnows contribute substantially to the "aquarium" trade of fishes, and cyprinids support commercial and subsistence (especially in Asia) fisheries wherever they occur (Welcom, 1985). The most prized freshwater game fishes of all Asia are the Indian cyprinids, the mahseers (Sen and Jayaram, 1982).

What follows is a discussion of the development of cypriniform classification, a short section on methods, a new classification of the Cypriniformes at the family level and a discussion of evidence embodied in the new classification.

A HISTORY OF THE DEVELOPMENT OF PHYLOGENETIC
CLASSIFICATION OF CYPRINIFORMS

Classifications of fish groups that reflect phylogeny have been an explicit aim of ichthyologists since Garstang (1931) and have become more popular at least since Hennig (1966). Presentation of such a classification is the aim of this work. A phylogenetic objective is not likely to be taken as a controversial goal but what constitutes a phylogenetic classification may be open to debate. I have chosen to take as phylogenetic a classification that consists of an hierarchical arrangement of monophyletic groups and have chosen to employ Patterson's (1982) criterion of monophyly. Groups are monophyletic by this criterion if they are characterized by synapomorphy. Poly- and paraphyletic groups are not allowed.

With this in mind I have chosen to review the development of phylogenetic classification, as defined above, of cypriniform fishes (Cypriniformes of Fink and Fink, 1981). Others, especially Hensel (1970), have examined the history of cypriniform classification from a different perspective. Implicit in the development of a phylogenetic classification of cypriniforms has been a logical method of systematics. Such development, as with fish classifications in general, has been nothing more than the recognition, with subsequent corrective action by elimination, of para- and polyphyletic groups.

Throughout, the key to this progress has been, and remains, the discovery and recognition of characters (synapomorphies) that define natural groups. That a phylogenetic classification of cypriniforms wasn't established before now seems to have stemmed, initially, from a lack of character information across the great array of cypriniform fishes and, especially later, from a lack of explicit use of a logical method of systematics.

The development of cypriniform classification during the late eighteenth century and during the first three quarters of the nineteenth century was coincident with the development of fish classification in general. Then, as now, relationship was expressed by inclusion of a species within a group. Discovery of more and more cypriniform fishes and the recognition of more and more detailed relationships generated the need for a proliferation of classificatory levels. Linnaeus, dealing with relatively few organisms managed with just four categories, those of order, genus, species, and variety (Nelson and Platnick, 1981). Post-Linnean systematists, of necessity, exploited the territory between the categories of order and genus in their development of classifications.

The first unambiguous suprageneric but subordinal grouping of fishes that today we call the cypriniforms was that of Cuvier (1817), "des Cyprins" of "Ordre Malacopterygiens Abdominaux." Cuvier's "Cyprins" is not

unproblematic from a phylogenetic viewpoint but it does represent the first step forward in achievement of a phylogenetic classification of cypriniforms. His "des Cyprins", a family level category, contained cobitidids (loaches), cyprinids (carps), and what today are known as cyprinodontoids (some of the killifishes; Parenti, 1981). Classifications earlier than Cuvier's simply had listed cobitidids and cyprinids as two separate genera, Cobitis and Cyprinus, among the many but equal genera of malacopterygian fishes. It should be pointed out, however, that most of these early classifications did at least list Cobitis and Cyprinus sequentially (Linnaeus 1735, 1740; Artedi 1738; Gronovius 1754; Bloch and Schneider 1801). But to argue that the sequential listing of Cobitis and Cyprinus represents something of a grouping for cobitidids and cyprinids is imposing an ordering upon a list of genera in these early classifications in which groupings at this level, clearly, were not specified. More to the point, Linnaeus (1748, 1758, 1766) in the sixth, tenth, and twelfth and Gmelin (1788) in the thirteenth editions of Systema Naturae (and later C. C. Gmelin, 1818) placed Cobitis as one, if not the first, of the malacopterygian genera, but placed Cyprinus last with the whole range of remaining malacopterygian fishes interceding between the cobitidids and cyprinids.

Lacépède's (1803) ordering was, in the main, like that of Linnaeus and Gmelin.

Agassiz (1835,1838), after having observed that cobitidids and cyprinids possessed three branchiostegals, edentulous jaws, the characteristic pharyngeal mill of cypriniforms (features known to Cuvier), and a Weberian apparatus, removed all cyprinodontoids included by Cuvier in "des Cyprins" and put them in their own family (des Cyprinodontes, or der Cyprinodonten). Agassiz's family of cypriniforms, "der Karpfen", is today recognized as the Cypriniformes. The association of cyprinodontoids with cypriniforms that Agassiz redressed is itself interesting. Artedi, Gronovius, and Linnaeus, in his early editions of Systema Naturae, made no such association but listed what cyprinodontoids were known as separate malacopterygian genera. Then, Linnaeus (1758, 1766) and Gmelin (1788) included cyprinodontoids in Cobitis. But Bloch (1785), Bloch and Schneider (1801), and Lacépède (1803) continued to include cyprinodontoids in their classifications as separate genera without reference to any association with cypriniforms. Cuvier's inclusion of cyprinodontoids in "des Cyprins" in 1817 is mysterious except they, like cypriniforms, are malacopterygians lacking an adipose fin and possessing an abdominal placement of pelvic fins. Agassiz's disavowal of a close association between cypriniforms and

cyprinodontoids did not meet with universal acceptance. Müller (1842, 1846), in whose work definite signs of the beginning of the Ostariophysii can be found, and Heckel (1843) followed Agassiz but Valenciennes (in Cuvier 1836; Cuvier and Valenciennes 1842, 1846) pointedly retained Cuvier's grouping, as did McClelland (1838), Swainson (1838, 1839) and Bleeker (1859, 1860). Gill (1861) laid the discussion of an association between cyprinodontoids and cypriniforms to rest in a short assessment of the relationships among cypriniforms with clear approval of Agassiz's opinion on this particular matter.

Early classifications always recognized a distinction between cobitidids and cyprinids. Fitzinger (1832) amplified the distinction by suggesting a family level group and name, Cobitoidei, for them (he also associated them with catfishes rather than with cyprinids; as did Swainson, 1838, 1839). Agassiz (1835, 1838) suppressed Fitzinger's (1832) suggestion by recognizing, and emphasizing, the relationship among all cypriniforms as one family. For the most part once Cuvier had created a family level category for cypriniforms, progress was achieved by inserting additional classificatory levels between the family and genus levels. Along this vein McClelland (1838) proposed a classification of Cyprinidae that was a subfamily system for grouping of genera. One of the subfamilies he proposed, Apalopterinae, contained

primarily cobitidids along with cyprinodontoids, a grouping that maintained the tradition of a separation of cobitidids and cyprinids, but now within the family Cyprinidae. Heckel (1843, 1847) produced a tribe level system for Cyprinidae but, oddly, did not include any cobitidids in its formal presentation even though he did list cobitidid genera under Cyprinidae in various listings of regional faunas. This is a most intriguing aspect of his latter work (1847) as in it he suggested catostomids were near to cobitidids on the basis of pharyngeal arch structure, but did not so classify them. Bleeker (1859, 1860) progressed further than previous cypriniform workers in the development of classification. His cypriniform classifications contained three categories between family and genus, subfamilia, cohorts, and strips, that expressed a complex set of relationships for the entire range of cypriniforms within his "familia Cyprinoidei."

If Cuvier's and Agassiz's contributions are recognized as the first developmental step toward expressing relationship among cypriniforms, and the contribution of complex classifications by several workers as the second, Gill's contribution (1861) was the third, and for a long while the last, major advance toward a phylogenetic classification of cypriniforms. He performed two different, but related, actions. Gill (1861) restricted the limits of cyprinids to what today is a

demonstrably monophyletic group, the Cyprinidae. He accomplished this not so much by having discovered characters that define a cyprinid group though he did mention arrangement of pharyngeal teeth, but by having removed catostomids from Cyprinidae (the identification and correction of a polyphyletic group). Since their discovery by Forster (1773), up to Gill (1861), catostomids always had been recognized only as a subgroup of cyprinids. Gill's other contribution was to raise what since Cuvier had been recognized as a family (*des Cypins, der Karpfen, Cyprinidae, familia Cyprinoidei, etc.*) to the suborder level. A suborder level for all cypriniforms, Gill's "Eventognathi", allowed relationships to be expressed in a classification among what had become acknowledged generally as four familial level groups of cypriniforms: cyprinids, catostomids, cobitidids, and homalopterids. These four groups, in their essentials, have remained intact through to their continued existence today.

The view, from the vantage point of phylogenetic classification development, that Gill's contribution was the last step forward for a long while does not mean research on cypriniforms came to a stop or that classifications were not proposed for an extended period of time. Classifications were published but, fundamentally, they did not differ from Gill's.

Cypriniform research during the half century after Gill's 1861 paper yielded a wealth of anatomical data and a greater realization of the tremendous amount of cypriniform diversity that exists. Notable comprehensive classifications of cypriniforms were published by Günther (1868), Sagemehl (1891), Boulenger (1904), Goodrich (1909), and Regan (1911). While none of these was phylogenetically innovative, the growth of anatomical knowledge of cypriniforms can be traced through each classification, from classification to classification, by the greater detail in group diagnoses. Regan's investigation and proposal (1911) represents the acme of this trend, containing enough anatomical data to have been phylogenetically original. Why his classification wasn't so can only be subject to speculation. Perhaps lack of a clear logical systematic method with which to sort through all the accumulated information was the major deficiency that led to its lack of originality.

Günther's classification of this era (1868, and again in 1880) seems to have been strangely anacronistic. Regan (1911) credited Günther (1868) with the four major familial groups of cypriniforms recognized during the period but they can only be inferred to be present from the structure of the key Günther presented to the fourteen suprageneric groups of cypriniforms he admitted. Curiously, Günther (1868) did not cite Gill's 1861 paper

in his list of works consulted even though the list of Gill's other papers from the same year and journal as the "Eventognathi" paper was lengthy. Sagemehl's contribution (1885, 1891) of this period was especially large. His comparative study of cypriniform crania was remarkable and perhaps, like Regan later, his resultant classification suffered from a lack of precise methodology.

In 1902 Vaillant (1902a, 1902b) reported the existence of a new cypriniform genus, Gyrinocheilus, an event that in numerical terms did not loom large in expanding cypriniform diversity but does so in terms of its comprehension. So unusual was Gyrinocheilus that it soon (Boulenger 1904) began to be touted as the type of a new family, a reputation that was acted upon by Gill (1905) in a footnote, and more openly by Hora (1923). Vaillant, in the original description of Gyrinocheilus, prophetically suggested an alignment of the genus with noncyprinid cypriniforms. This suggestion that was not widely appreciated and was obscured by Hora's action since Hora did not at that time deal with the interfamilial relationships of gyrinocheilids in his paper.

By 1861 remarkable progress had been made toward a phylogenetic classification of cypriniforms. One tool utilized during that early period of achievement was the hierarchical arrangement of categories. It is notable that no attempt to express relationships among cypriniform

families with an hierarchical arrangement among them was made during the half century following Gill (1861). Cypriniform classification had achieved a sort of stasis with Gill's presentation (Gill, 1861), a stasis that would not be broken during the half century following Regan (1911) either. The fifty years following Regan (1911) can be characterized as an era of "evolutionary" classification, a period preoccupied with morphological specializations and a search for ancestry among cypriniform families. Many notions of ancestor-descendant relationships were postulated during this time but none was ever formalized into a written classification.

One of the major reasons the half century following Regan can be characterized as above is because the voluminous work of the era's most influential cypriniform worker, Sunder L. Hora, can be so characterized. Hora (1920), in one of his first published papers, presented notions of relationships among cypriniform families that are, in retrospect, amazingly perceptive, including the recognition of a relationship between cobitidids and homalopterids (fig. 2). But Hora, apparently influenced by Annandale, based his systematic decisions thereafter throughout his career on ideas of adaptive specializations and evolution (Hora, 1952). His feelings of relationships among cypriniform families changed dramatically during the decade of the 1920s, a period in which he undertook

studies of "the bionomics" of organisms living in fast flowing waters (Hora, 1930, 1932). Now, similarity of outward appearance among various cypriniform fishes likely was the result of adaptation to a particular environment and parallel evolution (Hora, 1923, 1925, 1932). Fishes that looked alike need not be closely related. Thus, he thought the Homalopteridae of previous workers was thought to be polyphyletic and divided it into the Homalopteridae (sensu stricto), said to have evolved from Cyprinidae, and the Gastromyzontidae, said to have evolved from Cobitididae (Hora, 1932, 1951, 1952), a conclusion far different from his ideas about cypriniform relationships presented in 1920. Hora's investigation of adaptive specialization also led him to suggest special recognition for small groups of fishes he felt were highly specialized. His proposal was to recognize Gyrinocheilus, Psilorhynchus, and the Gastromyzontinae as families (Hora, 1923, 1925, 1932, 1952). This action obscured the relationships of these taxa because even though definite ideas of relationship were often expressed (Hora felt Gyrinocheilidae was closest to Cyprinidae, Psilorhynchidae evolved from Cyprinidae and Gastromyzontidae from Cobitididae) the equal, coordinate rank afforded all cypriniform families in classification failed to express the hierarchical relationships among them. An Indian school of ichthyology developed around Hora, and

considerable effort by it was devoted in elaboration or defense of various aspects of his views regarding cypriniform relationships, including justification of family level recognition for small, highly specialized groups (Law, 1951; Hora and Jayaram, 1951; Silas, 1952; Ramaswami, 1952a, 1952b, 1952c, 1953, 1957). The enduring and widespread influence of Hora's views can be seen in a summary of views concerning evolution of cypriniforms published by Hensel (1970), much of which reads as a summary of Hora, and in J. Nelson's (1984) most recent summary of the views regarding cypriniform relationships. If coordinate recognition of many cypriniform groups tended to obscure their relationships, Hora's regional interest was another aspect of the overall problem. Relationships of the largely North American Catostomidae never really concerned him.

While Hora and the Indian school were preoccupied, mostly, with cypriniforms from India and other parts of Asia, some European, and North American ichthyologists in particular, were concerned with regional interests of their own, the relationships of the Catostomidae. A relationship among cobitidids, homalopterids, and cyprinids was accepted by them at one level or another; the question of primary interest for them was whether the Cyprinidae was ancestral to the Catostomidae or the Catostomidae ancestral to the Cyprinidae. It was as clear

to them as it was to Hora and the Indian school that specialized morphology was not likely to be ancestral to more generalized structure (Miller, 1959). Unfortunately their search for specialization of structure discovered, if taken as a whole, that all cypriniform families were specialized so as to preclude any family being ancestral to any other. Eaton (1935), commenting on upper jaw mechanism, found the Cyprinidae more primitive, and therefore ancestral, as did Jordan (1925) before him while Nichols (1930, 1938, 1943) felt the Cyprinidae were less primitive of the two and not likely the Catostomidae ancestor. Weisel (1960) reviewed these arguments, then opined that catostomids retained certain primitive habits but were highly divergent and therefore not good candidates for ancestors of other cypriniform groups. He argued that a comparative study of all cypriniforms together, or fossil clues which he did not specify, would be necessary to settle the question, an argument that in my view is in vain without an additional change in perspective. Like Hora and his colleagues, non-Indian cypriniform workers never transcribed their efforts into hierarchical classifications of families (Jordan, 1923; Nichols, 1930, 1938; Berg, 1947; Fowler, 1975).

The inertia that gripped cypriniform classification for a century following Gill (1861), began to dissipate during the decade of the 1960s. First Greenwood et al.

(1966) published a new classification of teleost orders in which they suggested a close relationship among cobitidids, homalopterids, and gastromyzontids, reviving an old idea of Hora's (Hora, 1920; fig. 2). But their thinking was yet grounded in ancestor-descendant relationships (they agreed with Jordan (1925) and Eaton (1935) that cyprinids were most primitive), and specializations of the Catostomidae, the Cyprinidae, and the Cobitididae-Homalopteridae-Gastromyzontidae group vexed them and precluded obvious resolution. Lundberg and Marsh (1976) reviewed the relationships of families of cyprinoid fishes (= cypriniforms) and published a diagram that summarized their view which could be described as the prevailing one of the times. The lack of resolution of relationships among families in their diagram is noteworthy, and characteristic of the prevailing view. The only relationship clearly expressed is one between "Gastromyzonidae" and "Cobitidae." The solution to the problem of perplexing distribution of morphological specializations among cypriniforms that denied ancestral status to any group of them has its beginnings in Nelson's (1969a) classification of teleostomes, a classification based on his investigations of gill arches. His specific contribution was the suggestion that catostomids might be related to cobitidids and homalopterids. But the most important contribution was a general one, one that allows

resolution of vexing distributions of morphological specializations among taxa. No longer were groups thought of as ancestral or descendant, but instead related as sister groups. This change in perspective is the crucial element missing from Weisel's (1960) and Greenwood et al.'s (1966) analyses. In this newer mode of thinking, all groups could be specialized and still related hierarchically as sister taxa. Nelson did not formally propose a classification of cypriniform families but his foundation was built upon by Wu et al. (1981), and Sawada (1982). They were the first to actually propose classifications in which cypriniform families were related hierarchically. Their tactic was to subordinate families in superfamilies, the same subordination tool exploited to such good end prior to Gill (1861).

Both Sawada (1982) and Wu et al. (1981) used cladistic methods in their studies. Sawada's study was more limited in scope, concentrating on homalopterid and cobitidid fishes. He supported G. Nelson's (1969a) view that cobitidids and homalopterids were closely related and suggested a superfamily grouping of them, the "Cobitoidea". Wu et al. (1981) investigated familial relationships among all cypriniform families, using a characoid model to polarize their morphoclines. Their results (fig. 3) are novel in some ways, yet embody many of the ideas prevalent during the post-Regan era when

evolutionism intruded into the classification of cypriniforms. Most notably, they argue for a close relationship between homalopterids and cyprinids (an old idea of Hora's, 1932) and a close relationship among gyриноcheilids, catostomids, and cobotidids, an argument that is novel in its totality and has its beginnings in Ramaswami (1957). The latter relationship was expressed in a classification as the Catostomidea. This choice of basing the superfamilial name on Catostomoidae was unfortunate (explained below in the A NEW CLASSIFICATION OF CYPRINIFORMES section) and their analysis of cypriniform morphology would have benefitted from a wider outgroup analysis than what they employed. Despite whatever criticism might be said of their result, it is significant that they recognized groups of families of cypriniforms and expressed these relationships as a hierarchical classification of families.

G. Nelson's (1969a) and Sawada's (1982) view conflicts with that of Wu et al. (1981). Nelson and Sawada did not study all cypriniform families and it is difficult to directly compare their view with that of Wu et al. on the totality of cypriniform relationships. However, a direct comparison of the relationships of the four families common to Nelson's (1969a), Sawada's (1982) and Wu et al.'s study is possible and illustrative (fig. 4) Such a comparison reveals the current state of affairs

regarding cypriniform relationships, and the need for further study.

METHODS

Systematic. This work seeks to establish a classification of cypriniform families, a base from which further study may proceed. The classification is based on a study of some aspects of the morphology of cypriniform fishes. Analysis of the morphological data uncovered during this study employed cladistic methods. Much has been written about this methodology (Hennig, 1979; Eldredge and Cracraft, 1980; Nelson and Platnick, 1981; Wiley, 1981) and considerable misunderstanding surrounds discussion of it (reviewed by Janvier, 1984; exemplified by Dawkins, 1986). So much has been written concerning cladistic methods that there is little need to detail their use, however even within the group of systematists who themselves profess to be cladists there is misunderstanding and a variety of objectives. This climate of misunderstanding and multiple intentions demands clear statements concerning aims and methods, even to the point of saying what has been said before elsewhere.

My thoughts and understanding of cladistic methods follow the expositions of Nelson and Platnick (1981) and Patterson (1982). Essentially I adhere to the taxic, rather than transformational, approach (Eldredge and Cracraft, 1980; Patterson, 1982) to the evolutionary questions addressed in systematic studies. This amounts to the identification of monophyletic groups, something

that is accomplished by studying the interrelationships among organisms and groups of organisms. In particular, I have sought, mainly, to recognize interrelationships at, and above, the family level group. These interrelationships are expressed in the classification by inclusion of a group within a more inclusive taxon. Recognition of these interrelationships depends on identification of synapomorphous features (synapomorphies = homologies; Patterson, 1982) among groups in question, synapomorphies being those features that characterize monophyletic groups.

Identification of synapomorphous features among groups is not an easy endeavor. At its simplest, it is the search for the level of generality at which an attribute can be considered a unique feature characterizing a group of organisms. As an example, all cypriniforms possess a set of particular modifications of the four anteriormost vertebrae. This set of modifications is called the Weberian apparatus yet the Weberian apparatus is not a synapomorphy of cypriniforms, even though they all have it. The level of generality at which it can appropriately be considered to characterize a monophyletic group is the one that includes Chanoides macrapoma, characiforms, gymnotoids and siluroids as well as cypriniforms (the group so characterized is the Otophysi). Clearly, as this example shows, to pick out

features that are synapomorphic at the particular level of generality appropriate to the systematics of cypriniforms requires knowledge wider than that of just cypriniforms. How wide a knowledge is necessary is not easy to specify, "wide enough to be sure about your decisions" is about all that can be said. Simple "immediate" outgroup consideration just within otophysans has led to synapomorphy hypotheses that are incorrect (eg., Lo and Wu, 1979; Wu et al., 1981). In my estimation to avoid the pitfalls that might be encountered along a path employing immediate outgroup methods, knowledge at the levels of generality of all otophysans, all ostariophysans, within lower euteleosts and even among lower teleosteans is desirable in efforts to identify synapomorphies among cypriniforms (fig. 5). These levels of ever increasing generality can be daunting but need not be. Each more inclusive level throws into the arena of investigation additional, sometimes huge, numbers of kinds of organisms, too many for any one investigator to examine individually (conservative estimates suggest there are over 6,000 ostariophysan species and within the realm of consideration among lower eutelosteans and lower teleosteans, another 2,000 species). Pragmatically, sampling is a necessity along with a good deal of reliance on previously published works. Even within cypriniforms sampling is required as there are, likely, more than 3,000

species of them. I have tried to obtain for examination representatives from as many genera of cypriniforms from as many different parts of the range of cypriniforms as I could. Defense as monophyletic of all genera included in this study is neither intended, nor implied. It is assumed that the species examined are representative of nominate genera, an assumption that ichthyologists familiar with cypriniforms know is not met frequently, at least not among cyprinids. This does not diminish the value of the study and resultant classification for two reasons. First, this is a classification at and above the family level, a level at which groups are shown to be monophyletic. Second, when suggestions of the interrelations below the family level are made, the classification of the species studied remains defensible even if the genera in which the species are currently placed are not monophyletic. This is a criticism of the efficacy of those particular genera; the classification of the individual species remains as a base from which to proceed with further studies of monophyly of questionable genera.

The classification presented here is a classification of cypriniform families. It is not intended as a phylogeny of the included groups. Such interpretations can be made of it and some argue that such classifications are isomorphic with phylogeny (Wiley,

1979a). This may be so in the sense that this sort of classification is about evolution in that it is a classification of organisms based on monophyletic groups. But it DEFINITELY is not so in any sense of ancestor - descendant relationships that often come into mind when the term phylogeny is bandied about. Those kinds of relationships have been shown not to be about monophyletic groups (Patterson, 1982) and have been exposed to falsification and shown false in the context of classifications (Nelson and Platnick, 1984).

Specimen Preparation. Most of the material examined for this study is what some call "alizarins" and others call "cleared and stained material." Material of this type has been prepared either by KOH maceration with staining of calcified and ossified tissue with alizarin red or enzyme maceration with counterstaining of calcified or ossified tissue with alizarin red and cartilagenous tissue with alcian blue. The latter technique is the more "modern" approach and does usually make study of certain types of cartilage easier. Most of the cleared and stained material used in this study was counterstained following the technique outlined by Dingerkus and Uhler (1977). Whenever possible several, or at least more than one, specimens were prepared and examined. Individual variation was not the focus of this study but by examining

more than a single specimen some attempt was made to discover whether the material examined could reasonably be considered representative and not aberrant. A glance at the material examined list will reveal however that this was not always possible.

Observations of myology were made on materials preserved in alcohol and dissected. Cleared and stained materials, even though macerated, also were examined because careful study of them, especially of KOH macerated material, often reveals myologic details.

Illustrations of osteology are tracings from pencil drawings made under a camera lucida attached to a Wild M8 zoom stereo-microscope.

Vernacular Usage. The following conventions are employed for the use of vernaculars in the stead of formal names of higher taxonomic groups. First, no vernacular begins with a capital letter, unless it is the initial word of a sentence. Second, vernaculars carry the following standardized endings:

- a) in endings indicate a vernacular for a tribal name (e.g. homalopterin for Homalopterini);
- b) ine endings indicate a vernacular for a subfamilial name (e.g. gastromyzontine for Gastromyzontinae);

- c) id endings indicate a vernacular for a familial name (e.g. catostomid for Catostomidae);
- d) oid endings indicate a vernacular for a subordinal or superfamilial name (e.g. cobitidoid for Cobitidoidea);
- e) form endings indicate a vernacular for an ordinal name (e.g. cypriniform for Cypriniformes);

Formal group name endings of taxonomic groups above the level of order are not bound by established convention. Vernaculars used here for those kinds of group names are simply those in current use (e.g. elopomorph for Elopomorpha, ostariophysan for Ostariophysi, and teleost or teleostean for Teleostei; see fig. 5 for other examples).

ABBREVIATIONS.

Institutional.

- AMNH - American Museum of Natural History; New York,
N. Y.
- ANSP - Academy of Natural Sciences; Philadelphia, Pa.
- ASU - Arizona State University; Tempe, Az.
- BMNH - British Museum (Natural History); London,
England.
- FMNH - Field Museum of Natural History; Chicago,
Il.
- UMMZ - Museum of Zoology, Univ. Michigan; Ann Arbor,
Mi.
- USNM - National Museum of Natural History;
Smithsonian Institution, Washington, D.C.

Anatomical.

- AA - afferent artery
- Ah - anterohyal
- alp - anterolateral lateral ethmoid process
- Bb 1-6 - basibranchial 1-6
- Bh - basihyal
- Boc - basioccipital
- BTP - basihyal tooth plate
- Cb I-IV - ceratobranchial I-IV
- cbVc - ceratobranchial V cartilage
- Cl - cleithrum

DA	- dorsal aorta
DP	- dermal plate
EA I-IV	- efferent artery I-IV
EAT	- efferent artery trough
Eb I-IV	- epibranchial I-IV
Epi	- epioccipital
Exo	- exoccipital
Fr	- frontal
Ib IV	- interbranchial IV
Ic	- intercalar
Ic-Pc	- infraorbital and preopercular canal interconnection
Ic-Tc-Sc	- infraorbital, temporal, and supraorbital canal interconnection
icno	- infraorbital canal neuromast ossification
ILC	- infraorbital laterosensory canal
Io 1-6	- infraorbital bone 1-6
Ipb I-IV	- infrapharyngobranchial I-IV
kbb	- ventral keel of basibranchial 4
Ke	- kinethmoid
Le	- lateral ethmoid
leb I-III	- laminar extension of epibranchial I-III
LExof	- lateral exoccipital fenestra
lio	- laminar infraorbital canal ossification
Mes	- mesethmoid
Mppl	- mesioprepalatine

Mx	- maxillary
nilo	- infraorbital 1 neuromast ossification
NR	- nasal ribbon ossification
nrf	- nasal ribbon foramen
oil	- ossified portion of infraorbital 1
Op	- opercular
OR	- orbital rim
Osp	- orbitosphenoid
Pa	- parietal
Pal	- palatine
Pas	- parasphenoid
PbTp	- pharyngobranchial tooth plate
Pcl	- postcleithrum
PCrF	- posterior cranial fontanelle
Pc-Tc	- preopercular and temporal canal interconnection
Pe	- pre-ethmoid
PLC	- preopercular laterosensory canal
Pmx	- premaxillary
Ppl	- prepalatine
Pop	- preopercular
Pro	- prootic
Pt	- posttemporal
Pto	- pterotic
PTF	- post-temporal fossa
2pe	- second pre-ethmoid

Qu	- quadrate
rcp	- rectus communis prong
Scl	- supracleithrum
SL	- sigmoid ligament
Sl	- sublingual
So	- supraorbital
Soc	- supraoccipital
Sos	- suborbital spine
SpO	- suprapreopercular
St	- supratemporal
SLC	- supraorbital laterosensory canal
STF	- subtemporal fossa
t	- tooth
Tc-Stc	- temporal canal and supratemporal comissure interconnction
TLC	- temporal laterosensory canal
tvp	- transversus ventralis process
UEb	- unciniate process of Eb I-IV
uil	- unossified portion of infraorbital 1
UL	- confluent unciniate process
UIpb I-IV	- unciniate process of infrapharyngobranchial I-IV
VA	- ventral aorta
Vo	- vomer

MATERIALS EXAMINED

GYRINOCHEILIDAE

<u>Gyrinocheilus aymonieri</u>	AMNH	77898SW	C/S	(12)
<u>Gyrinocheilus aymonieri</u>	AMNH	77898	Alch	(4)
<u>Gyrinocheilus</u> sp	USNM	272884	Alch	(1)
				(gill arches removed and C/S)

HOMALOPTERIDAE

Neomacheilinae

<u>Lefua echigonia</u>	AMNH	37356	C/S	(7)
<u>Noemacheilus barbatulus</u>	AMNH	37608	C/S	(4)
<u>Noemacheilus posteroventralis</u>	AMNH	29706	C/S	(5)
<u>Noemacheilus posteroventralis</u>	AMNH	10323	Alch	(57)
<u>Noemacheilus pulcher</u>	AMNH	10347	C/S	(3)
<u>Noemacheilus pulcher</u>	AMNH	10284	Alch	(30)
<u>Noemacheilus senlangoricus</u>	AMNH	48937	C/S	(2)
<u>Noemacheilus stoliczkai</u>	AMNH	10350SW	C/S	(4)

Ellopostominae

<u>Ellopostoma</u> sp	AMNH	55110	C/S	(1)
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Homalopterinae

Homalopterini

<u>Homaloptera amphisquamata</u>	AMNH	9257	C/S	(2)
<u>Homaloptera orthogoniata</u>	AMNH	77899	C/S	(1)
<u>Lepturichthys fimbriata</u>	AMNH	10335	C/S	(4)

Gastromyzontini

<u>Beaufortia zebroides</u>	AMNH	11054	C/S	(6)
<u>Beaufortia leveretti</u>	AMNH	10281	C/S	(2)
<u>Crossostoma davidi</u>	AMNH	10282	C/S	(4)
<u>Gastromyzon borneensis</u>	AMNH	77900	C/S	(2)
<u>Glanioptis denudata(?)</u>	AMNH	77901	C/S	(1)
<u>Pseudogastromyzon myersi</u>	AMNH	50152	C/S	(1)
<u>Vanmanenia caldwelli</u>	AMNH	11138	C/S	(5)

COBITIDIDAE

Cobitidinae

<u>Acanthopthalmus kuhli</u>	AMNH	77902	C/S	(3)
<u>Acanthopsis choirorhynchos</u>	FMNH	68146	C/S	(3)
<u>Cobitis aurata</u>	AMNH	20669SW	C/S	(4)
<u>Cobitis taenia</u>	AMNH	20366	C/S	(2)
<u>Lepidocephalichthys berdmorei</u>	AMNH	13808SW	C/S	(2)
<u>Lepidocephalus hasselti</u>	AMNH	9266SW	C/S	(2)
<u>Lepidocephalus thermalis</u>	AMNH	40956	C/S	(2)
<u>Misgurnus anguillicaudatus</u>	AMNH	77903	C/S	(1)
<u>Misgurnus mizolepis</u>	AMNH	17928	C/S	(5)
<u>Misgurnus mizolepis</u>	AMNH	10362	C/S	(25)

Botiinae

<u>Botia macracanthus</u>	AMNH	56394SD	Skel	(3)
(Aq. Mat.)				
<u>Botia macracanthus</u>	AMNH	77904SW	C/S	(2)
<u>Botia macracanthus</u>	AMNH	77904	Alch	(2)

<u>Botia modesta</u>	AMNH	77905	C/S	(1)
<u>Botia purpurea</u>	AMNH	10419SW	C/S	(2)
<u>Leptobotia fasciata</u>	AMNH	10298SW	C/S	(1)
<u>Vaillantella euepiptera</u>	AMNH	48938	C/S	(1)

CATOSTOMIDAE

Ictiobinae

<u>Carpiodes carpio</u>	UMMZ	180304	C/S	(17)
<u>Carpiodes cyprinus</u>	AMNH	45964	C/S	(1)
<u>Carpiodes sp</u>	AMNH	21694	Skel	(1)
<u>Carpiodes velifer</u>	UMMZ	67046	C/S	(5)
<u>Cycleptus elongatus</u>	AMNH	uncat.	C/S	(2)
<u>Cycleptus elongatus</u>	AMNH	77906SD	Skel	(1)
<u>Ictiobus bubalus</u>	AMNH	77907	C/S	(2)
<u>Ictiobus bubalus</u>	AMNH	77908	Xray	(1)
<u>Ictiobus labiosus</u>	UMMZ	189565	C/S	(13)
<u>Ictiobus meridionalis</u>	AMNH	27804SD	Skel	(1)
<u>Ictiobus meridionalis</u>	AMNH	27940SD	Skel	(1)
<u>Ictiobus sp</u>	AMNH	22711	Skel	(1)
<u>Myxocyprinus asiaticus</u>	AMNH	10612	Xray	(1)
<u>Myxocyprinus asiaticus</u>	AMNH	37501	Xray	(1)
<u>Myxocyprinus asiaticus</u>	AMNH	10437	Xray	(1)
<u>Myxocyprinus asiaticus</u>	AMNH	11629	Xray	(1)
<u>Myxocyprinus asiaticus</u>	AMNH	11629SW	C/S	(1)
<u>Myxocyprinus asiaticus</u>	AMNH	77909	C/S	(1)

Catostominae

<u>Catostomus</u> <u>bernardini</u>	AMNH	77910SD	Skel	(1)
<u>Catostomus</u> <u>catostomus</u>	AMNH	41156	C/S	(3)
<u>Catostomus</u> <u>columbianus</u>	AMNH	36281	C/S	(1)
<u>Catostomus</u> <u>commersoni</u>	AMNH	40549	C/S	(1)
<u>Catostomus</u> <u>commersoni</u>	AMNH	43509	C/S	(2)
<u>Catostomus</u> <u>commersoni</u>	AMNH	43520	C/S	(1)
<u>Catostomus</u> <u>commersoni</u>	AMNH	43551	C/S	(3)
<u>Catostomus</u> <u>commersoni</u>	AMNH	43638	C/S	(2)
<u>Catostomus</u> <u>insignis</u>	ASU	64-1236	Skel	(1)
<u>Catostomus</u> <u>occidentalis</u>	AMNH	21699	C/S	(2)
<u>Catostomus</u> <u>wigginsii</u>	AMNH	77911SW	C/S	(2)
<u>Erimyzon</u> <u>oblongus</u>	AMNH	43772SW	C/S	(12)
<u>Erimyzon</u> <u>oblongus</u>	AMNH	42802SW	C/S	(1)
<u>Erimyzon</u> <u>oblongus</u>	AMNH	39405	C/S	(1)
<u>Erimyzon</u> <u>oblongus</u>	AMNH	42433	C/S	(3)
<u>Erimyzon</u> <u>sucetta</u>	AMNH	27254	C/S	(1)
<u>Hypentelium</u> <u>etowanum</u>	AMNH	53009	C/S	(11)
<u>Hypentelium</u> <u>nigricans</u>	AMNH	49057	C/S	(1)
<u>Hypentelium</u> <u>nigricans</u>	AMNH	44529	C/S	(1)
<u>Hypentelium</u> <u>roanokense</u>	AMNH	70818	C/S	(3)
<u>Minytrema</u> <u>melanops</u>	AMNH	22208SW	C/S	(1)
<u>Minytrema</u> <u>melanops</u>	AMNH	52995	C/S	(1)
<u>Minytrema</u> <u>melanops</u>	AMNH	65313	Alch	(5)
<u>Minytrema</u> <u>melanops</u>	USCRC98SU57		Xray	(4)
<u>Moxostoma</u> <u>anisurum</u>	AMNH	42088	C/S	(5)

<u>Moxostoma anisurum</u>	AMNH 39315	C/S	(4)
<u>Moxostoma ariommum</u>	USNM 203034	Xray	(1)
<u>Moxostoma ariommum</u>	USNM 203108	Xray	(1)
<u>Moxostoma cervinum</u>	AMNH 70821	C/S	(9)
<u>Moxostoma cervinum</u>	AMNH 70819	C/S	(2)
<u>Moxostoma erythrurum</u>	AMNH 45976	C/S	(2)
<u>Moxostoma erythrurum</u>	AMNH 42932	C/S	(4)
<u>Pantosteus clarki</u>	AMNH 27286	C/S	(1)
<u>Pantosteus clarki</u>	ASU 64-1214	Skel	(1)
<u>Thoburnia atripinne</u>	AMNH 54633	C/S	(3)
<u>Thoburnia hamiltoni</u>	AMNH 70822	C/S	(3)
<u>Thoburnia rhothoecum</u>	AMNH 8010	C/S	(4)
<u>Thoburnia rhothoecum</u>	AMNH 65885	C/S	(5)
<u>Thoburnia rhothoecum</u>	AMNH 66449	C/S	(7)
<u>Xyrauchen texanus</u>	AMNH 30848SD	Skel	(1)

CYPRINIDAE

<u>Abramis ballerus</u>	AMNH 20380	C/S	(2)
<u>Abramis brama</u>	AMNH 37594	C/S	(2)
<u>Acanthorhodeus guichenoti</u>	AMNH 10233	C/S	(2)
<u>Acheilognathus intermedius</u>	AMNH 26933	C/S	(5)
<u>Acrocheilus alutaceus</u>	AMNH 54631	C/S	(4)
<u>Agosia chrysogaster</u>	AMNH 17288	C/S	(4)
<u>Agosia chrysogaster</u>	AMNH 27250	C/S	(5)
<u>Alburnus alburnus</u>	AMNH 20536	C/S	(4)
<u>Aopidoparia sp</u>	AMNH 55112	C/S	(1)

<u>Aphyocypris chinensis</u>	AMNH	10969	C/S	(5)
<u>Balanteocheilus melanopterus</u>	AMNH	77920SD	Skel	(1)
<u>Barbus ablades</u>	AMNH	32726	C/S	(3)
<u>Barbus barbus</u>	AMNH	54635	C/S	(3)
<u>Barbus conchoniuis</u>	AMNH	14622	C/S	(1)
<u>Barbus matsudai</u>	AMNH	11104	C/S	(5)
<u>Barilius barna</u>	AMNH	13794	C/S	(3)
<u>Barilius ubangensis</u>	AMNH	12411	C/S	(2)
<u>Blicca bjoerkna</u>	AMNH	37599	C/S	(2)
<u>Brachydanio albolineatus</u>	AMNH	54630	C/S	(3)
<u>Campostoma anomalum</u>	AMNH	4902	C/S	(4)
<u>Campostoma anomalum</u>	AMNH	40260SW	C/S	(1)
<u>Capoeta damascina</u>	AMNH	40951	C/S	(2)
<u>Chela anomalurus</u>	AMNH	36373	C/S	(1)
<u>Chela oxygastroides</u>	AMNH	36368	C/S	(1)
<u>Chelaethiops elongatus</u>	AMNH	6212	C/S	(2)
<u>Chondrostoma nasus</u>	AMNH	55111	C/S	(1)
<u>Chondrostoma nasus</u>	AMNH	18078	C/S	(2)
<u>Chondrostoma ohridanus</u>	USNM	257748	C/S	(2)
<u>Cirrhinus chinensis</u>	AMNH	37021	C/S	(2)
<u>Clinostomus elongatus</u>	AMNH	45955	C/S	(5)
<u>Couesius plumbeus</u>	AMNH	41266	C/S	(5)
<u>Ctenopharyngodon idella</u>	AMNH	77912SW	C/S	(2)
<u>Ctenopharyngodon idella</u>	AMNH	77913SD	Skel	(4)
<u>Culter alburnus</u>	USNM	86997	C/S	(2)
<u>Cyclocheilichthys armatus</u>	AMNH	48918	C/S	(1)

<u>Cyprinion irregulare</u>	AMNH	35528	C/S	(2)
<u>Cyprinus carpio</u>	AMNH	48088	C/S	(1)
<u>Cyprinus carpio</u>	AMNH	10160SD	Skel	(1)
<u>Cyprinus carpio</u>	AMNH	77914	Skel	(1)
<u>Dangila festiva</u>	AMNH	77919SW	C/S	(1)
<u>Danio aequipinnatus</u>	AMNH	15761	C/S	(2)
<u>Danio malabaricus</u>	AMNH	77915	C/S	(2)
<u>Dionda episcopa</u>	AMNH	17873	C/S	(1)
<u>Elopichthys bambusa</u>	USNM	130383	C/S	(1)
<u>Engraulicypris sardella</u>	AMNH	31917	C/S	(5)
<u>Epalzeorhynchus kalopterus</u>	AMNH	10202	C/S	(2)
<u>Ericymba buccata</u>	AMNH	42928	C/S	(5)
<u>Ermichthys acros</u>	AMNH	27236	C/S	(3)
<u>Esomus metallicus</u>	AMNH	40851	C/S	(4)
<u>Exoglossum maxillingua</u>	AMNH	45747	C/S	(5)
<u>Exoglossum maxillingua</u>	AMNH	40253SW	C/S	(2)
<u>Garra rossica</u>	AMNH	35533	C/S	(4)
<u>Gila atraria</u>	AMNH	27262	C/S	(5)
<u>Gila ditaenia</u>	AMNH	27263	C/S	(4)
<u>Gila orcutti</u>	AMNH	27264	C/S	(4)
<u>Gila robusta</u>	AMNH	27245	C/S	(4)
<u>Gnathopogon caeruleus</u>	AMNH	26735	C/S	(2)
<u>Gobio gobio</u>	AMNH	37609	C/S	(3)
<u>Gobiobotia puppenheimi</u>	AMNH	10311SW	C/S	(7)
<u>Hampala macrolepidota</u>	USNM	107827	C/S	(2)
<u>Hemibarbus barbus</u>	USNM	45234	C/S	(2)

<u>Hemiculter leucisculus</u>	AMNH	10846	C/S	(2)
<u>Hemitrema flammea</u>	AMNH	54632	C/S	(3)
<u>Hesperoleucas symmetricus</u>	USNM	67255	C/S	(2)
<u>Hybognathus nuchalis</u>	AMNH	2175	C/S	(2)
<u>Hybognathus nuchalis</u>	AMNH	53425	C/S	(5)
<u>Hybopsis biguttatus</u>	AMNH	33525	C/S	(3)
<u>Hybopsis micropogon</u>	AMNH	21159	C/S	(5)
<u>Hypophthalmichthys molitrix</u>	AMNH	10222	C/S	(1)
<u>Ischikauia hainanensis</u>	AMNH	10986	C/S	(5)
<u>Labeo erythrurus</u>	AMNH	77916	C/S	(1)
<u>Labeo niloticus</u>	AMNH	9548	C/S	(1)
<u>Lavinia exilicauda</u>	AMNH	54637	C/S	(1)
<u>Lavinia exilicauda</u>	AMNH	22088	C/S	(2)
<u>Leptocypris niloticus</u>	AMNH	54634	C/S	(1)
<u>Leucaspius delineatus</u>	AMNH	20667	C/S	(4)
<u>Leuciscus leuciscus</u>	AMNH	36884	C/S	(2)
<u>Lobocheilus bo</u>	AMNH	36378	C/S	(2)
<u>Meda fulgida</u>	AMNH	27241	C/S	(3)
<u>Microphysogobio labeoides</u>	AMNH	10588	C/S	(4)
<u>Mirogrex terraesanctae</u>	AMNH	40965	C/S	(2)
<u>Moralius chrysophekadion</u>	AMNH	77917	C/S	(2)
<u>Moroco steindachneri</u>	AMNH	34765	C/S	(1)
<u>Mylocheilus caurinus</u>	AMNH	37966	C/S	(2)
<u>Mystacoleucas marginatus</u>	AMNH	48922	C/S	(1)
<u>Notemingonus crysoleucas</u>	AMNH	44665	C/S	(6)
<u>Notropis atherinoides</u>	AMNH	41051	C/S	(3)

<u>Notropis bellus</u>	AMNH	66965SW	C/S	(13)
<u>Notropis spilopterus</u>	AMNH	40307SW	C/S	(3)
<u>Ochetobius elongatus</u>	AMNH	10891	C/S	(2)
<u>Opsariichthys bidens</u>	AMNH	10955	C/S	(1)
<u>Opsariichthys uncirostris</u>	AMNH	11115	C/S	(2)
<u>Opsopoedus emiliae</u>	AMNH	54638	C/S	(4)
<u>Osteochilus melanopleurus</u>	AMNH	14574	C/S	(1)
<u>Osteochilus salsburyi</u>	AMNH	10624	C/S	(3)
<u>Oxygaster hypophthalmus</u>	AMNH	48924	C/S	(2)
<u>Oxygaster oxygastroides</u>	AMNH	14508	C/S	(1)
<u>Pachychilon pictum</u>	AMNH	40973	C/S	(1)
<u>Paracrossocheilus acerus</u>	AMNH	36375	C/S	(1)
<u>Paracrossocheilus vittatus</u>	AMNH	48926	C/S	(1)
<u>Pelecus cultratus</u>	AMNH	20543	C/S	(2)
<u>Phenacobius mirabilis</u>	AMNH	8892	C/S	(1)
<u>Phoxinus erythrogaster</u>	AMNH	42937	C/S	(5)
<u>Phoxinus phoxinus</u>	AMNH	36873	C/S	(4)
<u>Plagopterus argentissimus</u>	AMNH	64579	C/S	(5)
<u>Platygobio gracilis</u>	AMNH	22408	C/S	(3)
<u>Ptychocheilus grandis</u>	AMNH	46007SD-C	Skel	(1)
<u>Ptychocheilus oregonensis</u>	AMNH	64560	C/S	(4)
<u>Ptychocheilus oregonensis</u>	AMNH	70053	C/S	(4)
<u>Pseudogobio esocinus</u>	AMNH	11005	C/S	(3)
<u>Pseudoperilampus hainanensis</u>	AMNH	10769	C/S	(5)
<u>Pseudorasbora parva</u>	AMNH	34796	C/S	(5)
<u>Psilorhynchus balitora</u>	AMNH	13811	C/S	(3)

<u>Psilorhynchus gracilis</u>	AMNH	43097SW	C/S	(1)
<u>Psilorhynchus sucatio</u>	AMNH	43096	C/S	(2)
<u>Puntius filamentosus</u>	AMNH	40954	C/S	(1)
<u>Rasbora daniconius</u>	AMNH	13818	C/S	(3)
<u>Rasbora helfrichi</u>	AMNH	48936	C/S	(1)
<u>Rasbora pauciperforta</u>	AMNH	48933	C/S	(4)
<u>Rasbora steineri</u>	AMNH	10935	C/S	(3)
<u>Rhinichthys cataractae</u>	AMNH	41122	C/S	(4)
<u>Rhinichthys cataractae</u>	AMNH	40719SW	C/S	(1)
<u>Rhinogobio typus</u>	AMNH	11632	C/S	(2)
<u>Rhodeus sericeus</u>	AMNH	39117	C/S	(2)
<u>Rhodeus sinensis</u>	AMNH	10785	C/S	(5)
<u>Rhyncocypris variegatus</u>	AMNH	10912	C/S	(5)
<u>Richardsonius balteatus</u>	AMNH	36272	C/S	(3)
<u>Richardsonius balteatus</u>	AMNH	64559	C/S	(6)
<u>Richardsonius egregius</u>	AMNH	64563	C/S	(4)
<u>Rutilus rutilus</u>	AMNH	36897	C/S	(4)
<u>Saugogobio dumerilli</u>	USNM	130296	C/S	(2)
<u>Sarcocheilichthys variegatus</u>	AMNH	26742	C/S	(2)
<u>Scardinius erythrophthalmus</u>	AMNH	37607	C/S	(1)
<u>Semotilus atromaculatus</u>	AMNH	45990	C/S	(5)
<u>Spinibarbus hollandi</u>	AMNH	10719	C/S	(2)
<u>Squalidus intermedius</u>	AMNH	11024	C/S	(1)
<u>Squaliobarbus curriculus</u>	AMNH	10890	C/S	(2)
<u>Thynnichthys thynnoides</u>	AMNH	14570	C/S	(1)
<u>Tinca tinca</u>	AMNH	37597	C/S	(1)

<u>Tor putitora</u>	USNM 257749	C/S	(2)
<u>Tor tambora</u>	AMNH 36370	C/S	(2)
<u>Tribolodon hakuensis</u>	AMNH 12999	C/S	(1)
<u>Varicorhinus robustus</u>	AMNH 11634	C/S	(2)
<u>Varicorhinus tamusuiensis</u>	AMNH 10691	C/S	(2)
<u>Xenocypris davidi</u>	AMNH 10933	C/S	(2)
<u>Zacco platypus</u>	AMNH 10945	C/S	(1)
<u>Zacco spilurus</u>	AMNH 10932	C/S	(6)

A NEW CLASSIFICATION OF THE CYPRINIFORMES

The following classification of cypriniforms, based on this investigation into the relationships among the families of the order Cypriniformes, is advocated herein.

Order Cypriniformes

Superfamily Cyprinoidea

Family Cyprinidae

Superfamily Cobitidoidea

Family Gyrinocheilidae

Genus Gyrinocheilus

Family Catostomidae

Subfamily Ictiobinae

Subfamily Catostominae

Family Cobitididae

Subfamily Botiinae

Subfamily Cobitidinae

Family Homalopteridae

Subfamily Noemacheilinae

Subfamily Ellopostominae

Genus Ellopostoma

Subfamily Homalopterinae

Tribe Gastromyzontini

Tribe Homalopterini

Two conventions for the expression of hierarchical relationships among taxa have been followed here, subordination and coordinate ranking with sequencing (Nelson, 1973). Fig. 6 is the diagrammatic representation of the classification above. I have also followed Wiley (1979b) in keeping redundant group names to a minimum. Even so, there are three such redundancies present (Cyprinoidea = Cyprinidae, Gyriinocheilidae = Gyriinocheilus, Ellopostominae = Ellopostoma). I also agree with Wiley (1979b) that a classificatory ediface can be burdensome and often results in a proliferation of group names. Therefore, I have chosen to call all non-cyprinid cypriniforms cobitidoids (see below for a discussion of this choice of name rather than a name based on Catostomus), and to leave some subgroups of them innominate (the cobitidid-homalopterid and catostomid-cobitidid-homalopterid groups; see fig. 7). All information regarding their relationships can be expressed by adopting the conventions cited above and to do otherwise and argue for a complete coordinate ranking of groups based on Sawada's proposal of "Cobitoidea" for the cobitidid-homalopterid group would require at least an additional two familial level group and three ordinal level group names in the non-cyprinid cypriniform clade alone. Such a collection of would-be names hardly seems worthwhile.

Readers familiar with the names of cypriniform groups will have noticed the spelling of group names based on Cobitis and Gastromyzon. Steyskal (1980), after becoming aware of the publication of J. Nelson's (1976) Fishes of the World in which over 400 familial level group names are readily accessible, reviewed the grammar of these names of fishes. He pointed out the correct stem of the familial level names based on Cobitis is Cobitid-, not Cobiti-, therefore Cobitidinae, Cobitididae and Cobitidoidea, and the correct stem for such names based on Gastromyzon is Gastromyzont-, therefore Gastromyzontinae. J. Nelson, in his 2nd Ed. (1984) of Fishes of the World, has chosen to follow this corrected grammar and since his work is widely read I will follow suit. Sawada's (1982) conclusion to subordinate the gastromyzontin and homalopterid fishes within the Homalopterinae is followed here, and elaborated as the Gastromyzontini and Homalopterini.

There is another matter concerning a higher group name of non-cyprinid cypriniforms that needs comment. Wu et al. (1981) published the name Catostomoidea for a gyrinocheilid-catostomid-cobitidid group of families. Sawada (1982) published the name "Cobitoidea" for a cobitidid-homalopterid group a year later. J. Nelson (1984) chose to follow Wu et al. and used Catostomoidea as the higher level familial group name for some non-cyprinid

cypriniforms. Art. 27, paragraph (d) of the Code of Zoological Nomenclature, 3rd Ed., clearly states family group names are subject to the Principle of Priority and when larger groups are made by combining several already existent groups, the oldest available name according to this principle is the correct one to use. Art. 34, the Principle of Coordination, states that all family level group names based on the same type genus are proposed simultaneously with authorship. Fitzinger's (1832) "Cobitoidei" is the oldest family level group name for non-cyprinid cypriniforms (Catostomidae dates from Heckel, 1843), therefore any superfamilial group name of non-cyprinid cypriniforms that is inclusive of cobitidids must be Cobitidoidea.

SYSTEMATIC DISCUSSION

One manner of presenting the evidence for the relationships embodied in the above classification would be to discuss information relevant at particular levels of generality level by level (e.g., with reference to fig. 7 discuss synapomorphies of Cobitidoidea, then innominate group A, etc.). If this plan were followed synapomorphies would be clearly layed out, a definite plus if weighing possibilities. This work is, however, a comparative one. I prefer to approach the discussion of it character system by character system, treating each system in its entirety at single setting among all cypriniforms. Evidence of relationships appropriate at several levels of generality may reside within a single morphological complex and it seems more efficient to discuss all the evidence from a single system in the same place rather than to have the reader search back and forth from group to group to find reference to, for example, gill arch structure. A summary diagram will be presented as a conclusion that will lay out the evidence in the manner referred to above. Another advantage to this latter approach is that the sister-taxa, rather than ancestor-descendant, relationships among cypriniform groups become clear. There are many examples throughout this discussion of cypriniform morphology of divergent specialization of several groups so that to think of them as standing one to another as ancestor to

descendant would be to sink back into the mire that G. Nelson's (1969a) change in perspective extracted investigations of cypriniform systematics from in 1969.

The thrust of this work was to investigate the interrelationships among cypriniform families and most effort was directed toward that end but some consideration initially of the monophyly of the group as a whole is warranted as a prelude to discussion of intra-Cypriniformes relationships. Cypriniforms, as we know them today, have been recognized as a "natural" group for a long time (Agassiz, 1835, 1838; Gill, 1861), and no one yet has been able to demonstrate that some of them are most closely related to other fishes rather than to other cypriniforms. Evidence of the naturalness of the Cypriniformes has accumulated since the early 1800s (Cuvier, 1817) and is still being uncovered (Fink, 1981; Fink and Fink, 1981). A great deal was known about cypriniforms by the early 1900s (Boulenger, 1904; Goodrich, 1909; Regan, 1911), but the style of presentation of the information as diagnoses tended to obscure those features that are synapomorphic of cypriniforms because many anatomical features that are characteristic of fishes generally were intermingled with them. Fink and Fink (1981), utilizing the clear style of presenting only synapomorphies pursuant to cladistic methods, sifted through the lists of features reported by

earlier workers and clarified the situation to the degree that Lauder and Liem (1983) wrote that the Cypriniformes were "clearly monophyletic."

Much of the evidence for cypriniform monophyly can be categorized into two sets of modifications related to feeding, and as such is a listing of various aspects of two functional complexes. One set of modifications is associated with food gathering and another with the processing of food before it is swallowed. Six of the nine features listed by Fink and Fink (1981) as unique to cypriniforms (kinethmoid, pre-ethmoid, dorsomedial palatine process, "ball and socket" articulation between the palatine and endopterygoid, reduced ectopterygoid and premaxillary ascending pedicels), and possibly four of eight features they hypothesized as synapomorphic for cypriniforms on parsimony grounds but as convergent in other ostariophysan groups (no jaw teeth, no teeth associated with the branchial basket anterior to the fifth branchial arch, no infrapharyngobranchial tooth plates and no basibranchial tooth plates) are modifications associated with the "pipette" method of suction feeding universal among cypriniforms (Alexander, 1969, 1970; Gosline, 1973; others have referred to certain aspects of this system as the protrusibility or protractability of the cypriniform mouth). Yet another feature in the list Fink and Fink (1981) hypothesized as synapomorphic of

cypriniforms but as convergent in other groups as well, sensory barbels located around the mouth, is also associated with food acquisition.

Two of the remaining features in the list of unique characters of cypriniforms (enlarged fifth ceratobranchials and teeth ankylosed to this bone) are part of the "pharyngeal mill" of cypriniforms and are elements of the set of modifications associated with the processing of food before it is swallowed. In sum, 13 of the 17 features (9 unique, 8 convergent) listed by Fink and Fink (1981) as characterizing cypriniforms are associated with the feeding apparatus in one or another way. Only four are not associated with the feeding apparatus and three of these are reduction characters also postulated to be convergent (no adipose fin, 1 postcleithrum and 1 epural). Clearly, what distinguishes cypriniforms from other fishes is their specific set of modifications associated with feeding and many other features discussed below that characterize various subgroups of them are variations on the two main themes within this set of modifications.

TEMPORAL FOSSAE.

Posttemporal fossa. Two posterior cranial fossae, the subtemporal and the posttemporal, have played an important role in the assessment of relationships among

cypriniform families and are still subjects of active investigation. Patterson (1975) described and discussed the posttemporal fossa of teleosts generally. This fossa occupies the space above the horizontal semicircular canal. It is floored by the pterotic, walled anteriorly, laterally, and medially by the sphenotic, dermopterotic and epioccipital respectively, and is usually roofed by the dermopterotic laterally and the parietal medially. Normally the posttemporal fossa is open from the rear lateral to the course of the posterior semicircular canal through the epioccipital, though among ostariophysans characiforms possess an additional, dorsomedial opening as well (Weitzman, 1962; Roberts, 1969; Fink and Fink, 1981) and in Chanos there is an opening into the posttemporal fossa through the interior of the arch of the posterior semicircular canal in the epioccipital besides the usual one (Rabor, 1938; Plate 2, fig. A). Epaxial musculature enters through these openings to insert in the fossa, presumably contributing to the epaxial-neurocranium coupling characteristic of actinopterygians (Lauder, 1982) that functions to elevate the head during feeding.

A posttemporal fossa occupying the space above the horizontal semicircular canal in the pterotic is primitively present and widespread among cypriniforms (Howes, 1978, 1979, 1980, 1981, 1983, 1984, 1984b; Sagemhel, 1891; Weisel, 1960; Wu et al., 1981) though it

is greatly modified in various taxa and has not always been recognized as a homologous structure among them. Among cypriniforms the posttemporal fossa of cyprinids (fig. 8), when it is not obliterated from below by the expansion of the subtemporal fossa, and of the homalopterid Ellopostoma most closely conforms to that typical of teleosts described by Patterson (1975). By this I mean that there is a spacious vault above the horizontal semicircular canal, with a rear opening, in which epaxial muscle fibers insert. As just noted many cyprinids lack a posttemporal fossa, and many homalopterins lack one as well, but for a different reason. The homalopterin skull is very broad and greatly compressed dorso-ventrally. The result is a cranium with a shallow temporal region in which the space for the posttemporal fossa seems to have been squeezed out of existence. There is, however, a shallow depression of the skull roof of homalopterins in the region of the posttemporal fossa of other cypriniforms that could be considered a posttemporal fossa (fig. 9), but it is not an internal skull space. It is merely a depression that is actually floored by the skull roofing bones rather than being roofed by them as is the case for the posttemporal fossa of teleosts in general.

The remaining familial and subfamilial cypriniform taxa, gastromyzontins, gyrinocheilids, catostomids,

botiines, noemacheilines and cobitidines, each possess a characteristic, derived posttemporal fossa. The gastromyzontin posttemporal fossa is open from the rear (fig. 10) but is shallow and the usual sphenotic contribution to the fossa is lacking. The fossa is bounded ventrally, laterally, anteriorly and dorsally by the pterotic and medially and dorsomedially by the epioccipital. Glanioptis denudata is unusual among gastromyzontins, its posttemporal fossa lacks the roof over the fossa of other gastromyzontins and extends further forward. This forward extension of the fossa of Glanioptis appears to be a consequence of the lack of a pterotic and epioccipital roof over the fossa and the absence of any ossifications around the cephalic laterosensory canals. Both these conditions allow epaxial musculature to invade further onto the posterolateral skull roof of Glanioptis than in other gastromyzontins.

The posttemporal fossa of Gyrinocheilus is large (fig. 11). It is roofed principally by the parietal with only a small lateral contribution of the pterotic associated with the temporal sensory canal. Musculature enters the posttemporal fossa of Gyrinocheilus from two directions. Epaxial and epaxial derivative (levator pectoralis) fibers enter from the rear, running into the fossa beneath the posttemporal bone. Fibers of the muscle that mainly fills the fossa, the adductor operculi, enter

through a large lateral opening, running between the horizontal semicircular canal and the temporal sensory canal. This lateral access is so large that the fossa effectively has no lateral wall and this has led some workers to label it the lateral temporal fossa, confounding its homology with the posttemporal fossa of other ostariophysans.

The catostomid posttemporal fossa has been described in detail by Weisel (1960). Except for its most medial extent which is covered by the parietal (fig. 12) it is unroofed and effectively open only laterally.

Catostomids, excepting Minytrema, fill the posttemporal fossa with the levator operculi, rather than with epaxial musculature. Minytrema, however, fills it chiefly with the levator pectoralis which enters through the lower posterior corner of the opening into the fossa. Jenkins (1970), Smith (1966) and Weisel (1960) have identified the muscle filling the posttemporal fossa of catostomids as the adductor operculi, of which the levator operculi is a derivative (Winterbottom, 1974).

Botiines possess a rather spacious posttemporal fossa, with the parietal and pterotic both contributing extensively to its roof (fig. 13A). Entry of the epaxial musculature into the fossa is through a lateral opening positioned at the posterior corner of the skull. The opening is tucked beneath the posttemporal bone (not

illustrated) in such a way that it is not visible from lateral view when the posttemporal is in place.

Vaillantella euepiptera is an exception to what appears to be a standard botiine configuration of the fossa. It does have a vault above the horizontal semicircular canal but an entry-way into it could not be detected. Vaillantella possesses a remarkable cephalic laterosensory canal system with great, capacious canals (fig. 13B) and the opening into the posttemporal fossa characteristic of other botiines is blocked by the extrascapular and posttemporal canal ossifications (ossifications that are present only on the medial side of these canals).

Noemacheiline homalopterids have a dorsolateral depression of the skull roof over the horizontal semicircular canal that can be described as an unroofed posttemporal fossa (fig. 14). This unroofed fossa of noemacheilines may result from the absence of a dermopterotic in these fishes. A dermopterotic is normally present in teleosts but Lekander (1949) failed to find one during his study of the ontogeny of the cephalic laterosensory canal system of some cypriniforms. He felt he could identify three separate ossifications in the pterotic region of cypriniforms, an endochondral pterotic, a dermal pterotic and another dermal ossification surrounding the temporal canal apart from the dermal pterotic. In cyprinids all three ossifications, when

present, eventually fuse to form a single compound bone. In material examined during the present study, an ossification around the temporal sensory canal (not illustrated) does sometimes fuse to the pterotic above the horizontal semicircular canal but this ossification never was extensive enough to roof the fossa, it merely provides a lateral wall. If Lekander's observations, and interpretations, are correct this canal ossification of noemacheilines that fuses with the endochondral pterotic might not be the dermopterotic of most teleosts. Lefua echigonia, an East Asian noemacheiline, has no cephalic laterosensory canals, ossified or unossified, so such questions concerning it never arise. Epaxial musculature, entering from the rear, extensively fills the posttemporal fossa of noemacheilines. In N. barbatulus fibers run beneath the posttemporal bone but in N. posteroventralis, N. pulcher and L. echigonia fibers run above the posttemporal as well as beneath it. In N. pulcher the ossified supratemporal laterosensory canal is not closely associated with the skull roof and the layer of musculature running into the fossa above the posttemporal bone is quite thick.

Cobitidine cobitids are a morphologically varied group of fishes. Their skulls, generally, are quite deep, rounded and posteriorly produced. Like noemacheilines and Glanopsis they have a posttemporal fossa that is unroofed

but some of them, such as Misgurnus and Acanthopthalmus, possess skulls that are rounded to such a degree that identification of a discrete posttemporal fossa is equivocal. Among cobitidines examined, Acanthopsis choirorhynchus (fig. 15) and Cobitis taenia, possess a well developed posttemporal fossa. The posttemporal fossa of A. choirhynchus is roofed along its anteriomedial, medial, and posteromedial edges by a shallow shelf of bone contributed to by the sphenotic, parietal, and epioccipital respectively. Its fossa is quite like that of botiines in its extent, but simply lacks any pterotic contribution to its roof. Other cobitidines examined completely lack roofing of the fossa. The Acanthopsis material examined in the present study was from Borneo and does not exhibit the sphenotic intercession between the parietals and pterotics illustrated by Sawada (1982; Fig. 12). Sawada's material was from the mainland of Asia so what looks to be a mistake in interpretation of his material may in fact be an indication that fish now recognized as Acanthopsis choirorhynchus should be considered as more than one species. Epaxial musculature does insert in the posttemporal fossa region of cobitidines. In fact it generally encroaches onto the skull roof, in some cases (Cobitis taenia) as far forward as the sphenotics and frontals, completely covering the supraoccipital and parietals.

Among cypriniforms there seems to be a relationship between the supratemporal commissure of the laterosensory system and the invasion onto the skull roof of epaxial musculature. Epaxial musculature does not normally encroach onto the skull roof of cypriniforms beyond a limit set by the supratemporal commissure when the supratemporal commissure is associated with the surface of the parietals and the supraoccipital. When the commissure is wanting, as in most cobitidines, Lefua and Glaniopsis, deeply buried in the parietals and supraoccipital as in A. choirorhynchos and many botiines, or disassociated from the skull roofing bones and free in the tissues above the bones as in N. pulcher, epaxial fibers do advance anteriorly onto the skull roof beyond the course of the supratemporal commissure. Among cyprinids, Chela oxygaster is noteworthy and instructive. Epaxial musculature has invaded forward as far as the anterior extent of the frontal, and has pushed the canals of the supratemporal commissure ahead of it (fig. 16).

Posttemporal fossa discussion. Ramaswami (1957) briefly summarized his series of papers on cypriniform anatomy and intrarelationships in the discussion of the last paper in the series, a paper that considered catostomid cranial and Weberian apparatus structure. In that summary he noted that the families Catostomidae,

Gyrinocheilidae and "Cobitidae" possess a well developed supratemporal fossa but that the "Gastromyzontidae", Homalopteridae and Cyprinidae do not. Whether he recognized its homology in general to the posttemporal fossa of other fishes is not clear. He did not specifically suggest the three families with a well developed supratemporal fossa were closely related but did identify their temporal fossae as the same structure, a supratemporal fossa. Wu et al. (1981) took the step Ramaswami did not and treated the posttemporal fossa of catostomids, gyrinocheilids and cobitidids including noemacheilines as a synapomorphy characterizing them as a group. They went even further and suggested that the absence of a posttemporal fossa among homalopterids, excluding noemacheilines, and cyprinids was a synapomorphy indicative of a sister group relationship between these two families. Of the two postulates advanced by Wu et al., the second is most easily falsified. Homalopterids, at least gastromyzontins and Ellopostoma among those that Wu et al. considered to be homalopterids (like Ramaswami they included noemacheilines in cobitidids), do in fact possess a posttemporal fossa and primitively cyprinids do as well. The statement of absence of the posttemporal fossa is then true for only some homalopterids (homalopterins) and some cyprinids. Evidence presented below will show that the Homalopteridae and the Cyprinidae

are each monophyletic and that absence of the posttemporal fossa among some members of these families is most fruitfully viewed as an indication that some members of these might be most closely related among themselves rather than that homalopterins and some cyprinids are most closely related to each other among cypriniforms. The other postulate, that catostomids, gyrinocheilids and cobitidids including noemacheilines are characterized as a group by a particular configuration of the posttemporal fossa is not so easily dismissed. As above though, evidence will show these fishes in and of themselves are not a monophyletic group. The implication of this is that the nature of the similarity of the posttemporal fossa among these taxa is superficial. Wu et al. (1981) did not specifically state what they thought the similarity of the posttemporal fossa among these taxa is (neither did Ramaswami) but it seems to be no more than a realization that the opening into the fossa is unconventional. This is certainly true, but this unconventionality is not the same in all these fishes. Cobitidines (fig. 15) and noemacheilines (fig. 14) lack a posttemporal fossa roof, for it is open from above. The botiine condition is to open the fossa somewhat laterally but still essentially from the rear. Gyrinocheilids and catostomids have what is effectively a lateral opening into the fossa, and most unusually, opercular muscles that originate in it though

not the same muscle in the two cases (see above). But the lateral opening seems to be an absence of a lateral wall (dermopterotic?) to the fossa that, although certainly derived in and of itself relative to the primitive ostariophysan condition, is hard to maintain as a synapomorphy in light of other evidence. My conclusion is that family or subfamily groups of cypriniforms do possess characteristic posttemporal fossae but that groups of cypriniform families and subfamilies do not. Hypotheses of similarity of the posttemporal fossae among these groups have to date been based upon consequences of the absence of some element (dermopterotic?) and do not withstand close scrutiny.

Subtemporal fossa. As with the posttemporal fossa, Patterson (1975) has discussed, and described, the subtemporal fossa of actinopterygians. There are, certainly, several lower teleostean taxa with a well developed subtemporal fossa but the occurrence of such a structure is not as widespread as the occurrence of the posttemporal fossa. It seems that among taxa considered relevant for consideration in "outgroup comparison" in this study, elopiforms and some characins (Patterson, 1975) have a well developed subtemporal fossa. Greenwood (1970) has illustrated the subtemporal fossa of some elopiforms. It is a cone- or pyramid-shaped indentation

in the ventral surface of the posterior region of the skull. The base of the cone or pyramid fills the interior of the arch of the horizontal semicircular canal in the pterotic. The cavity does not rise straight up into the skull but rises obliquely with the apex of the fossa pointing toward the midline of the skull. It is deep enough to bulge up into the posttemporal fossa, raising a bump in its medial floor. The subtemporal fossa of elopiforms is walled by the prootic, pterotic, and exoccipital, with a minor contribution from the epioccipital in some taxa. Generally, dorsal gill arch musculature and the adductor operculi originate from this region of the skull. Patterson (1975) included cyprinoids (= cypriniforms) among those fishes with a well developed subtemporal fossa and commented that in them it was most likely a secondary feature related to pharyngeal arch dentition and its associated musculature, a conclusion Gosline (1971) had reached too. Such a blanket statement concerning the nature of the subtemporal fossa as that above does not hold for all cypriniforms; it is certainly true for some. Those for which it is true, in fact, possess what might be the largest and deepest subtemporal fossa among all fishes.

Cyprinids exhibit a most remarkable subtemporal fossa (fig. 17). Many authors have illustrated it for various cyprinid taxa (Eastman, 1971; Harrington, 1955:

Howes, 1980, 1981, 1983, 1984b, 1985a; Ramaswami, 1952b, 1955a,b; Sagemhel, 1981; Sibbing, 1982; and others) so it is fairly well known in the family. The subtemporal fossa of Engraulicypris sardella (illustrated by Howes, 1981) is directly comparable with that observed in elopiforms, but E. sardella has the smallest subtemporal fossa of all cyprinids examined. Among other cyprinids the subtemporal fossa rises vertically, up through the interior of the arch of the horizontal semicircular canal not as a cone or pyramid as in elopiforms, but more as a cylinder. It is a great, capacious vault. In many, perhaps most, cyprinids it is so extensive it largely, or even completely, supplants the posttemporal fossa, obliterating the space of its superiorly positioned neighbor by its upward and lateral expansion. It is walled by the prootic, pterotic, exoccipital and occasionally by the sphenotic. Its ceiling is usually formed from the epioccipital but sometimes the sphenotic forms part of the ceiling and in very deep subtemporal fossae, the parietal, a dorsal roofing bone of the skull, forms part of the ceiling too. No other fishes that I know of have such a large subtemporal fossa. The levator arcus branchialis V, the muscle that adducts the toothed fifth ceratobranchial of cypriniforms, has its origin deep within the medial side of the subtemporal fossa, largely filling it (Eastman, 1971; Sibbing, 1982; Takahasi, 1925). The adductor

operculi originates in the lateral side of the fossa, but is not nearly as large as the levator arcus branchialis V (Takahasi, 1925; Winterbottom, 1974). Howes (1980, 1983) and Fink and Fink (1981) have identified a passageway between the subtemporal fossa and the posttemporal fossa of a few cyprinids through which epaxial fibers enter and insert in the subtemporal fossa. This is a most unusual feature and one Howes (1983) uses to characterize a "bariliine" cyprinid group. No other group of cypriniforms demonstrate such a subtemporal fossa, as a group, as do cyprinids. Gyrinocheilus (fig. 18) possesses a shallow indentation in the region of the ventral surface on the skull where the pterotic, prootic, and exoccipital meet to form a triple joint, but it is not a discrete feature like that found in cyprinids. Catostomids often possess a similar depression in which the adductor operculi originates. Cobitidids vary considerably. Botiines show a distinct indentation in this region, sometimes quite deep in large individuals (fig. 19; see Sawada, 1982, for additional illustrations), but some cobitidines show no trace of a subtemporal fossa, even in large individuals (fig. 20). Among homalopterids, noemacheilines (illustrated by Ramaswami, 1953; Sawada, 1982) and gastromzontins (illustrated by Ramaswami 1952d; Sawada, 1982) are quite similar to the non-cyprinid cypriniforms just described, but Ellopostoma and

homalopterins have a discrete indentation in the region of the horizontal semicircular canal (fig. 21). In some homalopterins, Lepturichthys and some Homoloptera (illustrated by Hora, 1932, Ramaswami, 1952c; Sagemhel, 1891), it is quite deep and includes the epioccipital in its ceiling. This latter condition is unusual among non-cyprinid cypriniforms. Usually their subtemporal fossa is roofed only by the prootic, pterotic and exoccipital.

Subtemporal fossa discussion. In spite of the fairly large body of descriptive work that has been published on cypriniforms that has included information on the subtemporal fossa, the implication for systematics of its various forms among all cypriniforms has never been examined in detail. The vast subtemporal fossa with the epioccipital ceiling, which also sometimes includes the sphenotic, parietal or both sphenotic and parietal, is characteristic and synapomorphic for cyprinids, as Ramaswami (1955b) seemed to indicate. Howes (1981) has discussed it among cyprinids, but among all his works (1978, 1979, 1980, 1981, 1983, 1984a, b, 1985a) has never compared it to that of other non-cyprinid cypriniforms. Ramaswami (1957) did note the distribution of a deep subtemporal fossa among the taxa he considered in his work (1952a-d, 1953, 1955a, b, 1957) but did not draw any

systematic conclusions from his observations. Hora (1932) took note of the deep subtemporal fossa of some homalopterins, and believing it to be a character warranting special consideration, revised his previous notions of relationships (Hora, 1920) and suggested homalopterins were descendent from cyprinids rather than being closely related to gastromyzontins and cobitidids. Wu et al. (1981) concurred, and in the process had to employ a burdensome explanation of degeneracy for the shallow subtemporal fossa of gastromyzontins because they believed gastromyzontins and homalopterins belonged to the same family, the Homalopteridae. However, only some homalopterins, Lepturichthys (fig. 21) and some Homaloptera, have a subtemporal fossa comparable to that found among cyprinids, i.e., it is discrete, deep, and includes the epioccipital in its roofing (compare figs. 17 and fig. 21). It is an untenable hypothesis, though, that all homalopterids are most closely related to cyprinids when only a very few homalopterins possess the feature that is put forward as the evidence of such a relationship. As before with the posttemporal fossa, the resemblance among some homalopterins and cyprinids is most fruitfully viewed as an indication of the close relationship of those particular homalopterins among themselves within all homalopterids rather than as a synapomorphy between them and the Cyprinidae.

GILL ARCHES.

Dorsal elements. Even though they are highly derived in certain respects, the gill arches of Chanos chanos (fig. 22), minus their median pharyngobranchial, will serve to illustrate the basic structure of the dorsal endoskeletal elements, and the relationships among these elements, of the branchial arches of teleosts. The elements of interest, epibranchials and infrapharyngobranchials (of Nelson, 1969a), are all bilaterally paired. There are four pairs of epibranchials that normally ossify (Eb I-IV) and four pairs of infrapharyngobranchials, usually of which only three ossify (Ipb I-III), the fourth remaining cartilaginous (branchial arches are enumerated in the anterior to posterior direction). An additional pair of cartilaginous elements of doubtful homology is often present in teleosts, the pair of so-called Eb V associated with the posterolateral end of Eb IV. Additional, secondarily derived, elements other than these just mentioned above appear sporadically among the dorsal elements of certain fishes and particular elements of those basic for teleosts may be highly modified in certain taxa.

In Chanos (fig. 22), and most other teleosts (Rosen, 1973, 1974), epibranchials I-III are of similar structure. They are slender and elongate with a dorsally projecting uncinata process situated on the posterior side

near their medial end. In dorsal view epibranchials are trough shaped, the trough accommodating an efferent artery (EA) that runs mesiad atop each of these first three epibranchials. Depending on the arch in question, each efferent artery proceeds in front of the uncinete process before it joins the circulus cephalicus circulation or the arterial trunk that leads to the middorsal aorta (for discussion see Nelson 1967a, 1969a). Despite its typical teleostean nature in many respects, Eb I of Chanos does have associated with its tip an accessory cartilage (fig. 22) that is not representative of teleostean gill arch structure. This accessory cartilage is, apparently, a secondarily derived feature. Epibranchial IV of Chanos is not representative of generalized teleostean structure either, but is highly modified in support of an epibranchial organ. Chanos is, however, representative in one respect, and that is that among teleosts Eb IV is of a modified nature relative to its three anterior neighbors (Nelson 1967a; Rosen 1974). It is often shorter, narrower, may or may not be trough shaped superiorly to accommodate an efferent artery running atop it and often possesses a levator process near its lateral end. Rosen (1974), writing about Eb IV generally, commented that presence of an uncinete process on Eb IV in front of a distinct levator process is characteristic of eutelosteans.

Associated with the lateral end of Eb IV of

teleosts, and the tip of its levator process when one is present, is a usually independent cartilaginous element called epibranchial V. It is so named because it is thought to be a rudimentary remnant of the epibranchial of a fifth functional branchial arch and therefore homologous with Ebs I-IV. Interpretation of the efferent blood supply associated with Eb IV has been central in such conclusions. Some lower teleosts, Chanos being one of them, have two efferent arteries associated with Eb IV (Nelson 1967a, 1967b). Epibranchial IV seems to be tipped on its anterior edge relative to Ebs I-III and in those fishes with two efferent arteries associated with it, one runs on its anterior side (interpreted as positionally atop Eb IV) and one runs behind it through a canal formed by the juxtaposition of Eb V along the posterolateral border of Eb IV. This posteromost EA passing through this canal is interpreted as EA V, the remnant of the blood supply of the proposed fifth functional arch (Nelson, 1967a). Other fishes, maybe even most, have only a single EA associated with Eb IV. However, when such is the case, it runs through the Eb IV-V canal and along the posterior edge of Eb IV. Since Nelson (1967a), this has been labeled the EA V and it follows then, that EA IV is secondarily absent in such cases. Bertmar (1959), in a study of the development of the chondral portion of the head of the characiform Hepsetus odoe, inspired such a

fifth arch point of view with the observation that in H. odoe, Eb V originated atop ceratobranchial V and migrated to its position along the posterolateral end of Eb IV. My observations of whole mount alcian blue preparations of series of larval catostomids and cyprinids do not indicate such an origin for the structure termed Eb V among cypriniforms. In my material, it is instead always associated with the fourth branchial arch. Recently, Claeys and Varraes (1985) studied the gill arch ontogeny of Salmo gairdneri, and observed that the development of the structure most workers today call Eb V never involves an association with the fifth ceratobranchial and they termed it an interbranchial (Ib IV). One can not conclude definitely from this that what is called Eb V in teleosts is not serially homologous with Ebs I-IV but it does indicate the conjectural nature of the use of such a name for an element that is topographically misplaced (it should be positioned in its place in the fifth arch).

Primitively Chanos, along with other teleosts, (Nelson 1969a; Rosen 1973) possesses infrapharyngobranchials that articulate with the medial tip of each ossified epibranchial (fig. gdl). Infrapharyngobranchials II-IV articulate directly with the medial tip of their respective epibranchials so as to appear simply as anteromedially directed extensions of them. Infrapharyngobranchials II and III each possess,

usually, a dorsally directed uncinat process. These three elements, Ipb II-IV, often abut one another and meet their bilateral counterparts in the midline above the pharynx. Infrapharyngobranchial I, sometimes referred to as the suspensory infrapharyngobranchial, has an orientation different from that of its three posterior neighbors. Rather than projecting medially, it projects dorsally, and somewhat posteriorly, from the tip of Eb I (fig. 22) to articulate with the skull, thereby contributing to the attachment of the branchial arches to the braincase. A survey of literature in which dorsal elements of branchial arches are carefully illustrated (Allis, 1897; Forey, 1973; Nelson 1966, 1967a,b, 1968a,b, 196a9, 1970; Rosen 1973; Vari 1983) reveals that such an orientation of Ipb I is definitely characteristic of at least elopcephalan fishes, and most likely is a synapomorphy of teleosts.

Chanos demonstrates most of the relationships among its dorsal elements that Nelson (1967d, 1969a) and Rosen (1973) describe as general for most teleosts. These relationships are summarized as follows.

Infrapharyngobranchials articulate with the medial end of their respective epibranchials and in general, each branchial arch has an association of one sort or another with its neighbors. The uncinat process of Eb I usually meets the uncinat process of Ipb II and that of Eb II

meets that of Ipb III. Branchial arches III and IV associate through contact between the anterior end of Ipb IV abutting Ipb III's posterior end and, rather than their uncinatate processes meeting Ipb uncinatate processes as in branchial arches I and II, through an association between their uncinatate processes directly (Chanos does not exhibit this). Vari (1983; Fig. 14, Brycon falcatus) has described and illustrated the structure of and the relationships among dorsal gill arch elements he considered primitive for characiforms. They are as those found in Chanos and among teleosts generally. An implication of this is that following Fink and Fink (1981) on interrelationships of ostariophysans (fig. 1), this kind of gill arch structure with its relationships among the individual elements can be considered primitive for ostariophysans and for the otophysan subgroup of the Ostariophysi as well. It is against this general structure and arrangement that the dorsal elements of the gill arches of cypriniforms will be compared.

The dorsal gill arch elements of cypriniforms are one of the underutilized complexes of structures in investigations of the interrelationships among cypriniforms. They are often included and illustrated in general osteological descriptions of cypriniforms but are rarely included in analytical discussions of relationships among taxa within the Cypriniformes. This sort of

attention, when directed at gill arch structures at all, has been mainly directed toward the ventral elements (discussed below).

No cypriniform examined in this study nor any ever reported on in the literature possesses the complete set of dorsal endoskeletal gill arch elements, or has relationships among those elements like that described above as general among teleosts and primitive for otophysans. Nevertheless cypriniforms do possess, certainly, many of the features described as general among teleosts. Among these are the generally anteromesial orientation of the epibranchials, the progressive decrease in size from Eb I to IV (see fig. 23 and Vari, 1983, Fig. 14, for this characteristic among members of other otophysan groups that are considered to show the primitive condition for their respective lineages), the modified nature of Eb IV relative to its three anterior neighbors, and the trough-like aspect of the dorsum of the epibranchials to accommodate efferent arteries.

One feature immediately stands out during comparison of cypriniform dorsal endoskeletal gill arch components with those of teleosts generally and that is no cypriniform possesses uncinata processes on any of their infrapharyngobranchials. Such uncinata processes usually contact uncinata processes of epibranchials and are normally present on the infrapharyngobranchials among

teleosts. Although such uncinata processes may be absent sometimes from fishes in other ostariophysan groups, they are found in all other major groups of ostariophysans including otophysan subgroups and are probably primitive for them. This absence of infrapharyngobranchial uncinata processes probably characterizes cypriniforms as a group though in and of itself it is difficult to analyze by its very nature as "absence" or negative evidence. It is however congruent with other "positive evidence" features that characterize all cypriniforms and is therefore interpretable as a synapomorphy. At this point another feature, though not concerning endoskeletal elements related to dorsal gill arch structure nonetheless, of all cypriniforms should be pointed out and that is their lack of any upper pharyngeal dentition or upper pharyngeal tooth plates, both of which are primitive for otophysans. Fink and Fink (1981) have pointed out such is the case for gonorynchiforms as well but argue that it is most parsimonious to interpret this as independent loss in separate ostariophysan lineages. Loss of various elements is something that is notable of the dorsal gill arch elements of cypriniforms and will be discussed when appropriate in group structure descriptions. None of these losses, however, are as easily defended as synapomorphic as the two cases discussed above applicable for all cypriniforms.

Of all cypriniforms, gyrinocheilids possess the most complete set of elements and relationships among the elements of any yet they are in some ways the most aberrant (fig. 24). They are the only cypriniforms that possess what can be unambiguously indentified as an infrapharyngobranchial I. It is rod-like (though bent), associated with the medial tip of epibranchial I and posterodorsad in its orientation. Their Ipb II and III are, however, highly derived and the largest of all dorsal elements. Rather than being directed anteromesially, they simply point mesiad and possess long processes that meet each other toward the midline (fig. 24). An Ipb IV could not be positively identified as a separate element in my material.

Gyrinocheilid epibranchials are remarkable too, the first three being of subequal length and very short, not much longer than they are wide. Epibranchial IV is much longer than it is wide and as usual among teleosts and otophysans, of a modified nature relative to its anterior fellows. All four epibranchials possess uncinata processes but only those of Eb III and IV exhibit the primitively teleostean relationships of meeting each other. Obliquus dorsalis fibers originate from the uncinata process of Eb III and insert on Ipb III, a common situation among cypriniforms (Ballintijn and Punt, 1985; Takahasi, 1925; Winterbottom 1974). The uncinata

processes of Eb I and II are stout cartilage capped rods with a posterodorsal orientation and each associates with the anterior edge of its posterior epibranchial neighbor. Efferent arteries are not illustrated but are four in number. The first three course mesiad atop Eb I-III and the fourth runs along the posterior side of Eb IV. This fourth efferent artery associated with the posterior border of Eb IV is herein identified as EA IV. Evidence of a fifth functional arch is equivocal (see above) and to call this artery EA V would involve postulation of retention of a fifth arch rudiment and loss of the fourth arch efferent artery. The simplest view is that the efferent artery associated with Eb IV of cypriniforms is just an EA IV (peculiarly positioned?).

Catostomids (fig. 25) have as many dorsal gill arch elements as gyrinocheilids and are just as derived, but in very different ways. In some respects, even though highly derived in their own right, catostomids are more conventional than gyrinocheilids. They possess four infrapharyngobranchials, or at least three elements that can be clearly interpreted as such and a fourth, Ipb I, that is best interpreted as one. This so-called Ipb I of catostomids is a nodule of alcian blue staining cartilage positioned medially to the head of the first epibranchial. It is never observed to ossify as the Ipb I of other teleosts usually does and is not rod-like with a

posterodorsad orientation as is usual. This interpretation of it as homologous to the Ipb I of other teleosts is based on its position medial to the tip of Eb I, its cartilaginous composition (infrapharyngobranchials preform in cartilage before they ossify) and its articulation with the base of the skull (Fink and Fink, 1981) as is usual for an Ipb I. With the information presently at hand identifying it as some structure other than Ipb I (as a neomorph) offers no advantages. Its unconventional nature as an Ipb I already characterizes the catostomids as a group (calling it something besides Ipb I would add nothing to this) and it is not likely to be confused with any other structure among cypriniforms. Infrapharyngobranchial IV among catostomids is an independent cartilage associated with the medial margin of Eb IV.

Castostomid epibranchials are conventionally sized, that is they are much longer than wide and decrease in size from Eb I to IV (this is one of the ways catostomids are more conventional than gyrinocheilids). They are, however, much modified (strongly arched and with expanded heads, especially the head of Eb I) and wrap around the basioccipital process found among catostomids and aid in the support of a sizable palatal organ (Eastman, 1971; Weisel, 1960). Epibranchial IV is conventional as a modified epibranchial and has associated with its

posterolateral margin an interbranchial element (Ib IV). This Ib IV of catostomids is a slender elongate structure and unlike that found in any other group of cypriniforms. All catostomid epibranchials usually possess an uncinat process. Those of Eb I and II project posterodorsad and are cartilage capped like those of Eb I and II of gyri-nocheilids but do not associate with Eb II and III respectively as in Gyrinocheilus. Those of Eb III and IV are associated with one another, at least among catostomines, as is usual and obliquis dorsalis fibers originate from both to insert on Ipb III (see Winterbottom, 1974, for a discussion of terminology and the problems of exactness concerning these fibers). Each epibranchial has an associated efferent artery. Epibranchial I-III are trough shaped superiorly and EA I-III run in the grooves of their respective arches and each hooks posteriad around the uncinat process to eventually contribute to the middorsal aorta (fig. 26). Efferent artery IV ascends along the juxtaposition of Eb IV and Ib IV to pass through the notch between them near the terminus of the latter element. Efferent artery III, after hooking posteriorly around the uncinat process of Eb III, passes over the head of Eb IV beneath the base of the uncinat process of Eb IV and joins EA IV just posterior to the Eb IV head. The common trunk formed from EA III and IV then joins with that of EA I+II and the

bilateral counterparts from the opposite side to form the middorsal aorta.

No cobitidid examined in this study possessed an Ipb I, an uncinata process on epibranchial I or II (some lacked one on Eb III as well) and in a few a separate Ipb IV could not be identified. This is an unusual state of affairs among teleosts but is problematic in and of itself for characterizing cobitidids as a group because some of the "same" absences are also observed among all homalopterids and all cyprinids. However, even without considering these loss features of cobitidid dorsal gill arch elements, there are still other non-loss features of them that do uniquely characterize cobitidids, and subgroups of them (botiines and cobitidines). Cobitidid gill arches vary a lot and discussion of them, for now, will concentrate at the subfamily level.

Leptobotia fasciata (fig. 27) exemplifies many of the features of botiines generally.

Infrapharyngobranchial III is the largest of the infrapharyngobranchial series and overlaps the posteromedial portion of Ipb II and Eb II. It is characteristically elongate, especially so in Vaillantella, and an independent Ipb IV makes contact with its posterolateral corner. Infrapharyngobranchial IV of teleosts usually remains cartilaginous but all botiines examined for this study except Vaillantella in which no

Ipb IV could be identified, demonstrated granular alizarin staining particles within Ipb IV. Whether these result from a calcification process or some sort of endochondral ossification process was not determined but it makes little difference to the systematics of cypriniforms which process, or some other, is responsible for these bodies within the Ipb IV of botiines. The phenomenon is characteristic of botiines regardless of its specific cause.

Botiine epibranchials are unusual in some ways too. The size relationships among Eb I-III are conventional, Eb I is the largest of the three but Eb IV is nearly as large as Eb I and is larger than Eb II and III. Epibranchial IV possesses a levator process, not found in catostomids or gyrinocheilids, near its lateral end that is expansive to the degree of being flange-like. Interbranchial IV articulates with the dorsolateral corner of the levator process and with the posterolateral corner of Eb IV, forming a canal through which EA IV passes on its journey toward the midline. Anterior to the levator process of Eb IV is an uncinat process under which the posterior section of EA III runs. Epibranchial III has an uncinat process as well and obliquis dorsalis fibers originate on it and on that of Eb IV to insert on Ipb III. Efferent arteries I-III course atop Eb I-III, and Eb I and II are trough shaped to accommodate them. Epibranchial I however

has the anteromedial corner of its head twisted ventrad so that it cups around Ipb I, and the heads of Eb II and III have their posteromedial corners depressed, that of Eb II in conjunction with the overlap of it by Ipb III. Among botiines the morphology of Leptobotia appears representative, but is not universal. As mentioned above, Vaillantella lacks an identifiable separate Ipb IV and has an especially elongate (posteriorly) Ipb III (not to be interpreted as in any way compound, i.e. Ipb III+IV; see Nelson, 1969, for discussion of fusion of endoskeletal elements of successive arches). It also lacks an Eb III uncinat process and the Botia macracantha material examined for this study lacked an Eb IV uncinat process.

The dorsal gill arch elements of Acanthopsis choirorhynchos (fig. 28A,B) will serve to discuss representative structure of cobitidines. There are usually three infrapharyngobranchials present in cobitidines. When three independent infrapharyngobranchial elements are not identifiable it is Ipb IV that has failed to develop. Infrapharyngobranchial II is a small nodule-like element among cobitidines and its foreshortening has brought the medial tip of Eb I into close approximation with that of Eb II. Infrapharyngobranchial III among cobitidines is a waisted element with its anterior end deflected upward nearly 90° (fig. 28B). This dorsally turned end of Ipb III and

Ipb II are closely associated and appear to form a functional unit that braces the gill arches against the braincase, not a surprising observation since Ipb I, at times referred to as the suspensory infrapharyngobranchial, is absent among cobitidines.

Size relationships among the epibranchials of cobitidines are as described for botiines, Eb I and IV being the longest of the quartet. The anteromedial tip of Eb I is deflected ventrally as in Leptobotia though not as much but the depression of the posteromedial corner of the head of Eb II is exaggerated compared to botiines. This downward twist in Misgurnus is of an extent so as to render the tip of its head of Eb II vertical and that of Eb III nearly so. Acanthopthalmus was the only cobitidine to possess a structure on Eb III recognizable as an uncinata process. All cobitidine taxa examined reveal a levator process on Eb IV confluent with the uncinata process normally distinct from and anterior to it, the confluence of the two structures forming a large flange-like process. The head of Eb IV of cobitidines is unusually large and expansive and is in fact the largest of all epibranchial heads. As in botiines an Ib IV element is present among cobitidines and forms the posterior portion of an EA IV canal.

Consideration of the relationships between the efferent arteries and the underlying skeletal elements of

Lepidocephalis thermalis (fig. 29) may provide insight into the specializations of cobitidine dorsal gill arch elements and into such specializations of cypriniforms generally. Among cobitidines, the deflections of Eb I and II are followed by the courses of EA I and II. They closely track the curves and twists of the bones and the beginning of the posteriorly running arterial trunk formed by the union of EA I and II is accommodated within the hollow of the waisted region of Ipb III. The expanded head of Eb IV appears to support the posteriorly coursing section of EA III, and the confluence of the levator process and unciniate process of Eb IV to form a flange overlies EA IV. Such relationships between efferent arteries and obvious specializations of the underlying bones are provocative of functional explanations for the origin of such specializations. This study and discussion are geared to exploring the implications of such specializations for the systematics of cypriniforms and as intriguing as it might be, digression into the relationships between function and origin are considered inappropriate, at least until a much more thorough study of the vascularization of the gill arches is completed.

Variation of dorsal gill arch elements among homalopterids is as great as among cobitidids. Like cobitidids, no element that can be identified as Ipb I or as an unciniate process on Eb I and II is to be found among

them, and most lack an uncinata process on Eb III as well. Absence of Ipb IV, excepting the single species of Ellopostoma, is uniform among homalopterids and, once again excepting Ellopostoma, a peculiar relationship between epibranchials I and II and Ipb II is universal as well.

Noemacheiline homalopterids can not be characterized as a group if the dorsal gill arch elements are the sole character complex examined. They are similar amongst themselves and different from any group described so far but that similarity amongst them is one that characterizes all homalopterids (noemacheilines might not be monophyletic). Consequently, illustrations (fig. 30A-D) of four species of them, Noemacheilus barbatulus, N. pulcher, N. stoliczkai and Lefua echigonia, are presented as a basis for discussion of their dorsal gill arch anatomy. All four, and all other noemacheilines examined, have but two infrapharyngobranchials and there is a common pattern of an end-to-end arrangement of those present that is not found among the other cypriniforms so far described. Infrapharyngobranchial II is usually smallest but that of N. stoliczkai is subequal in size with its Ipb III.

Size relationships among noemacheiline epibranchials is as described for cobitidids but only N. pulcher among the material examined in this study possessed an uncinata

process on Eb III, and possession of it varied among specimens and even between right and left sides within a single specimen. Without exception, all noemacheilines possess a prominent flange on Eb IV, best interpreted as a confluence of a levator and an uncinat process as obliquis dorsalis fibers originate from it and insert on Ipb III. In all examined materials except Lefua, an Ib IV and an EA IV are associated with this flange (IB IV is missing from Lefua). The deflection of the anteromedial corner of the head of Eb I ventrad and of the posteromedial corner of Eb II also ventrad, is apparent in at least N. pulcher, N. stoliczkai and N. barbatulla. It is not so clear of Lefua in which the medial ends of its Eb I and II are rod-like rather than bar-like, therefore making it difficult to discern if they have been twisted.

The relationship between the infrapharyngobranchials and Eb I and II is different among noemacheilines from what has been described previously.

Infrapharyngobranchial II and III abut solidly end-to-end, presenting a longitudinal bar against the side of which Eb I and II articulate. Among other cypriniforms without such a consolidation between Ipb II and III, Eb I and II tend to articulate with Ipb II solely rather than with an Ipb II and III unit.

Homalopterine dorsal gill arch elements present some of the same features as those of noemacheilines and others

that are distinctive of them as a group. Illustrations of Crossostoma davidi and Homaloptera orthogoniata (fig. 31A,B) are presented as a basis for discussion of gastromyzontins and homalopterins. Both demonstrate the consolidation of Ipb II and III into a single unit (Ipb IV is not identifiable among them or amongst other homalopterines examined) with the consequent characteristic relationship between this unit and Eb I and II just described above for noemacheilines. All homalopterins examined extensively ossify the normally cartilaginous posterior region of Ipb III that occupies the space of an Ipb IV. The result is a characteristic posteriorly elongate Ipb III (fig. 31B) common to all homalopterins.

Uncinate processes are lacking on all epibranchials of all material examined of homalopterines. A posterolateral levator process on Eb IV and an associated Ib IV was identifiable in all material. The epibranchials of homalopterines are all remarkably short, and all show the modification from flat bar-like to rod-like of the medial ends of Eb I and II as seen in Lefua. Commonly among them, Eb IV is the longest of all epibranchials.

Homalopterines show a change in the orientation of their epibranchials compared to that found among other cypriniforms. The epibranchials of other cypriniforms are oriented anteromedially; homalopterines show a mesiad

orientation of Eb II and III and a posteromesiad orientation of Eb I (fig. 31A,B). This particular epibranchial orientation is characteristic of them as a group.

Ellopostoma sp. (fig. 32) appears enigmatic, and unique, among homalopterids. It possesses an independent Ipb IV normally positioned, does not show the consolidation among the infrapharyngobranchials demonstrated by all other homalopterids, has an uncinata process only on Eb III and exhibits a broad, sheet-like cartilaginous extension of ceratobranchial IV that extends up along the posterior border of Eb IV instead of an Ib IV in this position as is found among other cobitidoids. Its Eb I is an interesting structure. Epibranchial I of Ellopostoma extends anterior to Ipb II so that Ipb II articulates with its posterior edge and its lateral half is oriented posteromedially like Eb I of homalopterines, but the medial half of it projects directly mesiad if not slightly anteromedially (fig. 32). Features of the lower gill arch elements will suggest that the posteromesiad orientation of the lateral half of Eb I of Ellopostoma is part of a common heritage it shares with homalopterines.

Cyprinids present a common pattern of dorsal gill arch elements yet exhibit a lot of variation of these elements amongst themselves. Illustrations of the dorsal gill arch elements of Abramis brama, Acrocheilus

alutaceus, Cyclocheilichthys armatus, Cyprinis carpio, Dangila festiva, Elopichthys bambusa, Gobio gobio, Labeo niloticus, Notropis atherinoides, Rasbora pauciperforta and Zacco spilurus (fig. 33A-K) are presented as a basis for discussion. Cyprinids possess, at most, three infrapharyngobranchials. Infrapharyngobranchial I appears to be absent universally from them and in many a separate Ipb IV is not identifiable either. As one would expect, when Ipb IV is present, it is present as a cartilage intervening between the posterior end of Ipb III and the head of Eb IV (fig. 33A,B,C,D,E,F,G). When a separate Ipb IV is not identifiable, there is often a cartilaginous extension of Ipb III that occupies this space (fig. 33I,J,K). As mentioned previously no cyprinid infrapharyngobranchial possesses an uncinata process, and all taxa examined except Psilorhynchus (not illustrated) revealed an overlap of Ipb II by the larger Ipb III (fig. 33A-K). Infrapharyngobranchial II is often modified in conjunction with this overlap, possessing a depression on its dorsal side into which Ipb III nestles. Of the two ossified infrapharyngobranchial elements, Ipb III varies the most. Organizing this variation and sorting out its implications for the systematics of cyprinids is not an easy task, and is left for further study. A common pattern of connections of cyprinid dorsal gill arch efferent arteries and their relationships to their

underlying skeletal elements is shown in fig. 33F, an illustration of Elopichthys. The combined trunk formed from the union of EA I and II passes over Ipb III and Ipb III appears to have been modified to accommodate it, becoming a somewhat, to decidedly, waisted element (fig. 33 G,C,F) as also observed for cobitidines. Other sorts of Ipb III variation among cyprinids, such as the distinctive semicircular shape of that of Abramis (fig. 33A) and the roughly triangular form of that of Zacco and Acrocheilus (fig. 33K,B), are not as easy to appreciate but are perhaps clues to relationships among some cyprinids, as might be the rather extensive cartilaginous edging of the lateroposterior margin of Ipb III of these and other cyprinids like Notropis (fig. 33I). Failure to develop an independent Ipb IV may also be indicative of relationships among some cyprinids but needs further study as some taxa vary in its possession among specimens or even between right and left sides of the branchial basket.

Size relationships among cyprinid epibranchials are mostly conventional with Eb I the largest and a graded series decreasing in size posteriorly from arch to arch after Eb I though Eb IV is a little longer than Eb III in some taxa. No cyprinid possesses a clearly identifiable uncinata process on Eb I or II. The uncinata process of Eb III approximates that of Eb IV which nearly always is distinct from the more lateral levator process. Obliquus

dorsalis fibers originate from the uncinata processes of Eb III and IV to insert on Ipb III (Takahasi, 1925; most clearly illustrated in Ballijtin and Punt, 1985). An Ib IV element is present among cyprinids, and with the levator process of Eb IV, forms a canal through which EA IV passes (fig. 33F). Roberts (1986) figured a tiny cyprinid species (Danionella translucida), illustrating a cartilaginous structure interposed between the junction of Eb IV and CB IV and the dorsal tip of CB V. I have not examined material of that species but suspect what he labels as an Eb V is the Ib IV of other cyprinids. In general the first three epibranchials of cyprinids are trough shaped and accommodate an associated efferent artery in their dorsal groove. The relationships among the epibranchials and infrapharyngobranchials of cyprinids is interesting, a relationship Roberts and Kottelat (1984) have described as 2+2, a pattern they intimated to be the result of Eb I and II articulating with Ipb II and Eb III and IV with Ipb III. Both Eb I and II do articulate with Ipb II as they described. The medial, or at least posteromedial tip of Eb I is nearly always inserted beneath Ipb II and this produces a concomitant ventrad deflection of its posteromedial corner, a deflection also produced on Eb II by the overlap of it and Ipb II by Ipb III. An aspect of the association between the medial tip of Eb I and Ipb II is the overall shape of Eb I.

Epibranchial I of cyprinids is oriented anteromedially as is usual for teleostean epibranchials but its medial half, or third, jogs posteriorly to make the articulation with Ipb II (fig. 33A-K). One effect of this is to produce the anterior half of the 2+2 pattern of Roberts and Kottelat (1984). Many cyprinids do in fact possess an Ipb IV which intervenes between Ipb III and Eb IV so the second half of the 2+2 pattern is not necessarily the result of an Ipb III-Eb IV articulation, and might simply be an illusion created by the association between Ipb II and Eb I and II. Reid (1982) identified a group of cyprinids he called "labeine" after an included genus, Labeo. Some of these labeines possess remarkable modifications of the epibranchials (fig. 33H,E). They possess a large laminar flange on the anterior side of their Eb I, a structure Reid (1985) suggested supported their glandular pseudobranch. That Dangila (fig. 33E) possesses flanges on the anterior edges of all its epibranchials might suggest these flanges have other functions as well, perhaps support of the very large vomero-palatine organ in the roof of the oral cavity these fishes all possess.

Dorsal gill arch elements discussion. Variation of dorsal endoskeletal elements of the gill archs has broad implications for the systematics of cypriniforms. One or another aspect of them provides characterization of nearly

all levels of generality considered in this study. Some of the obvious specializations of cypriniform dorsal gill arch elements involve loss, or absence, of particular features generally present among teleosts and are thus somewhat problematic in a systematic analysis. Groups of cypriniforms characterized by dorsal gill arch element features are: all cypriniforms; gyrinocheilids; catostomids; botiines; cobitidines; homalopterids; homalopterins; a cobitidid-homalopterid group (innominate group B of fig. 5); and cyprinids, but within some of these groups reside enigmatic taxa.

So far as is known, no cypriniform possesses uncinata processes on any of their infrapharyngobranchials, an obvious specialization within euteleosts.

Gyrinocheilids are unique for their Ipb II and III anatomy, very short and broad epibranchials and the relationship between the uncinata processes of Eb I and II with their posterior neighbors, Eb II and III respectively (these uncinata processes are usually associated with infrapharyngobranchial uncinata processes).

The nodule-like Ipb I, strongly arched epibranchials with expanded heads, posterodorsally oriented uncinata processes of Eb I and II with no connection between them and infrapharyngobranchials or epibranchials of a more

posterior arch and the slender elongate Ib IV characterize catostomids.

Botiines are unique for their mineralization of Ipb IV and cobitidines for their anteriorly upturned Ipb III with its tight association with Ipb II, and for an Eb IV with a very expansive head and confluent levator and uncinata processes.

Homalopterines all possess short broad epibranchials with either a mesiad or posteromesiad orientation and the uncinata process of Eb IV is absent. Among them, homalopterins show a posterior elongation of the ossified portion of Ipb III.

All homalopterids including noemacheilines, but excepting Ellopostoma, exhibit a consolidation of their infrapharyngobranchial series with an end-to-end relationship between Ipb II and III with a consequent modification of the Eb I and II articulations with infrapharyngobranchials, and lack a separate Ipb IV. Within homalopterids, homalopterins, Ellopostoma and some noemacheilines possess a modification of the medial end of Eb I and II, possibly an indication that noemacheilines, as now known, are not monophyletic.

A cobitidid-homalopterid group is indicated by size relationships among the members of the epibranchial series, by Eb IV consistently being larger than Eb II and III, producing the unique appearance of a pair of short

internal epibranchials (Eb II and III) bracketed by a pair of larger ones (Eb I and IV), (the shortening of the epibranchials of homalopterines, especially of Eb I, tends to obscure this). The twist of the medial tip by the deflection of its anteromedial corner also characterizes this group though the modification of some homalopterines' Eb I makes this hard to discern. All except botiines, Ellopostoma and Noemacheilus pulcher (among noemacheilines examined) lack an uncinata process on Eb III.

Cyprinids are characterized by the insertion of the medial tip of Eb I beneath Ipb II, a posteriorly directed bend of Eb I (not to be confused with the similarly appearing Eb I of cobitidines which is an illusion resulting from the twisting of its medial end) and overlap of Ipb II by Ipb III.

There is a pattern of resemblance between the dorsal gill arch elements of the cobitidid-homalopterid group and cyprinids. Absence of of an Ipb I and uncinata processes on Eb I and II pertains directly to this resemblance and though absence of such elements is obviously derived within fishes of the general organization of cypriniforms, it must be treated as homoplasious and not as indicative of relationship between the two groups. In the context of the classification of cypriniforms advocated herein, an alternative of treating this (or these) absence (s) as characteristic of all cypriniforms with subsequent

reappearance in gyrinocheilids and catostomids is not as parsimonious as treating them as homoplasious between a cobitidid-homalopterid group and cyprinids.

Roberts and Kottelat (1984) suggested a pattern of epibranchial-infrapharyngobranchial articulations they described as 2+2, briefly mentioned earlier, was primitive for cyprinoids (= cypriniforms). Their pattern involves the appearance of anterior and posterior pairs of epibranchials rather than an evenly spaced quartet of them and was said to involve Eb I and II articulating with Ipb II and Eb III and IV articulating with Ipb III (they reported most cypriniforms to have but two infrapharyngobranchials, Ipb II and III). I have suggested above that the 2+2 pattern does not hold in and of itself because of the general presence among cyprinids, and cypriniforms, of an Ipb IV and now further suggest that the anterior half of the 2+2 pattern admitted as apt for cyprinids (above) is not primitive for all cypriniforms. The association between Eb I and II in this 2+2 pattern seems dependent on the absence of Ipb I or on a foreshortened Ipb II that would bring Eb I and II together if both were to articulate with it. Among non-cyprinid cypriniforms not all lack an Ipb I and only cobitidines among them have a small enough Ipb II to make the association of Eb I with II obvious. The suggestion by Roberts and Kottelat (1984) of a cypriniform-siluroid

relationship based on this 2+2 pattern is thus strained.

Ventral Gill Arch Elements. Due to the complete lack of any dermal skeletal elements among the upper pharyngeal structures of cypriniforms, discussion of the dorsal components of their gill arch necessarily was restricted to endoskeletal structures. Such is not the case for a discussion of the lower elements of their gill arches. Dermal elements are present among the lower gill arch skeletal components of cypriniforms, namely, as teeth associated with the fifth ceratobranchial. Gyrinocheilus possesses what are herein considered dermal elements associated with its third copula (C 3; see below), these "extra ossifications" being the only other dermal pharyngeal skeletal elements known among cypriniforms. Endoskeletal elements under consideration are: The median series of unpaired elements; bilaterally paired hypobranchials (usually three pairs, Hb I-III); and the bilaterally paired ceratobranchials (always five pairs, Cb I-V). The ventral gill arch elements of Chanos chanos are illustrated in fig. 34, and will serve as a basis for discussion of features of ventral gill arch elements considered primitive for teleosts and ostariophysans.

Included among the components of the lower halves of the branchial arches of teleosts are five pairs of ceratobranchials and three pairs of hypobranchials.

Ceratobranchials are usually elongate structures, trough shaped below to accommodate afferent arteries, and are the structures with which epibranchials articulate. Gill rakers often adorn their oral surface, and sometimes teeth or tooth patches do as well. Gill lamellae extend ventrally from their lower surface. Among teleosts teeth or tooth plates are often associated with CB V (Fink and Fink, 1981).

The presence of three pairs of hypobranchials, all of which normally ossify, is general among teleosts, though occasionally a pair associated with branchial arch IV sometimes appears. Why only three pairs, instead of five pairs, are present is unknown. The size relationships among the hypobranchials of Chanos appear representative of teleosts, and of ostariophysans. Hypobranchial I is usually longest and Hb III is often very much shorted than its two anterior serial homologues. The medial ends of Cb I-III articulate with the lateral ends of Hb I-III.

The lower half of the branchial arches of fishes are anchored to the unpaired median series of elements, known collectively as the basibranchial series. Nelson (1969a) provides the best discussion of this complex series of median elements. This series includes both dermal and endoskeletal components, and workers have not always taken care to carefully identify structures in the material under study. This is not problematic in the cypriniform

literature since gyrinocheilids are the only known cypriniforms to have any dermal components in the median series. However, workers on cypriniforms often have been careless with identification of the endoskeletal elements. The following discussion is aimed at clarifying the situation with the hope that future identification of the median elements of cypriniforms will be more precise, and more consistent.

The median series of unpaired elements in the lower gill arches of teleostomes fundamentally consists of three independent elements, termed copulae (C 1-3) (Nelson, 1969a). More attention has been devoted to the series of elements, the basihyal and basibranchials, that develop from these copulae than to the copulae themselves. It is generally the case that the hyoid arch articulates with C 1, or at least the posterior end of C 1. Branchial arches I-III articulate with C 2 (arch III with its posterior end) and arches IV and V with C 3. Little attention, apparently, has been paid to the relationships among these copulae and it seems not to have been reported before that it is only among teleosts that the anterior end of C 3 overrides the posterior end of C 2 though among osteoglossomorphs this is not universal (fig. 35). This particular observation of the positional relationship between the posterior end of C 2 and the anterior end of C 3 proves to be important in interpretation of homologies

among lower gill arch elements among non-cyprinid cypriniforms when some of the elements that normally appear are absent. As mentioned above the basihyal and basibranchials develop in or from pre-existing copulae. Nelson (1969a) pointed out that traditionally these elements are named or numbered according to which paired elements articulate just posterior to them. Thus, basihyal (Bh) is from the hyoid arch's articulation with C 1; basibranchials (Bb 1-3) take their number from the arch that articulates just posterior to them. Copula 3 normally remains unsegmented, and unossified, but the non-independent elements are still sometimes identified as Bb 4-5, or Bb 4-6 if a section of C 3 extends posteriorly between the medial tips of the Cb V pair, no implication of a sixth branchial arch being made (Nelson, 1969a). Segmentation of C 3 into separated elements does sometimes occur, and among teleosts is considered derived when it does occur. In this work the unsegmented cartilaginous structure with which branchial arches IV and V articulate is referred to as C 3. The terms Bb 4-6 are reserved for derivatives (separate segments) of C 3.

In this work a distinction is made between paired and unpaired elements of the lower portion of the gill arches. Paired elements are thought to be serial homologues and herein are identified to arch by a Roman numeral designation. Unpaired elements are of unknown

homology and do not seem to fit within the serial homology scheme of the paired elements. Therefore, unpaired elements herein carry an Arabic number designation.

Dermal plates, usually tooth bearing, are normally associated with the endoskeletal median elements of the lower gill arches, at least with those elements that develop from C 1 and C 2. The plate associated with C 1 is referred to as the basihyal tooth plate and that associated with C 2 is referred to as the basibranchial tooth plate, or if segmented, as the specific tooth plates of the basibranchial elements they overlay. Confusion sometimes arises for a not uncommon situation concerning these tooth plates of the median series. The confusion results from the retention of dermal plates associated with the basihyal or basibranchials even when teeth are absent, and is manifested as an identification of a tooth plate, a dermal element, as a basihyal or basibranchial, which are endoskeletal structures.

Cypriniforms and subgroups of cypriniforms depart characteristically from general teleostean and general ostariophysan lower gill arch structure in various ways. Fink and Fink (1981) have pointed out that none possess any basihyal teeth, nor do any reveal a tooth plate associated with copula 2 (Bb 1-3). They did not mention that no cypriniform yet has been discovered to possess a basihyal tooth plate either. Possession of such a plate,

toothed or not, is primitive for teleostomes (Nelson, 1969a) and for ostariophysans (fig. 34 for Chanos; Vari, 1983 and Roberts, 1969 for characiforms). Fink (1981) noted that cypriniform teeth are fully ankylosed to Cb V. Although this mode of tooth attachment is primitive for teleosts, it is not so for fishes of the general organization of ostariophysans (lower euteleosts) and Fink and Fink (1981) argued that this ankylosis of teeth to bone was synapomorphous for cypriniforms.

Among cypriniforms, gyrinocheilids are unique (fig. 36A,B; also illustrated by Ramaswami, 1952a). Their basihyal is a slender rod of bone, nearly vertical in its orientation. Only Bb 2 and Bb 3 segment and ossify from C 2 (sometimes a small nodule of bone appears between the posterior end of the basihyal and Bb 2). In my material C 3 was not observed to have segmented, was always cartilaginous, and ended between the anterior tips of the paired Cb V elements. Its anterior tip is positioned superiorly to the posterior tip of Bb 3 (the posterior end of C 2) as is conventional for teleosts (fig. gv 3B). Unconventionally, C 3 of gyrinocheilids supports two plate-like ossifications applied to its dorsal surface in the positions of Bb 4 and 5. These ossifications appear independent of C 3 (they can be moved, wiggled, independently of the underlying cartilage) and are regarded as dermal ossification. These two plates are the

only known dermal structures of the medial series of elements of the lower gill arches of cypriniforms.

Size relationships among gyриноcheilid hypobranchials are as those primitive for teleosts and except for one oddity, they are, overall, rather conventional. The oddity lies in Hb III. Gyrinocheilus has been reported to have but two pairs of hypobranchials (Ramaswami, 1952a) but careful study reveals the cartilage mass intervening between the ossified portion of Cb III and the posterior end of Bb 3 to be segmented. The medial most cartilage segment undoubtedly is an unossified, albeit small, Hb III.

Ceratobranchials of gyриноcheilids are long slender bars. Ceratobranchial I and II are shorter than Cb III and IV, a conventional arrangement considering that Hb I and II are quite long. Ceratobranchial V is decidedly unusual among cypriniforms. It is smallest among the pairs of ceratobranchials and no teeth or tooth plates are associated with it, a row of gill rakers lining its posterior edge instead.

Catostomid ventral gill arch components present several unusual features (fig. 37A,B). Of the median series of elements the basihyal develops from C 1 but beneath it lies an extra element which Nelson (1969a) termed a sublingual. Its origin is unknown but it appears to fall into the class of bones called sesamoid bones that

appear variously in the skeletons of vertebrates in ligaments, tendons or the gaps of joints. Occasionally the sublingual appears to preform in cartilage but Patterson (1977) has pointed out cartilages sometime appear in skeletal stress points as bones do. There is little reason to suspect the sublingual (s) of some cypriniforms is anything other than an adventitious structure.

Basibranchials 1-3, elements which ossify from copula 2, are rod-like. Basibranchial 1 in catostomids is uniformly small, a mere nodule of bone. Copula 3 usually segments in catostomids (fig. 37B), into three elements here termed Bb 4-6, but sometimes the posterior most element (Bb 6) is absent. As its name implies, Bb 6 lies longitudinally between the lower arms of Cb V posterior to the articulations of Cb V with the median series of elements. Basibranchial 4 is a rod-like element with a large laminar ventral keel. Positionally, Bb 4 maintains its place as the anterior end of C 3, that is its anterior tip lies superiorly to the posterior end of Bb 3 (C 2). These C 3 segments (Bb 4-6) were never observed to ossify in my material.

Catostomid hypobranchials are much like those of Gyrinocheilus. Hypobranchial I and II are bar-like bones, and Hb III is a small cartilaginous element, sometimes overlooked by previous workers (e. g., Ramaswami, 1957,

reported presence of just two pairs of hypobranchials).

Ceratobranchials I-IV of catostomids are bar-like too, as in Gyrinocheilus and other cypriniforms generally, and the size relationships among them are like those found in gyrinocheilids. Hypobranchial I and II are major elements, meaning they contribute substantially to the overall length of the lower portions of branchial arches I and II thereby reducing the length of Cb I and II (fig. 37A). Ceratobranchial V of catostomids is a large element, its lateral tip curving upward to approach the floor of the braincase. Its posteromedial margin bears a single row of teeth (fig. 37A, 38) that, due to the curve of the bone, bear against a basioccipital masticatory process (Weisel, 1960; Eastman, 1972). Catostomid pharyngeal teeth are small, and numerous enough (generally more than 30 per arch) to be described as comb-like. Only Ellopostoma among all other cypriniforms bears as many teeth on its Cb V as catostomids do, and tooth number in Ellopostoma is comparable only to the catostomids with the fewest Cb V teeth.

Cobitidid lower gill arches reveal features of the median series of elements that are similar to the specializations of the same series in catostomids.

Cobitidine lower gill arches are highly specialized (fig. 39). A basihyal is present, and beneath it lie sublingual ossifications. In Misgurnus (fig. 39B), a pair

of them appears rather than the large single ossification found in catostomids. The first element that usually develops from the anteromost section of C 2 (Bb 1) is normally absent among cobitidines. In some individuals (including the one figured in fig. 39A) tiny ossifications appear in series between the basihyal and Bb 2. These extra ossifications are treated as individual peculiarities since their frequency of appearance is low and their number varies and does not correspond to known structures of other fishes (Bb 1 is the element that normally appears in this position). Basibranchial 2 and 3 are normally present, though modified in shape. Basibranchial 2's anterior margin fans out so that it can no longer be considered a rod-like element, but rather as a plate lying in the floor of the mouth. Its posterior neighbor, Bb 3, exhibits some of the same shape tendencies, but not to the same degree it does. Copula 3 is segmented into Bb 4 and 5, and in Acanthopsis and Misgurnus into Bb 6 as well. Basibranchial 4 is shaped like Bb 4 in catostomids. It is a rod shaped element above with a pronounced ventral keel, and it is solidly ossified, an unusual occurrence for a C 3 derivative.

Cobitidine hypobranchials are unlike those of gyриноcheilids or catostomids. As a transverse element Hb I is short. As a longitudinal element it is long. Among cypriniforms the rectus I muscle that spans between Hb I

and the hyoid arch is usually small but among cobitidines it is bulky, originating from a long anteroventrally produced prong of Hb I that approaches the anterohyal, the site of attachment for the rectus I on the hyoid arch. Hypobranchial II has a similarly anteroventrally produced prong, not associated with the rectus I, that meets its bilateral counterpart in the midline beneath Bb 2. Hypobranchial III is small, ossified and with its bilateral counterpart, forms a canal in which the posterior end of Bb 3 is seated.

Cb I of cobitidines is long, necessarily so since Hb I is short. It is a slender element that arches ventrad to a much greater degree than its posterior fellows or that of previously described groups. A hooked process is located on its ventral surface near its medial end. This process serves as the attachment site for the obliquus ventralis muscle. Ceratobranchials II-IV progressively decrease in size from arch to arch posteriorly. Ceratobranchial V bears a single row of teeth on its posteromedial margin, and curves dorsally above the height of Cb I-IV, but not nearly as much as the Cb V of catostomids. Its underside bears a ventrally directed spike (fig. 40A-C) that serves as the site of insertion for the transversus ventralis V muscle.

Botiine lower gill arch elements (fig. 41A,B) are similar to those of cobitidines in some respects and

different from them in others. The basihyal of botiines is a large element with an expanded anterior end. It sits in a lower horizontal plane than its posterior fellows of the median series. Below it lies a pair of sublinguals. Basibranchial 1 is absent from the basibranchial series and Bb 2 and 3 have fan shaped anterior ends like those of cobitidines, Bb 3 of botiines to a greater degree than Bb 3 of cobitidines. Copula 3 is segmented into Bb 4 and 5; no Bb 6 was observed among botiines examined. The botiine basibranchial 4 possesses the rod-like shape with a ventral keel like the one seen in catostomids and cobitidines, and its anterior end is positioned as is conventional for the anterior portion of C 3 of a teleost relative to the posterior end of C 2. Basibranchial 4 of botiines remains cartilaginous, though many examples of it contained alizarin staining bodies within it, as sometimes did Bb 5 too.

The hypobranchial series of botiines, with all three pairs ossified, is very similar to that of cobitidines. Hypobranchial I is the largest element of the series. Its orientation is strongly ventral, rendering it nearly vertical (fig. 41B). Like cobitidines it possesses a prong for attachment of a hypertrophied rectus I muscle. Hypobranchial II is strongly ventral in its orientation too, and so is Hb III. Hypobranchial III is a rather

small element that fits snugly around the rod-like posterior end of Bb 3.

Botiine ceratobranchials are not as slender as cobitidine ceratobranchials and their Cb I does not arch ventrad as much as Cb I in cobitidines. Size relationships among botiine ceratobranchials, with Cb I the longest and Cb IV the shortest, are like those in cobitidines. Ceratobranchial V bears a single row of teeth and possesses the ventral spike to which the transversus ventralis V attaches (fig. 42A,B).

The lower elements of the gill arches of homalopterids are arranged much like those of cobitidids. Noemacheilines (fig. 43a,B) present a basihyal with an expanded head, beneath which lies a pair of sublinguals (fig. 44). Basibranchial 1 is absent from the series of elements that segment from C 2 and Bb 2 and 3 are similar to the fan shaped structures seen among cobitidids. Lefua's Bb 2 is further differentiated into a nearly cross shaped element. Copula 3 segments into Bb 4 and 5. Basibranchial 4 is shaped as that of catostomids and cobitidids. It occupies the position of the one found in the two just mentioned groups and is solidly ossified as in the latter. Basibranchial 5 lies anterior to the anterior tips of the pair of Cb V, and remains cartilaginous although occasionally alizarin staining particles can be observed within it.

Noemacheiline hypobranchials are short squarish ventrally oriented elements. Hypobranchial I does not possess the rectus I process of cobitidids. Among noemacheilines, N. posteroventralis is most unusual, possessing a pair of ossified Hb IV.

Noemacheiline ceratobranchials are like those found among botiines, Cb I clearly largest. Ceratobranchial V bears a single row of teeth and ventrally, the spike that serves as part of the attachment for the transversus ventralis V.

Homalopterines (fig. 45A-C) and Ellopostoma (fig. 46) all reveal a peculiar Y-shaped basibranchial below which lie sublinguals. Basibranchial 1 is absent, and Bb 2 and 3 are further modified in the plan of Lefua into T-shaped elements, or pulled out into elongate transverse bars as in Gastromyzon (fig. 45C). Basibranchial 4 is ossified, shaped and positioned as described for catostomids, cobitidids and noemacheilines (fig. 47). Basibranchial 5 is represented as a cartilage located anterior to the tips of the pair of Cb V.

Hypobranchials of homalopterids and Ellopostoma are similar to those of noemacheilines, as are their ceratobranchials. However the expansion of Bb 2 and 3, especially in gastromyzontins, tends to separate hypobranchials of the same arch from one another in the floor of the pharynx. Ceratobranchial V among

homalopterines bears a single row of teeth and possesses the transversus ventralis V spike (fig. 48A,B) seen in cobitidids and noemacheilines.

Non-cyprinid cypriniforms present a variety of lower gill arch element structure, and so do cyprinids yet some lower gill arch features do unite all cyprinids.

Illustrations of Barbus barbus, Cyprinus carpio, Labeo niloticus, Notropis atherinoides, Opsariichthys bidens and Saurogobio dumerillii (fig. 49A-F) are presented as a basis for discussion. The three basic independent elements of the median series of elements of the lower gill arches primitive for teleosts (C 1-3) are all present among cyprinids. A basihyal develops from C 1 and beneath it in some cyprinids, such as Gobio (fig. 50A) and Saurogobio, develops a sublingual ossification (see also Sawada, 1982). Barbus and Labeo show some sort of expanded basihyal tip but no cyprinid examined revealed any basihyal modification as unusual as that of homalopterines and Ellopostoma. Nearly all cyprinids possess Bb 1-3. Two types of basibranchial series seem apparent among cyprinids, a series of slender rods of nearly uniform diameter (when viewed from above) as in Notropis and Opsariichthys (fig. 49D,E) or a series of elements with expanded articular ends as in Barbus, Cyprinus, Labeo and Saurogobio (fig. 49A,B,C,F). The basibranchial series of Labeo deserves further comment.

Basibranchial 1 is lacking and Bb 2 is a cross-shaped element. A reduction in size of, or a loss of, Bb 1 is characteristic of the group of cyprinid fishes Reid (1982) called labeines, as is the cross-shaped Bb 2 too.

Copula 3 of cyprinids is a varied element also. Species of Psilorhynchus were the only taxa examined to exhibit ossification of it and among cyprinids it was not observed to segment. In Cyprinus, Saurogobio (fig. 49A,F) and Phoxinus (fig. 50C) it is a substantial cartilaginous rod with positional relationships as expected for teleosts. In Zacco (fig. 50D) C 3 is much reduced, being just a slender rod extending between the end of Bb 3 and the tips of Cb V. Labeo (fig. 49C) and labeines possess an extremely elongate C 3, with Cb V posteriorly removed from Cb I-IV.

Cyprinid hypobranchials, of which there are normally three ossified pairs, are characteristically small. Opsariichthys (fig. 49E) possesses about as large and as unmodified a pair of Hb I as is observed among cyprinids. The cyprinid Hb III is highly unusual. It is a curved spike, vertically oriented, that extends below Bb 3 to form a canal through which the afferent arterial trunk that supplies blood to the gill arches passes (fig. 49E). In many cyprinids it does not articulate with the basibranchial series, Bb 3 residing within the canal above the afferent trunk (fig. 50C,D). Hypobranchial II is

often modified among cyprinids, in a similar way as Hb III, but never as dramatically as Hb III.

Ceratobranchials I-IV of cyprinids are quite ordinary bar-like bones. Ceratobranchial I is longest, with the remaining ceratobranchials progressively decreasing in length posterorly among themselves following Cb I. There is nothing ordinary about Cb V in cyprinids. It is an enormously hypertrophied, massive falcate bone that bears from one to three rows of teeth. Many authors have described it, especially Chu (1935). It extends far dorsally to a level even with the dorsal tip of the levator process of epibranchial IV. A massive posterior levator branchialis V muscle inserts on its dorsal tip. Rather than "biting" against upper pharyngeal elements, Cb V teeth of cyprinids bear against a basioccipital masticatory process (in many cyprinid taxa, the basioccipital masticatory process bears a horny masticatory pad) positioned beneath, or even posteriorly to, the basioccipital condyle.

Ventral Gill Arch Elements Discussion. Lower elements of the gill arches of cypriniforms provide characterization of nearly all levels of generality considered in this study. Historically Cb V, and its teeth, has been most important. It figured in Agassiz's establishment (1835) of a natural group including just

cypriniforms as we know them today, and it is prominent among features mentioned in general group descriptions of cypriniforms (eg. Regan, 1911; Greenwood et al., 1966; Fink and Fink, 1981; Lauder and Leim, 1984). Its size and shape and the fact that Cb V teeth in cypriniforms do not oppose upper pharyngeal teeth are the aspects of Cb V that have drawn attention to it.

The teeth of Cb V of cypriniforms are a study in and of themselves. They are arranged in definite rows (1-3 rows) and are unlike teeth associated with Cb V in other teleosts, not being clearly identifiable as derivative of the tooth plates and patches of Cb V of other teleosts. Heckel (1843) erected a classification of the entire order of cypriniforms, as then known, based solely on the different types of their Cb V teeth. Agassiz (1855) and Weisel (1960) felt the resemblance between the single row of comb-like teeth in catostomids and rows of gill rakers was compelling and suggested the two kinds of structures were homologous. In this view multiple rows of teeth, as found among cyprinids, then would be more advanced than a single row and the teeth of cypriniforms then might not be homologous with those of other teleosts. Others (Chu, 1935) simply asserted that multiple rows were primitive and that the single row found among catostomids, cobitidids and homalopterids more advanced. Nelson (1969a) argued forcefully so, noting that the Cb V teeth

of cypriniforms were to be ultimately derived from tooth plates or patches, not gill rakers, and that this meant multiple rows were more general, and a single row less so. Nakajima (1984, 1987) has made great progress in making available detailed enough information in a comparative manner to settle such questions. His conclusion reiterates the necessity of thinking of cypriniform subgroups as sister taxa, and not as ancestors or descendants of one another. Nakajima studied the ontogeny of the adult tooth row pattern among cyprinids and cobitidids and compared his observations with those of Weisel (1967) for catostomids. He found that a pattern of alternate-tooth replacement waves was common to all cypriniforms, but that the single tooth row pattern found among non-cyprinid cypriniforms and the multiple tooth row pattern of cyprinids were each specializations of a more general, multiple rowed larval pattern.

Other lower gill arch features that characterize cypriniforms as a group are the absence of basihyal teeth (Fink and Fink, 1981), absence of a basihyal tooth plate, absence of the Bb 1-3 tooth plate (Fink and Fink, 1981) and ankylosis of teeth to Cb V (Fink and Fink, 1981).

Subgroups of cypriniforms that are characterized by specializations of their lower gill arch elements are: gyrinocheilids, cyprinids and a catostomid-cobitidid-homalopterid group; within the latter

group subgroups of catostomids, cobitidids, cobitidines, botiines, a cobitidid-homalopterid group and an Ellopostoma-homalopterine group are characterized by lower gill arch features too.

Gyrinocheilids are characterized by an unossified Hb III, uniquely so by the dermal ossifications associated with copula 3. Among cypriniforms they are also unique for their small, completely toothless Cb V.

Cyprinids are notable for their hypertrophied Cb V with multiple rows of teeth and for the modification of Hb III into vertical spikes that form a canal for the afferent trunk that courses forward below the median series of gill arch elements.

A catostomid-cobitidid-homalopterid group is characterized by a single row of teeth (often numerous), sublingual ossifications and the segmentation of C 3 into Bb 4-6. The shape of Bb 4 is unusual and universal among members of this group, and appears related to the afferent blood supply (fig. 51a,B). The common afferent arterial trunk of afferent arteries (AA) III and IV rises from the ventral aorta below and just anterior to the keel on the underside of Bb 4. Afferent artery III branches off anteriorly to run laterally beneath Cb III, AA IV branches off but courses posteriorly along the keel before turning laterally to run beneath Cb IV.

Catostomids are characterized by their specialized tooth structure (Weisel, 1967) and by the abundance of those teeth. All catostomids have an unossified Hb III.

A cobitidid-homalopterid group is characterized by ossification of Bb 4, a copula 3 derivative that usually is not ossified among teleosts, and by the fan-shaped anterior ends of Bb 2 and 3. Basibranchial 1 is absent from this group, as reported by Nelson (1969a). Sawada (1982) suggested that the basibranchial series of this group was in fact complete, containing Bb 1-3, but that it was shifted backwards one arch, creating the false impression of a missing Bb 1. But the ossified element Sawada (1982) identifies as "Bb 3" is in fact Bb 4, clearly so by its shape and position as the derivative of the anterior endpiece of copula 3. All members of this group also possess the ventral spike on the underside of Cb V that serves as an attachment site for the transversus vantralis V muscle.

All cobitidids are characterized by the anterior prong of Hb I to which a bulky rectus I attaches. Cobitidines are characterized by their long ventrally arching Cb I and by the anterior extension of Hb II that meets its counterpart below Bb 2. Botiines, on parsimony grounds, are characterized by their unossified Bb 4.

Ellopostoma and homalopterines possess a remarkable Y-shaped basihyal and a T-shaped Bb 2 that among some

gastromyzontins is drawn out into a transversely lying bar between a widely separated pair of Hb II. Nelson (1969a) suggested that the expanded basihyal found among noemacheilines might be an indication they are closely related to homalopterins and gastromyzontins. Some noemacheilines, such as Noemacheilus selangoricus, show a basihyal that is suggestively Y-shaped, and Lefua reveals a suggestively T-shaped Bb 2. This might be an indication that these noemacheilines are more closely related to the Elopostoma-homalopterine group than they are to other noemacheilines.

ETHMOID REGION

Lateral Ethmoid. The lateral ethmoid is a paired endoskeletal bone of great systematic interest. It has often been described as a compound bone, consisting of endoskeletal and dermal components (see Harrington, 1955, and Weitzman, 1962, for examples of this for otophysans), but Patterson (1975, 1977) has concluded they are entirely of endoskeletal origin among teleosts. Generally, the lateral ethmoid forms part of the lateral wall of the cranium at the rear of the "ethmoid" region. It extends between roofing and flooring elements of the cranium in the "ethmoid" region and extends laterally from the brain case as an anteroventrally inclined transverse plate that separates the orbital and nasal regions. Starks (1926)

has described and illustrated the lateral ethmoid of many fishes, including some cypriniforms. Weitzman (1962), Roberts (1969), Fink and Fink (1981) and Patterson (1984) have described or figured it for a variety of ostariophysans.

Among cypriniforms, cyprinids possess a lateral ethmoid like that primitive for teleosts (fig. 52A,B; see also illustrations in Sagemhel, 1891, Ramaswami, 1952a,b, 1955a,b, Howes, 1978, 1979, 1980, 1981, 1982, 1984b, and Roberts and Kottelat, 1984). It preforms in cartilage and its transverse plate defines the anterior wall of the orbit and the posterior wall of the nasal capsule.

All non-cyprinid cypriniforms deviate from the general teleostean structure found among cyprinids. In gyриноcheilids the lateral ethmoid divides the orbital and nasal regions of the head as is usual, but the lateral edge of their lateral ethmoid is anteriorly produced into a long spine-like process (fig. 53; see also Ramaswami, 1952a). As a result, the lateral ethmoid forms a cup in which the nasal capsule sits, and alongside of which the first infraorbital lies.

Catostomids reveal a lateral ethmoid similar to that found in Gyrinocheilus (fig. 54A,B; see also Ramaswami, 1957). In some catostomid taxa the anterolateral process extends as far forward as the level of the anterior margin of the supraethmoidal wings, and the gap between the

ventral, medial, and lateral margins of the lateral ethmoid is floored with bone (see also Starks, 1926).

Homalopterids exhibit the same type of anterolateral process on their lateral ethmoids as was seen in gyri-nocheilids and catostomids (fig. 55A-D: see also Ramaswami, 1952c,d, and Sawada, 1982).

Cobitidid lateral ethmoids are unlike those found among all other fishes. Their lateral ethmoid is modified into a movable, erectile suborbital spine (fig. 56, 57; see also Ramaswami, 1953, Nalbant, 1963, Sawada 1982). Among material examined Vaillantella was the only one to possess a substantial anterolateral spine (fig. 58). All others lack the anterolateral spine, and except for Misgurnus, have a stout, usually bifid, suborbital spine. When retracted the spine points caudad. When erected it projects laterally from beneath the anterior edge of the eye. Functional considerations of this suborbital spine are anecdotal, but speculate it to be used for defensive purposes.

Cobitidids, except Acanthopthalmus, possess another peculiarity of the ethmoidal region, a ribbon-like ossification, here called the nasal ribbon, that wraps around the anterior and lateral margins of the nasal capsule. This nasal ribbon is not an obvious derivative of other ethmoidal bones. One possibility of derivation, however, is that the lateral ethmoid of cobitidoids is in

fact a compound bone and that an intramembranous prefrontal portion (the anterolateral process of non-cobitidid cobitidoids) has become disassociated from the endoskeletal lateral ethmoid proper and left in position around the nasal capsule in the process of the modification of the cobitidoid lateral ethmoid into a suborbital spine. However, this is not the hypothesis of choice and the nasal ribbon is instead homologized with the first infraorbital of other cypriniforms (see below).

Lateral Ethmoid Discussion. The lateral ethmoid of cypriniforms has not previously figured in discussions of interfamilial cypriniform systematics. The modification of it into a suborbital spine has long been recognized as a specialization and an indication of relationship (Agassiz, 1835), but only among some cobitidids (those that have it). The anterolateral process of gyrinocheilids, catostomids and homalopterids is unusual among teleosts generally, and considered herein to characterize the Cobitidoidea, with the suborbital spine of cobitidids being a further modification of it. Starks (1926) did in fact study the ethmoidal region of a number of cypriniforms but did not judge it to be very noteworthy systematically. The ethmoidal regions of catostomids, cyprinids, and the cobitidid he examined, Misgurnus, are hardly very similar and in isolation did not suggest to

him any particular relationships among taxa. Only when a wider range of cypriniform taxa are studied, and other features examined, do the systematic implications of the cypriniform lateral ethmoid become clear.

Greenwood, et al. (1966), Lenglet (1974) and Howes (1985) have illustrated a structure similar to the anterolateral process of cobitidoids in some gonorynchiforms (Kneria, Parakneria and Comeria). Howes (1985b) considered the structure of the lateral ethmoid of these three genera an indication they were most closely related to each other among gonorynchiforms. I have not examined material of these taxa, and cannot comment about how the lateral ethmoid morphology of these gonorynchiforms corresponds to that of cobitidoids. The interrelationships among all ostariophysans does suggest however, that resemblance between some gonorynchiforms and cobitidoid cypriniforms is homoplasious, and not indicative of relationship.

Palatomaxillary Elements. Non-cyprinid cypriniforms possess structures, not usually present in other fishes, that intervene between the maxillaries and the palatines and pre-ethmoids. Two of these structures have been known for a long time (Regan, 1911; Starks, 1926) but they have not been used as indicators of relationship.

Benjamin (1986) described two palatomaxillary elements in Gyrinocheilus, a chondroid meniscus that intervenes between the pre-ethmoid region of Gyrinocheilus and its maxillary, and one that intervenes between its palatine and maxillary. The latter stains with alcian blue in material included in this study, the former does not.

Catostomids possess the two palatomaxillary elements similar to those found in Gyrinocheilus, and another (fig. 59). The one communicating between the pre-ethmoid and the maxillary, called the 2nd pre-ethmoid, is rod-like and usually cartilaginous but does occasionally ossify, or at least mineralize with alizarin staining materials. That which communicates between the palatine and the maxillary is called the prepalatine and is usually cartilaginous. A third structure located medial to the prepalatine and communicating between the kinethmoid and the palatine is here called the mesioprepalatine.

Sawada (1982) has described the palatomaxillary elements of cobitidids and homalopterids, in which except for Ellopostoma, they are always solidly ossified. Botiines possesses a prepalatine and 2nd pre-ethmoid, and a separate mesioprepalatine ossification which Sawada (1982) called a sesamoid bone. Cobitidines possess a single palatomaxillary structure. It is elongate and its posterior end is bifurcate. The lower limb of its posterior bifurcation articulates with the pre-ethmoid,

the upper limb with the palatine (see Sawada, 1982, Fig. 32b). The posterior bifurcation, with its double articulation, of this single palatomaxillary element in cobitidines gives the appearance that it is the result of fusion of the prepalatine and 2nd pre-ethmoid ossifications.

Noemacheilines and homalopterins possess ossified prepalatines and 2nd pre-ethmoids like those found in botiines. The gastromyzontin Glaniopsis possesses ossifications like those of noemacheilines and homalopterins but all other gastromyzontin taxa examined (Gastromyzon, Beaufortia, Vanmania and Crossostoma) possess only the 2nd pre-ethmoid. Ellopostoma was found to possess only an unossified 2nd pre-ethmoid.

Palatomaxillary Elements Discussion.

Palatomaxillary elements, 2nd pre-ethmoids and prepalatines, characterize non-cyprinid cypriniforms as a group. They are the only ostariophysans to possess them consistently. Occasionally cyprinids and other fishes are found to possess adventitious structures like the palatomaxillary elements of cobitidoids but their origins do not appear tied to that of such structures of cobitidoids. Ossification of palatomaxillary elements characterizes the cobitidid-homalopterid subgroup of cobitidoids. An ossified mesioprepalatine characterizes

botiines and the single "compound" structure found among cobitidines characterizes them. A secondary "absence" of the prepalatine appears to be synapomorphic of a subgroup of gastromyzontins.

CEPHALIC LATEROSENSORY CANALS AND CIRCUMORBITAL BONES.

Discussion of the cephalic laterosensory canal patterns and of patterns of circumorbital bones of cypriniforms may be grounded in an understanding of general teleostean and general ostariophysan patterns. Circumorbital bones are the laminar dermal bones surrounding the orbit and include the antorbital, supraorbital and infraorbital bones. Nelson (1969b) reviewed patterns of infraorbital bones among a variety of teleost fishes and concluded that possession of an antorbital followed by six laminar infraorbitals (Io 1-6) was general for the Teleostei (he did not include the supraorbital in his considerations). This pattern occurs in characiforms (Weitzman, 1962; Roberts, 1969; Nelson, 1969b; Fink and Fink, 1981) and in Chanoides (Patterson, 1984), and is probably primitive for ostariophysans, or at least otophysans (see Fig. 7 of Fink and Fink, 1981, for illustrations of the circumorbital series of representatives from all major ostariophysan lineages). Nelson (1969b) also suggested that among teleosts not only was the dermal bone pattern apparent but that the number

of neuromasts associated with the last three infraorbitals (Io 4-6; Io 6 is called the dermosphenotic) was stable too, there being one per each of these three bones. Also, infraorbital 3 seems to be the largest of the infraorbital series.

The cephalic laterosensory system of teleosts includes laterosensory canals, pit lines and free organs. This study includes observations only of laterosensory canals, and primarily observations of connections among the different parts of the cephalic laterosensory canal system. The canals under consideration are the supraorbital, infraorbital, preopercular, temporal and supratemporal canals. Nelson (1972) reviewed the connections among these canals and concluded that the pattern primitive for teleosts included interconnections among the infraorbital, temporal, preopercular and supratemporal canals but considered the generality of a connection between the supraorbital and the rest of the cephalic laterosensory canals (specifically between the supraorbital and infraorbital canals) problematic as one does, or does not, occur throughout teleosts. Within ostariophysans the set of laterosensory canal interconnections Nelson (1972) felt were demonstrably general among teleosts occurs widely in all major lineages and is here considered to be general for them. Specifically, these connections are (fig. 60): 1) a

connection between the infraorbital and temporal canals; 2) a connection between the preopercular and temporal canals above the anterior edge of the operculum; and 3) a connection between the temporal and supratemporal canals near the posttemporal bone (a supratemporal bone is sometimes pertinent to this connection). When it occurs, the connection between the supraorbital canal and the infraorbital canal is made near the point where the infraorbital and temporal canals join.

Weitzman and Fink (1983) have hypothesized that a completely interconnected cephalic laterosensory canal system is general for characiforms, and such a completely interconnected system of laterosensory head canals occurs among some gonorynchiforms (Lenglet, 1974), cypriniforms (Lekander, 1949; Illick, 1956; Gosline, 1974) and siluroids (Kindred, 1919; Lekander, 1949). A completely interconnected system does not occur in chanids (Patterson, 1975), Phractolaemus (Thys van den Audenaerde, 1961) or Chanoides (Patterson, 1984). Even so, the widespread distribution of a supraorbital-infraorbital canal connection among ostariophysans is impressive and leads to the conclusion that it is general for them, and the widespread occurrence of this connection among lower teleosts (Nelson, 1972; Forey, 1973; Grande, 1985) suggests it is in fact general for all teleosts too.

The relationships between the cephalic lateralis

system and the laminar dermal bones that underlie or include it is complex and so intimate that it is sometimes hardly worthwhile to distinguish between the two systems (i.e. the identification of infraorbitals in most catfishes). There is some evidence that sense organs of the lateralis system even provide stimulus for bone formation. Ørvig (1972) has reviewed the relationship between these two systems and pointed out the intimate association between them is phylogenetically very old. Nevertheless, occasionally among teleosts the two systems are found largely to be unassociated, seemingly secondarily so. Such a disassociation seems to have occurred among cypriniforms, especially among non-cyprinid cypriniforms, principally in the circumorbital region but in other areas of the head as well. In these instances sense organs do not initiate laminar bone formation (Lekander, 1949; Reno, 1966, 1969; Ørvig, 1972) and one often finds tubular ossifications around laterosensory canals floating above, and well separated from, laminar dermal ossification, the two separate ossifications never having an ontogenetic connection (Lekander, 1949). It is also sometimes the case that laterosensory canal and infraorbital bone ossifications begin quite separately, but later the canal ossification secondarily becomes enclosed by growth of the underlying laminar bone. Homologizing canal ossifications with the laminar dermal

ossifications that normally underlie the canals in these instances of disassociation is probably a mistake.

In his review of infraorbital bones among teleosts, Nelson (1969b) noticed that cyprinids seemed to have only five, instead of six, infraorbital bones, and suggested that the reduction in infraorbital number was due to a "fusion" between Io 3 and 4. An indication that Io 3 and 4 were in some sense combined into a single element among cyprinids was that the third bone of the infraorbital series of cyprinids seemed to support a greater number of neuromasts than would normally be expected of an Io 3. Nelson (1969b) called the last element of the infraorbital series of cyprinids the dermosphenotic (fig. 61). Primitively, the dermosphenotic is the sixth bone of the series, and possesses an enclosed laterosensory canal with a characteristic fork (see Weitzman, 1962, Nelson, 1969b, and Patterson, 1984, for illustrations of it). The element Nelson identified as the dermosphenotic in cyprinids lacks this characteristic fork, is only the fifth element of the series and is often reduced to a bony tube with little or no associated laminar component. Identification of this element as a dermosphenotic might seem problematic except that the posteriorly directed branch of the laterosensory canal associated with the dermosphenotic of teleosts interconnects with the temporal canal (see Vari, 1979, for illustrations of this for some

characiforms) and this connection is made by the element Nelson labels as the dermosphenotic in cyprinids. Nelson did not say so, but cyprinids usually, perhaps universally, lack an antorbital too.

The implication of Nelson's (1969b) observations have not been widely appreciated by cypriniform workers, as has been pointed out by Patterson (1984). Only Gosline (1975) has followed Nelson's (1969) terminology, but Gosline did not comment on its correctness. Most workers (Hensel, 1978; Howes, 1978, 1979, 1980, 1981, 1984b; Roberts and Kottelat, 1984) have not accepted Nelson's identification of the fifth element of the cyprinid infraorbital series as a dermosphenotic, consistently labeling it Io 5, but none of them have dealt substantively with the issue which turns on the point of "fusion" of Io 3 and 4 into a single element. They have labeled as dermosphenotic, a tubular ossification that sometimes appears between the fifth element of the infraorbital series of cyprinids and the temporal canal. When such an element is absent the implication of their labeling is that the dermosphenotic is lacking in the taxa under study. Individual tubular ossifications not associated with any laminar component often appear among cyprinids, especially when neuromast numbers are secondarily increased (Lekander, 1949; Hensel, 1978). Homologizing these tubular ossifications that are the

result of a secondary tendency of the laterosensory system with laminar dermal elements with a long stable history among teleosts is questionable at best, and in my view, given the tendency for disassociation of the laterosensory canals from their underlying laminar bones to occur, mistaken. The element identified as a dermosphenotic by many cypriniform workers probably is not the dermosphenotic of other teleosts.

Another circumorbital element of cyprinids, the supraorbital, has received a certain amount of attention. It is absent from some cyprinids, but discussion centering around it mainly involves its sometimes large size and contact with other circumorbital series elements. It is sometimes large enough to roof the entire dorsal margin of the orbit (fig. 62). Such an elongate supraorbital is surely derived as the supraorbital is usually located over the anterodorsal margin of the orbit (fig. 61; see also fig. 52, 53, 54A).

A completely interconnected set of cephalic laterosensory canals (fig. 60) has been hypothesized as primitive for cyprinids (Lekander, 1949; Illick, 1956; Gosline, 1974). Such a set of interconnections occurs widely among cyprinids, non-cyprinid cypriniforms and other ostariophysans. There is, however, a remarkable tendency among cypriniforms for discontinuities to develop among the different canal system components.

Laterosensory canals begin as sense organs located in the skin. An invagination process encloses them in an epidermal tube, around which ossifications may, or may not, then develop (Lekander, 1949; Reno, 1966, 1969). Apparently, for unknown reasons, in regions where canals fail to interconnect and are thus discontinuous, the developmental invagination process just is not completed.

Gosline (1974) has pointed out that among cyprinids discontinuities of the cephalic laterosensory system occurs in a systematically interesting way in just two places, between the supraorbital and infraorbital canals (fig. 62) and between the preopercular and temporal canals (fig. 63; illustration in Illick, 1956, and Reno, 1966, 1969). Howes (1978, 1981) has stated that a connection between the supraorbital and infraorbital canals always occurs. His statement is incorrect and is best interpreted to mean between the infraorbital and temporal canals (Illick, 1956, labeled the temporal canal as part of the infraorbital canal) as there is an abundance of detailed evidence that a discontinuity occurs frequently among cyprinids in this region (Lekander, 1949; Illick, 1956; Reno, 1966, 1969; Hensel, 1976). There is little doubt that these gaps in the laterosensory canal system are derived, especially the discontinuity between the preopercular and temporal canal, but in and of themselves these gaps are difficult to evaluate systematically

because of their inherent nature as "loss" characters. Congruence with other features would erase doubts, but as things now stand that congruence with other features of cyprinids is lacking. A consequence of the lack of a preopercular-temporal canal connection in some cyprinids is the absence of suprapreopercular(s) in these taxa. A suprapreopercular is usually present, fused to the operculum, in cyprinids with a preopercular-temporal canal connection. Lekander (1949) recognized the unusual nature of a fusion between preopercular and opercular elements, suggesting it was derived.

The circumorbital series and cephalic laterosensory canal system of non-cyprinid cypriniforms is of systematic interest. Among them, only the first three elements of the infraorbital series, Io 1-3, can be identified with assurance, and only among some catostomids do Io 2 and 3 approach the form of Io 2 and 3 found among cyprinids and other ostariophysans with a generalized infraorbital series. Infraorbital 2 and 3 among non-cyprinid cypriniforms are usually greatly reduced, or even absent. There appears to be a very strong tendency among non-cyprinid cypriniforms for disassociation between the laterosensory canals of the head and underlying dermal bones. The laterosensory canals are then often found free in the skin, sometimes merely as epidermal tubes without any associated ossification or as tubular ossifications

referred to by some as "drainpipe" bones.

Gyrinocheilids possess a characteristic set of infraorbitals and associated laterosensory canals (fig. 64). Infraorbital 1 is largest, by a large margin. Its anterior portion is ovoid in shape, and its posterior end is drawn out into an attenuated process that lies against the anterolateral process of the lateral ethmoid. No antorbital lies ahead of, or dorsal, to it. Behind it lies a series of ossified tubes, some of which possess some associated laminar elements. The first two of these ossifications, and possibly the third, can be homologized with Io 2, 3 and 4? of other teleosts. At least three, sometimes more, additional tubular ossifications occur in the infraorbital series of Gyrinocheilus between the possible Io 4 and the temporal region canal. Homologizing these with Io 5 and 6 of other teleosts is problematic but it should be noted that the first two of these ossifications of Gyrinocheilus contain a single neuromast each, as Io 5 and 6 should (Nelson, 1969b).

The supraorbital canal always connects with the infraorbital and temporal canals in gyrinocheilids (fig. 64). The preopercular canal never joins the temporal canal as is usual. Instead it joins the infraorbital canal just posterior to the fourth element of the infraorbital series.

Catostomids, though not all, reveal the reduction of

Io 2 and 3 exhibited by Gyrinocheilus (fig. 65A-D). Their Io 1 is typically largest and no antorbital precedes it in the circumorbital series and Moxostoma, Hypentelium, Thoburnia, Erimyzon, Catostomus, Pantosteus, Xyrauchen, Deltistes and Chasmistes also lack a supraorbital. When a supraorbital is present in catostomids it is located over the anterodorsal part of the orbit. Identification of infraorbital series elements posterior to Io 1-3 is problematic in catostomids. Behind Io 3 a series of short tubular ossification containing the infraorbital canal leads up to the temporal region, which also may possess a series of short tubular elements instead of a pterotic temporal canal. These are the elements that inspired the term "drainpipe" bones.

The interconnection among various units of the laterosensory head canals of catostomids fall into several patterns (fig. 66). In this regard, as a group, catostomids are more variable than any other group of cypriniforms. One invariant connection of their cephalic laterosensory system is the one between the infraorbital and temporal canals. When the preopercular canal in catostomids does not end blindly it communicates with the infraorbital canal just posterior to the fourth element of the infraorbital series. This unusual pattern of connection may provide a point of reference for homologizing some of the tubular ossifications of the

catostomid infraorbital series with infraorbitals of other cypriniforms and teleosts generally.

Catostomids reveal another remarkable feature of their cephalic laterosensory system, one that might be related to their proclivity to enclose their head canals in "drainpipe" bones. Instead of a few neuromasts on Io 1-3 and one per element on Io 4-6, dozens of neuromasts lie, strung like beads, on the inner wall of the infraorbital and temporal canals. Among cypriniforms, cyprinids that secondarily increase numbers of neuromasts in head canals (Hensel, 1978), also secondarily increase numbers of infraorbital and temporal canal elements. The "drainpipe" bones of catostomids are likely a manifestation of their secondary increase of neuromasts in head canals.

The circumorbital series of cobitidids and homalopterids is largely non-existent and the disassociation of the cephalic laterosensory canals from their underlying dermal bones is marked in these two families. They all lack an antorbital and only Io 1 of their infraorbital series is clearly identifiable.

Among botiines Io 1 is elongate and always associated with the anterior end of the infraorbital canal and, posteriorly, with the lateral ethmoid (fig. 67, 68A,B, 69). It is not always wholly ossified and its unossified portion appears to be dense, sometimes fibrous,

connective tissue. Even so the infraorbital canal is closely, and intimately, associated with it anteriorly (they are never separate). In Botia macracantha (fig. 67) the anterior end of the infraorbital canal ossification fuses with the laminar component of Io 1 which has an unossified posterior end that lies alongside the lateral ethmoid. In B. purpurea (fig. 68A,B), Leptobotia (fig. 69) and Vaillantella (fig. 58, 70) it is the posterior part of Io 1 associated with the lateral ethmoid that is ossified and the anterior portion, the part associated with the infraorbital canal, that is not. Behind Io 1 lies a series of tubular ossifications that might be homologized with the infraorbitals of other fishes (based on numbers of contained neuromasts), or a series of weakly ossified patches on the medial side of the infraorbital canal (fig. c9), ossifications that appear in association with canal neuromasts.

The preopercular canal of botiines interconnects with the temporal canal, but in a manner that appears secondary. Two long tubular suprapreopercular ossifications, unfused to other elements, are present among most botiines. Their length is notable and in B. macracantha the lower one extends along the entire anterior edge of the operculum, not just over the anterodorsal arm of it as is usual among cyprinids. The shorter more dorsal second suprapreopercular spans some of

the distance between the dorsal edge of the operculum and the temporal canal.

The relationship between Io 1 and the infraorbital canal in noemacheilines is like that found among botiines (fig. 71). Lefua lacks head canals, but an elongate ossification positionally correct and associated with the anterolateral process of its lateral ethmoid is present and identified as Io 1. Other than an Io 1, noemacheilines possess little more in the way of an infraorbital series than weak neuromast associated ossifications on the medial side of their infraorbital canal. Homologizing these ossifications with infraorbitals of other fishes would be doubtful.

Discontinuity among canals is characteristic of the laterosensory canals of the head of noemacheilines. The nasal and frontal portions of the supraorbital canal are not always continuous and the supraorbital canal does not always join the infraorbital canal. The preopercular canal lies free in the skin, not fused with the underlying preoperculum, and never unites with any other unit of the cephalic laterosensory system.

Homalopterins possess an Io 1 similar to that of noemacheilines (fig. 72A,B). Usually it is only partly ossified. Its posterior end is ossified and is associated with the lateral ethmoid (fig. 73). The anterior end of the homalopterine Io 1 is not ossified but is associated

with the anterior end of the infraorbital canal, as in some botiines. Ossifications occur on the medial side of the infraorbital canal throughout its length and in Lepturichthys they are quite solid and enclose sections of the sensory canal.

The supraorbital, infraorbital and temporal canals all interconnect among homalopterins. The preopercular canal never joins the temporal canal, is free of the underlying preoperculum, and in Lepturichthys joins the infraorbital canal as individual variation.

Gastromyzontins possess an Io 1 independent of the infraorbital sensory canal (fig. 74A,B). That of Crossostoma is fairly conventional in shape and position for a non-cyprinid cypriniform, but that of Gastromyzon is hypertrophied and the largest element in the snout region, even of the whole head. The specimen of Glanioptis examined for this study lacked all infraorbital ossifications, and all other ossifications associated with laterosensory head canals. It lacked the preopercular canal entirely. Laminar bone development is associated with infraorbital canal ossifications of gastromyzontins in the region of the canal posterior to that portion that would normally be associated with Io 1. Those in Crossostoma might be homologous with infraorbitals of other teleosts but those of Gastromyzon probably are not.

The supraorbital, infraorbital and temporal canals

interconnect in gastromyzontins, including Glaniopsis. The preopercular canal is free from the preoperculum in gastromyzontins and when present, interconnected with the infraorbital canal.

Ellopostoma is unusual among homalopterids. Its Io 1 is as would be considered primitive for cypriniforms and its preopercular canal is associated with its preoperculum. Ossifications of the infraorbital series are nothing more than tubular ossifications around canals and the preopercular canal ends blindly. The infraorbital, supraorbital and temporal canals all interconnect.

Cobitidines are very unusual. Only Acanthopsis among them possesses any laterosensory head canals (fig. 75) and no cobitidine possesses what are clearly identifiable as infraorbital bones. Lekander (1949) studied Cobitis, and could say no more than that the canal invagination process that normally encloses neuromasts in canals just never occurred.

All cobitidine taxa except Acanthophthalmus possess peculiar ribbon-like ossifications in the region of the nasal capsule (fig. 56, 75, 76). These nasal ribbons are interpreted as remnant Io 1 bones. The possibility that they are an intramembranous remnant of the lateral ethmoid was discussed earlier. The interpretation of them as Io 1 is based on their position which is similar to that

occupied by the Io 1 of other cypriniforms (a position that is similar to the position of the anterolateral process of the lateral ethmoid too) and on the tendency among non-cyprinid cypriniforms of disassociation between the cephalic laterosensory system and its underlying dermal bones. Freeing Io 1 from its association with the infraorbital canal occurs in *gastromyzontins* and *Lefua* and would leave Io 1 available for modification into a nasal ribbon if such did occur in cobitidines. A pair of intriguing foramina occur in the nasal ribbons of *Misgunus*. If nerves that supply neuromasts of the infraorbital region were found to pass through them, it would lend support to the interpretation of these nasal ribbons as a modified Io 1.

Circumorbital Series and Cephalic Laterosensory

Canal Discussion. Cyprinids are characterized by their infraorbital series composed of five elements, including the dermosphenotic (Nelson, 1969b). A large supraorbital that contacts their dermosphenotic over the rear of the orbit probably characterizes a subgroup of them. Weitzman and Fink (1983) have discussed reductive tendencies of the cephalic laterosensory system among characiforms, pointing out the inherent difficulty of treating these reductive "losses" and "absences" systematically. Such reductions as they describe, failure to develop connections between

the supraorbital and infraorbital canal and between the preopercular and temporal canals, probably define subgroups of cyprinids (Gosline, 1974). However, corroborative evidence is yet wanting among cyprinids that would allow evaluation of these "losses" as characters of systematic importance. Another feature, investigated by Lekander (1949), fusion of a suprapreopercular to the operculum probably characterizes all cyprinids, but points to another problem. Such fusion can only be present in those cyprinids whose preopercular canal does not end blindly before crossing the dialator arm of the operculum. In other words, it is present only in those cyprinids with a preopercular-temporal canal interconnection. Implicit in the statement that fusion between a suprapreopercular and the operculum is characteristic of all cyprinids is that such a fusion would actually occur if all cyprinids had the preopercular-temporal laterosensory canal interconnection.

Non-cyprinid cypriniforms are characterized by an infraorbital series with Io 1 as its largest element (instead of Io 3) and with dramatic reduction, or absence, of all other infraorbital elements. Infraorbital 2 and 3 can be identified with assurance among some cobitidoids but posterior elements of the infraorbital series are of doubtful homology. Discontinuities among the laterosensory head canals and their disassociation from

underlying dermal elements are remarkable tendencies among non-cyprinid cypriniforms. All of them, except botiines, fail to develop a connection between the preopercular and temporal laterosensory canals, and as a group cobitidoids are characterized by this. The connection in botiines, evidenced by unusually long suprapreoperculars running over the operculum, appear to have the connection secondarily, and are thus characterized. Cobitidines carry reduction of the cephalic laterosensory canal system to an extreme, losing it entirely in all except Acanthopsis which possesses only the infraorbital and temporal canals. The nasal ribbon ossifications of cobitidines are hypothesized to be the result of this reduction, and they are hypothesized to be remnants of Io 1. Homalopterids, except Ellopostoma, possess a preopercular canal free from the preoperculum, and gastromyzontins also possess an infraorbital canal completely free from Io 1.

The lack of connection between the preopercular and temporal canals among non-cyprinid cypriniforms has another interesting aspect, one that is not reductive in nature. These fishes, when the preopercular canal does not end blindly, interconnect their preopercular and infraorbital canals (occurs in gyrinocheilids, catostomids, gastromyzontids, and some homalopterids). This connection is highly unusual among teleosts (it is

found among sarcopterygians; Hensel, 1986) and might involve enclosing the vertical pit line that normally spans between the infraorbital and preopercular canals of cypriniforms (Lekander, 1949) in a canal. This interconnection is taken as evidence that all non-cyprinid cypriniforms are closely related. As with fusion of a suprapreopercular with the operculum hypothesized to be characteristic of cyprinids, lack of such a connection among some cobitidoids is hypothesized to be a consequence of their extreme reduction of the preopercular canal, or in the case of botiines other secondary modifications of the cephalic laterosensory canal system, and as such is not considered very problematic as to relationships.

SYSTEMATIC DISCUSSION SUMMARY.

The morphology described above provides characterization for all groups of cypriniforms considered in this study. Not all of it, however, is pertinent to the question at hand of, how are groups of cypriniforms interrelated? Specializations unique to cyprinids, or those unique for gyrinocheilids or for that matter those unique to any other cypriniform terminal taxon, reveal nothing about how cyprinids and gyrinocheilids relate to other cypriniform groups. Accordingly, aspects of the anatomy of cypriniforms that appear to have relevance when considering group interrelationships (those not

unique to terminal taxa) were collected and coded as present/absent. Additional features described by Sawada (1982) in his study of cobitidids and homalopterids were included for analysis. The complete list of such features totaled forty-one characters (table 1) and was analyzed with the 2.4.0 version of PAUP (Il. Nat. Hist. Sur.) for microcomputers. Two trees emerged from the branch-and-bound procedure, each fifty-nine steps long and each with a consistency index of 0.695. One of the trees is that classification advocated herein (fig. 6, 7, 77; selection of the classification presented in fig. 6 is discussed below during the discussion of the systematic position of Ellopostoma). Translating the alternate tree into a classification would result in one in which the positions of the Ellopostominae and the Noemacheilinae are switched. A consensus tree resolution would result in a classification with a trichotomy among the three homalopterid subfamilies.

It was noted earlier that features said to characterize all cypriniforms were mostly different aspects of two related systems, one for food gathering and the other for food processing. The same can be said of the features that characterize subgroups of cypriniforms, especially interfamilial subgroups. Twenty-four characters of the forty-one considered relevant for analysis were features of the gill arches (evenly divided

between upper vs. lower portion elements) and seven were ethmoid region features (suspected of contributing to upper jaw protrusibility).

All non-cyprinid cypriniforms are characterized by a modified lateral ethmoid, palatomaxillary elements, the interconnection of infraorbital and preopercular canals, a peculiar circumorbital series, and an aspect of the Weberian apparatus (taken from Sawada, 1982).

The catosomid-cobitidid-homalopterid group is characterized by segmentation of the third copula of the median series of the lower gill arch elements, and their arrangement of ceratobranchial V teeth.

The cobitidid-homalopterid group is characterized by epibranchial structure, basibranchial structure, the transversus ventralis V prong of their ceratobranchial V, and ossification of their basibranchial 4 and palatomaxillary elements.

Cobitidids are characterized by their suborbital spine, hypobranchial structure, and supraethmoid (from Sawada, 1982).

Homalopterids are characterized by infrapharyngobranchial structure, epibranchial structure, basihyal shape, basibranchial shape, preopercular laterosensory canal specialization, and aspects of their Weberian apparatus (from Sawada, 1982).

Cyprinids emerge from this study as a monophyletic group. Their subtemporal fossa, enlarged specialized ceratobranchial V with its characteristic tooth pattern, dorsal gill arch elements, and unique circumorbital series all characterize the Cyprinidae. The Cyprinidae is a huge group of fishes, and other aspects of their anatomy not included in this study can be expected to corroborate its status as monophyletic. Further studies of cyprinids are needed to advance an intrafamilial classification of them. The approach to classifying cyprinids to date has been a piecemeal one and has not resulted in a widely accepted classification (Howes, 1985a; Gosline, 1978). It is doubtful that a piecemeal approach will ever produce a satisfactory classification of cyprinid subgroups. What is needed are extensive studies of character complexes among the range of cyprinids.

CONCLUSIONS

Systematic Position of Vaillantella. Nalbant and Banarescu (1977) erected a new subfamily, the Vaillantellinae, for the genus Vaillantella. Three species of Vaillantella are known and they are unusual both as cobitidids and as cypriniforms, possessing 59-71 branched dorsal fin-rays. Before the elevation to subfamilial level by Nalbant and Banarescu (1977), Vaillantella had been placed in the Noemacheilinae, mostly because they lack the suborbital spine of botiines and cobitidines. Even so, Nalbant and Banarescu (1977) noted that the gas bladder and pair of maxillary barbels of Vaillantella were similar to those found in Botia and Leptobotia. The absence of a suborbital spine provided impetus against their including Vaillantella in the Botiinae. On the other hand, the lack of an osseous encapsulation of the gas bladder in Vaillantella (a feature of all noemacheilines) provided impetus against their placing it in the Noemacheilinae. Nalbant and Banarescu's resolution of what in their view was contradictory evidence was the new subfamily Vaillantellinae, with a comment that since all of its members lacked a suborbital spine the subfamily probably was closer to the Noemacheilinae than to the Botiinae.

Sawada (1982) considered the conclusion of Nalbant and Banarescu (1977) concerning Vaillantella, and rejected

their arguments for its elevation to subfamily status. Sawada argued that it possessed none of the features he considered characteristic of cobitidids (modified supraethmoid, suborbital spine), and more specifically, those characteristic of botiines (ossified mesioprepalatines), and that it did possess a feature of the Weberian apparatus that suggested a relationship with noemacheilines. Consequently he suggested realignment of the genus within the Noemacheilinae.

I have cleared and counterstained a specimen of Vaillantella euepiptera AMNH 48938 (the counterstain did not take). This has allowed a much more detailed examination of its osteology than has been previously possible (Sawada examined only radiographs for examination of its internal anatomy). Vaillantella possesses none of the osteological features said in this study, or in Sawada's (1982), to characterize noemacheilines and homalopterines. It is not therefore a noemacheiline. It is true that Vaillantella lacks the suborbital spine characteristic of cobitidids, but contrary to Sawada's statement, its supraethmoid is like that of botiines and cobitidines. Vaillantella is a cobitidid.

The Weberian apparatus of Vaillantella is exactly like that of botiines regarding incorporation of particular components of it into the portion of the Weberian apparatus that interacts with the gas bladder

(cobitidines are unique among cobitidoids in this regard), its cephalic laterosensory canals interconnect in the same manner as botiines (derived within cobitidoids), and its basibranchial 4 is like that of botiines as well (derived within the cobitidid-homalopterid group). Vaillantella does not, however, possess ossified mesioprepalatines and without a successful counterstain I could not tell if cartilaginous mesioprepalatines were present. Nalbant and Banarescu's (1977) initial observations of the similarities between Vaillantella and botiines (especially of the maxillary barbels) were poignant. Vaillantella, based on maxillary barbel placement, cephalic laterosensory canal interconnections, basibranchial 4 structure, and supraethmoid morphology is a member of the Botiinae. Its lack of a suborbital spine (its lateral ethmoid is unusual in and of itself) and ossified mesioprepalatines can only be regarded as autapomorphic or homoplasious.

Systematic Position of Ellopostoma. Roberts (1972) examined the type material of Ellopostoma in an attempt to determine its relationships. Some of the type material is badly damaged (Roberts, 1972) and the specimen he designated as the lectotype was only radiographed. Roberts (1972) chose not to examine critical internal anatomical features of the type material of Ellopostoma,

and the radiograph of the lectotype did not provide sufficient detail for him to do other than suggest that Ellopostoma was most likely a cobitidid (it strongly resembled noemacheilines) rather than a kneriid (a gonorynchiform).

Gordon Howes of the BMNH sent two specimens of Ellopostoma AMNH 55110 to the AMNH on exchange for my examination. I have cleared and counterstained one of them and have been able to examine the critical internal anatomical features Roberts (1972) could not. Although Ellopostoma is a most unusual little fish deciphering its relationships is not as phylogenetically important as Roberts (1972) suggested it would be. Ellopostoma is a homalopterid. Its anterior vertebral modifications are a Weberian apparatus as Roberts suggested and Ellopostoma's Weberian apparatus possesses all of the features (Y-shaped tripus and gas bladder capsule formed of second and fourth vertebrae components) Sawada (1982) found to be characteristic of homalopterids.

Placement of Ellopostoma as a homalopterid is clear cut; its placement within the Homalopteridae is not clear cut. I advocate it as the sister group of the Homalopterinae (fig. 7 and 77). Two trees emerged from the PAUP analysis reported above because the placement of Ellopostoma as the sister taxon of homalopterines, or of noemacheilines + homalopterines, were equally parsimonious

(the consensus result is a trichotomy of the Ellopostominae, Noemacheilinae and Homalopterinae). Equivocation by PAUP over the placement of Ellopostoma centers on Ellopostoma lacking certain dorsal gill arch features that are suggestive of a relationship between noemacheilines and homalopterines and on Ellopostoma having its preopercular laterosensory canal conventionally fused to the preoperculum. The dorsal gill arch elements of Ellopostoma (fig. 37) are unique in and of themselves and their modification may have in fact been from a basic homalopterid plan. Fusion of the preopercular laterosensory canal to the preoperculum is a basic cypriniform condition, and does not preclude Ellopostoma as the sister taxon of the Homalopterinae. Ellopostoma does not possess the peculiarly enlarged pleural ribs of homalopterines (from Sawada, 1982) but with only seven pairs of them its ribs do not extend to the pelvic girdle where the modification occurs, nor does Ellopostoma possess the intimate shoulder girdle-Weberian apparatus relationship of homalopterines.

However, Ellopostoma does possess the Y-shaped basihyal, T-shaped basibranchial 2 of all homalopterines, and like gastromyzontins only a 2nd pre-ethmoid but like homalopterines, a discrete well-defined subtemporal fossa. These features are clear homalopterine characteristics, ones that the view of which is not fogged by Ellopostoma's

own specializations or by its retention of a very general condition. I therefore advocate Ellopostoma as the coordinate sister taxon of the Homaloterinae.

General Systematic Conclusions. This study and the classification presented (fig. 6,7) address the lack of consensus among conclusions reached regarding the interrelationships of cypriniform families (fig. 4) by workers who have examined the problem since Greenwood et al.'s (1966) provisional classification of teleosts. Sawada (1982) presented evidence, not universally accepted (J. Nelson, 1984), that G. Nelson (1969a) was correct in his assessment of interrelationships among members of a cobitidid-homalopterid group. Information developed during this study further corroborates their (Nelson's and Sawada's) point of view (i. e. monophyly of a cobitidid-homalopterid group and the monophyly of the Homalopteridae including the Noemacheilinae). G. Nelson's (1969) idea that catostomids are the sister group of the cobitidid-homalopterid group was also affirmed.

This result is counter to the view expressed by Hora (1932), and more recently by Wu et al. (1981), which would have the the Homalopterini (= Hora's Homalopteridae) more closely related to the Cyprinidae than to other non-cyprinid cypriniforms. Hora's early view however (1920; fig. 2), if set out as a branching diagram, is

exactly that come to by G. Nelson (1969a), Sawada (1982) and herein. In retrospect, Hora's delve into adaptationalism, his letting his subsequent adaptationalist viewpoint influence his systematics, and the continuation of his ideas of relationships among cypriniform families as party-line by subsequent workers and writers was, and has been, misadventurous.

Vaillant (1902b) suggested Gyrinocheilus was related to non-cyprinid cypriniforms when he described it. His suggestion was largely ignored (most workers claimed Gyrinocheilus to be closest to the Cyprinidae) until recently when Wu et al. (1981) suggested, and Rainboth et al. (1986) alluded to, a relationship for it more in line with Vaillant's original point of view. Wu et al. (1981), without any supporting evidence as was pointed out by Rainboth et al. (1986), related Gyrinocheilus most closely to the Catostomidae (part of a larger group consisting of the Gyrinocheilidae, Catostomidae and Cobitididae). This study does corroborate the relationship of Gyrinocheilus to other non-cyprinid cypriniforms rather than to the Cyprinidae. It does not corroborate, however, a sister taxon relationship between the Gyrinocheilidae and the Catostomidae. Instead it shows gyrinocheilids to be the sister group of all other non-cyprinid cypriniforms (fig. 5). Resemblances between Gyrinocheilus and catostomids (possession of Ipb I, Eb I and II uncinata processes, and

a cartilaginous pair of Hb III) are either sympleisiomorphic or homoplasious.

There are two great groups of cypriniforms, the Cobitidoidea (all non-cyprinid cypriniforms) and the Cyprinidae. Character distributions among all cypriniforms are such that they are best reconciled by a sister taxon view of the relationship between the groups (each large group of them possesses its own specializations); one group should not be viewed as ancestral to the other group. This result is satisfying as resolving vexing character distributions, but is less so for those who would like to find a quisesential cypriniform to use in comparative studies of other kinds of ostariophysans. No such cypriniform is likely to be found. Those desiring a comparative base for studies of other ostariophysans will have to come to understand cypriniforms as diphyletic, and will have to come to understand the basic morphology of both groups of cypriniforms rather than of just one group of them as the exemplar for all cypriniforms.

TABLES

Table 1. Data matrix analysed by PAUP. Characters¹ are coded as present (1) or absent (0) by group².

	Group	A	B	C	D	E	F	G	H	I	J
Charact.											
1		0	1	1	1	1	1	1	1	1	1
2		0	1	0	0	1	1	1	1	1	1
3		0	1	0	0	1	1	1	1	1	1
4		0	0	0	0	0	0	1	0	1	1
5		0	0	0	0	0	0	1	0	1	1
6		0	0	0	0	0	0	0	1	1	1
7		0	0	0	0	0	1	1	1	1	1
8		0	0	0	0	0	1	1	1	1	1
9		0	1	0	0	1	0	0	0	0	0
10		0	0	0	0	0	0	1	0	1	1
11		0	0	0	0	1	1	1	1	1	1
12		0	0	0	0	0	0	0	1	1	1
13		0	1	1	1	1	1	1	1	1	1
14		0	0	1	0	1	1	1	1	1	1
15		0	0	1	1	0	0	0	0	0	0
16		0	0	0	1	1	1	1	1	1	1
17		0	0	0	1	1	1	1	1	1	1
18		0	0	0	0	1	1	1	1	1	1
19		0	0	0	1	1	1	1	1	1	1
20		0	0	0	0	1	1	0	0	0	0

Table 1 continued.

	Group	A	B	C	D	E	F	G	H	I	J
21		0	0	0	0	0	0	0	1	1	1
22		0	0	0	0	0	0	0	1	1	1
23		0	0	0	1	1	1	1	1	1	1
24		0	0	0	0	1	1	1	1	1	1
25		0	0	1	1	0	0	1	1	1	1
26		0	0	0	0	1	1	0	0	0	0
27		0	0	1	1	1	1	1	1	1	1
28		0	0	1	1	1	1	1	0	1	0
29		0	0	0	1	1	0	0	0	0	0
30		0	0	0	0	1	1	1	1	1	1
31		0	0	1	1	0	0	0	0	1	1
32		0	0	1	1	1	1	1	1	1	1
33		0	0	0	0	0	0	1	0	1	1
34		0	0	1	1	1	1	1	1	1	1
35		0	0	0	0	0	0	0	0	1	1
36		0	0	0	0	0	0	1	1	1	1
37		0	0	0	0	0	0	1	1	1	1
38		0	0	0	0	1	1	0	0	0	0
39		0	0	0	0	0	0	0	0	1	1
40		0	0	1	1	1	1	1	1	1	1
41		0	1	0	0	0	0	0	1	1	0

Table 1 continued.

¹The characters are as follows (characters are discussed fully in the anatomical descriptions in the text): 1. absence of Ipb uncinata processes; 2. absence of Eb I and II uncinata processes; 3. absence of Ipb I; 4. consolidation of the Ipb series; 5. absence of Ipb IV; 6. medial tips of Eb I and II modified; 7. Eb I and IV largest of the Eb series; 8. anterior corner of the head of Eb I twisted ventrad; 9. overlap of Ipb II by Ipb III; 10. absence of Eb III uncinata process; 11. EA flange on Eb IV; 12. directly medial orientation of Eb's; 13. absence of BhTp; 14. absence of Bb 1; 15. cartilaginous Hb III; 16. sublingual ossifications; 17. segmentation of C 3; 18. Bb 4 ossified; 19 Bb 4 keeled; 20. rectus communis I process on Hb I; 21. Y-shaped Bh; 22. T-shaped Bb 2; 23. single row of Cb V teeth; 24. transversus ventralis V process on Cb V; 25. anterolateral process of the lateral ethmoid; 26. suborbital spine; 27. 2nd pre-ethmoid; 28. prepalatine; 29. mesioprepalatine; 30. ossified palatomaxillary elements; 31. ILC-PLC connection; 32. Io 1 largest of the infraorbital series; 33. preopercular laterosensory canal free from the preoperculum; 34. reduction of Io 2 and 3; 35. enlarged pleural ribs (from Sawada, 1982); 36. gas bladder division (from Sawada, 1982); 37. Y-shaped tripus (from Sawada, 1982); 38. supraethmoid (from Sawada, 1982); 39. shoulder girdle (from Sawada, 1982); 40. transverse shelf on 2nd neural arch; and 41. subtemporal fossa discrete.

²Group designations are as follows: A. outgroup; B. Cyprinidae; C. Gyrinocheilidae; D. Catostomidae; E. Botiinae; F. Cobitidinae; G. Noemacheilinae; H. Ellopostominae; I. Homalopterini; and J. Gastromyzontini.

FIGURES AND CAPTIONS

Fig. 1. Relationships among major groups of the
Ostariophysi (taken from Fink and Fink, 1981).

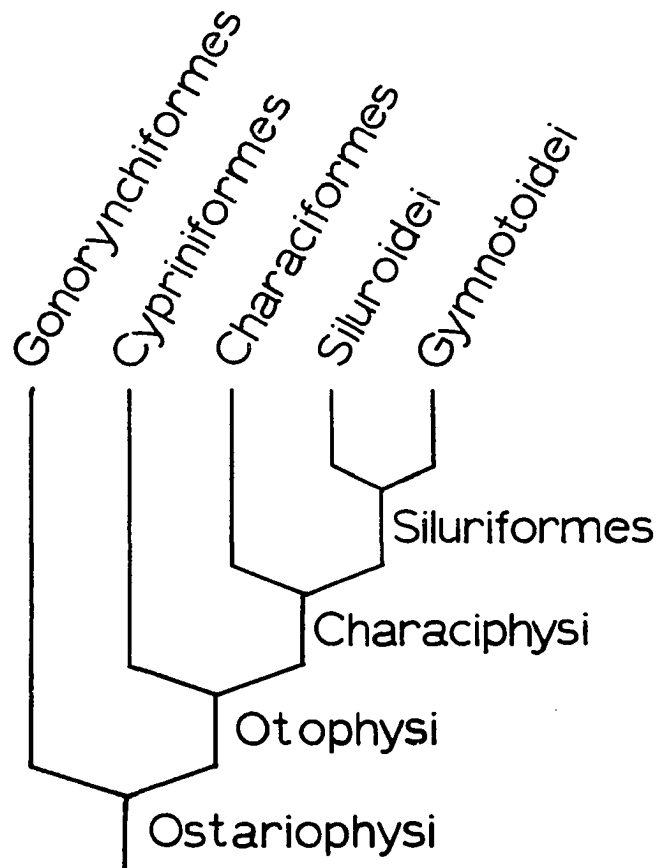


Figure 1

Fig. 2. A diagram (redrafted from Hora, 1920) expressing Hora's early views on relationships among Asian cypriniforms. At this time Hora felt homalopterins and gastromyzontins were closely related (both placed in the Homalopteridae) and descendent from Noemacheilus which he considered to be the central Cobitididae.

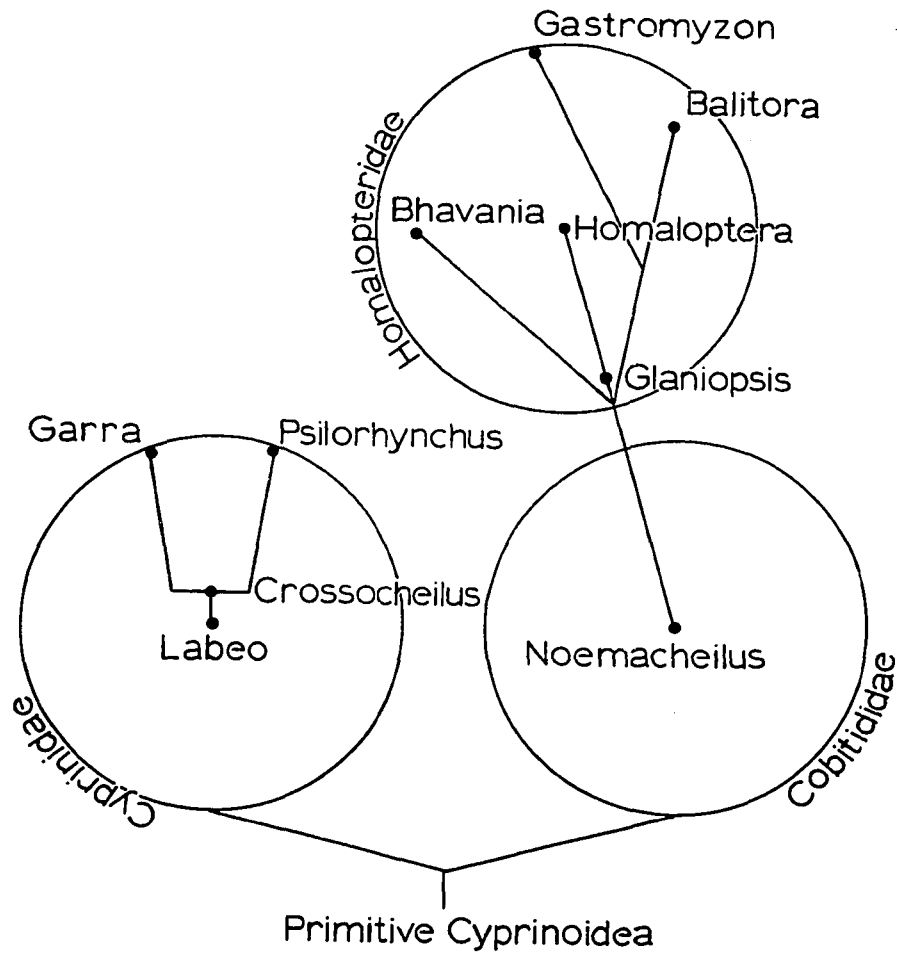


Figure 2

Fig. 3. Diagram of the interrelationships among cypriniform families according to Wu, et al. (1981). Their hypothesis of the relationship of the Gyrinocheilidae to the Catostomidae and Cobitididae is novel for post-Hora workers.

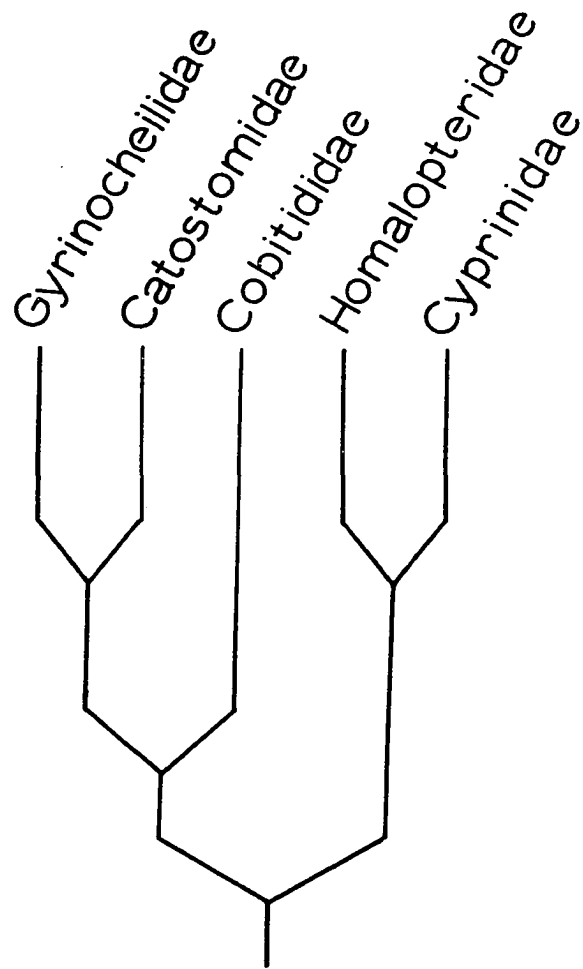


Figure 3

Fig. 4. Diagram of the consensus tree result of the comparison among conclusions regarding the relationships of the four cypriniform families common to the studies of G. Nelson (1969), Wu, et al. and Sawada (1982). No resolution was found.

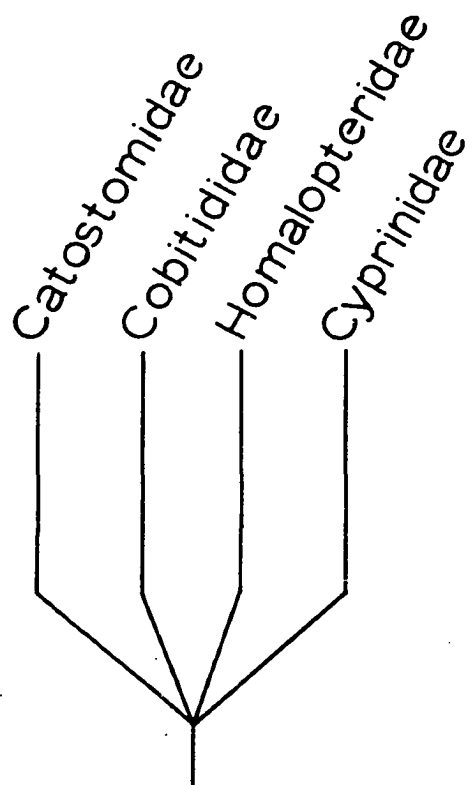


Figure 4

Fig. 5. Diagram of relationships among actinopterygian taxa considered relevant for "outgroup analysis" in this study. The relationships depicted are taken from the works of Patterson and Rosen (1977) and Fink and Weitzman (1982).

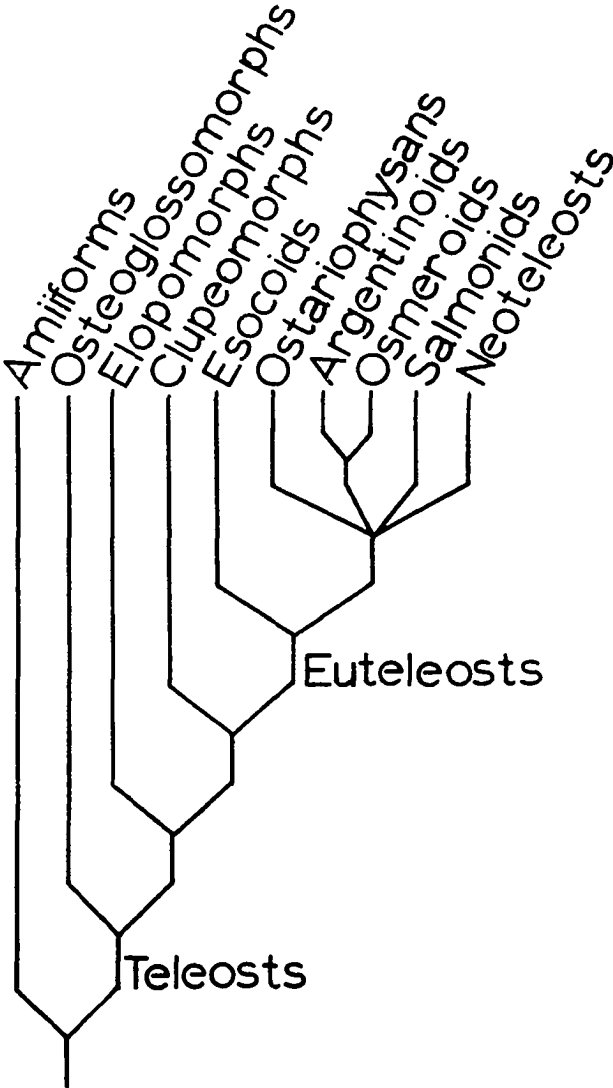


Figure 5

Fig. 6. Diagrammatic representation of the classification of the Cypriniformes advocated herein; groups A and B are left innominate (see text for discussion). Relationships are depicted at and above the family level.

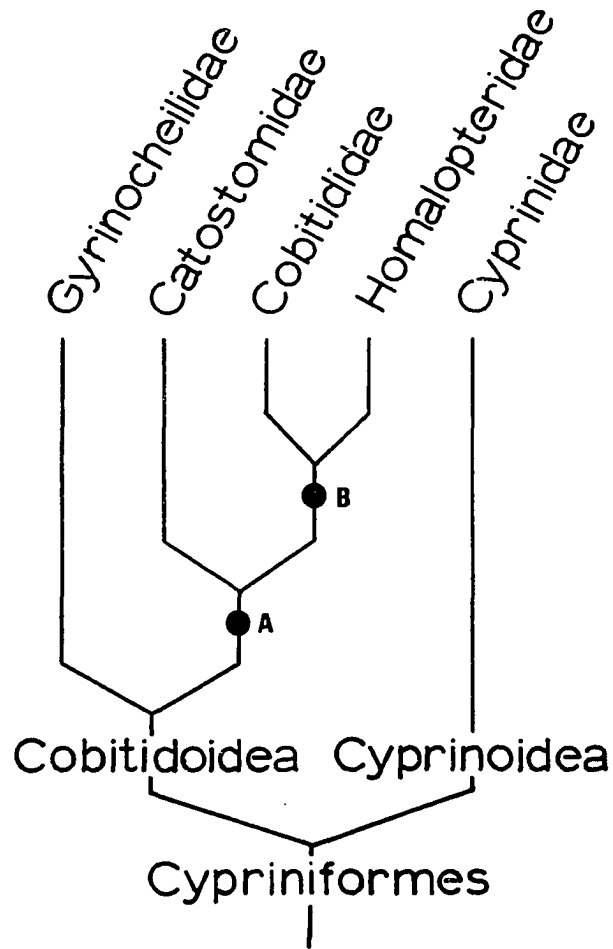


Figure 6

Fig. 7. Diagram of the relationships within the Cobitidoidea, at and above the tribal level, that are advocated here. Group A is the Catostomidae, group C is the Cobitididae, group D is the Homalopteridae, group E is the Homalopterinae and group B is left innominate.

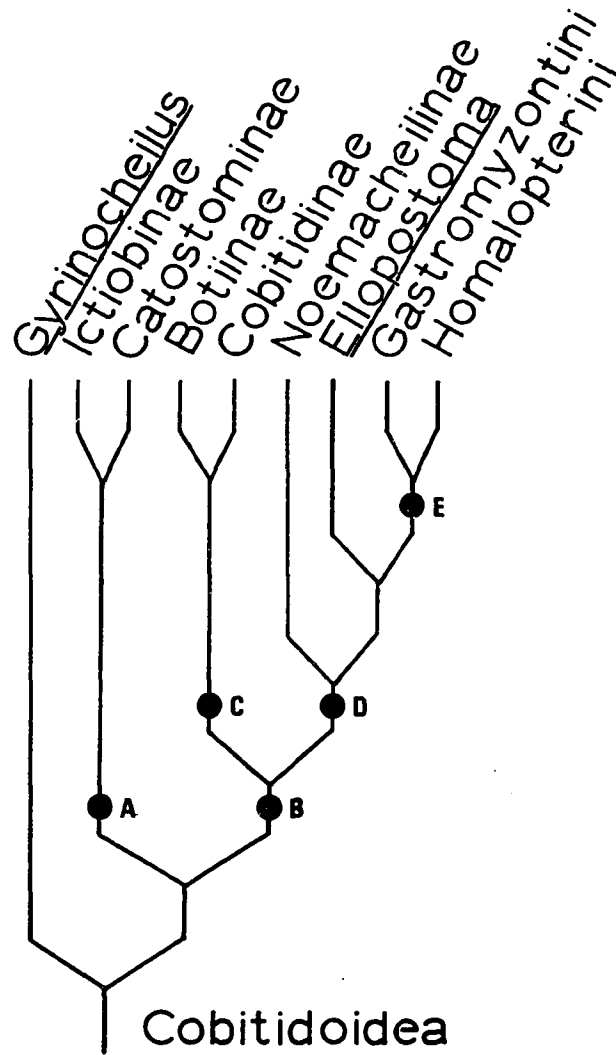


Figure 7

Fig. 8 Oblique dorsal posterior view of the skull of Ptychocheilus grandis AMNH 42007SD-C. The posttemporal fossa is well developed and the basioccipital masticatory process extends well posterior to the basioccipital condyle. An extensive blade-like crest projects directly back from the supraoccipital.

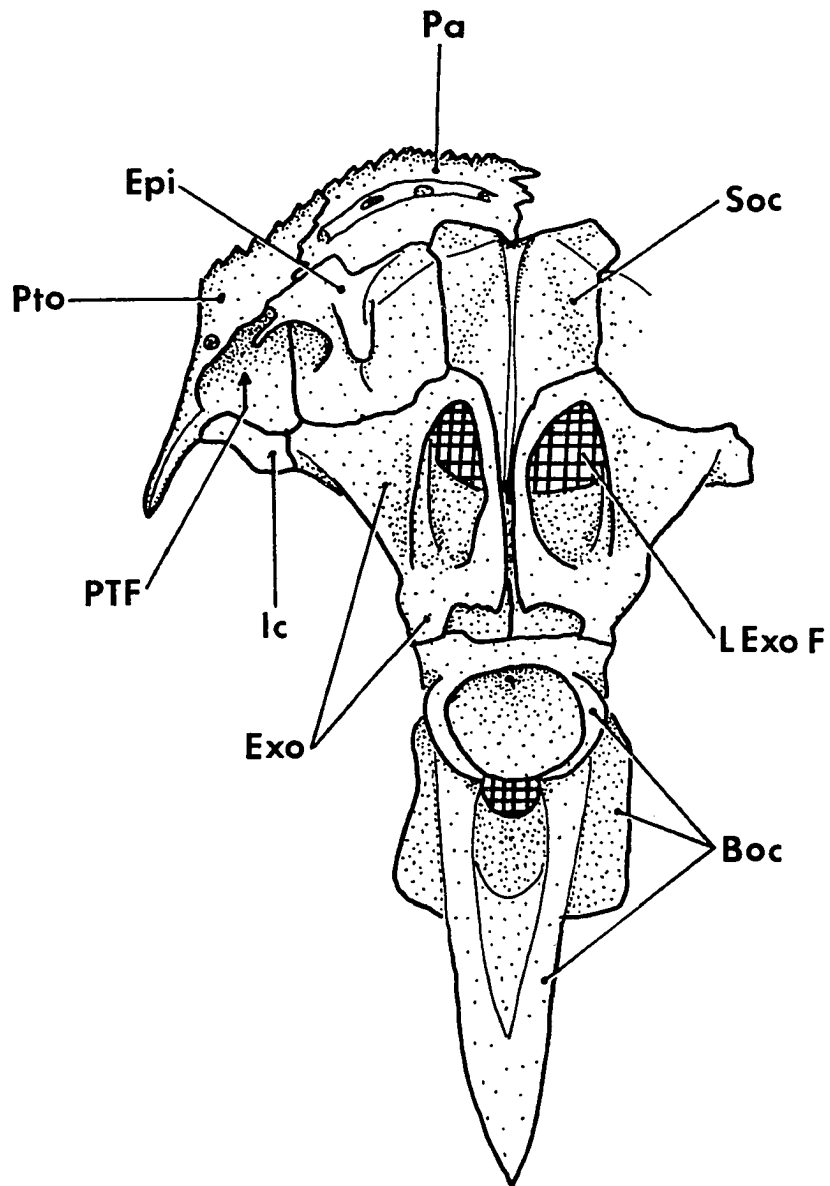


Figure 8

Fig. 9. Dorsal view of the right posterolateral region of the skull of Lepturichthys fimbriata AMNH 10335; anterior to the left. The exoccipital is hidden from view, tucked beneath the supra- and epioccipital. There is a shallow depression located within the interior confines of the arches of the semicircular canals.

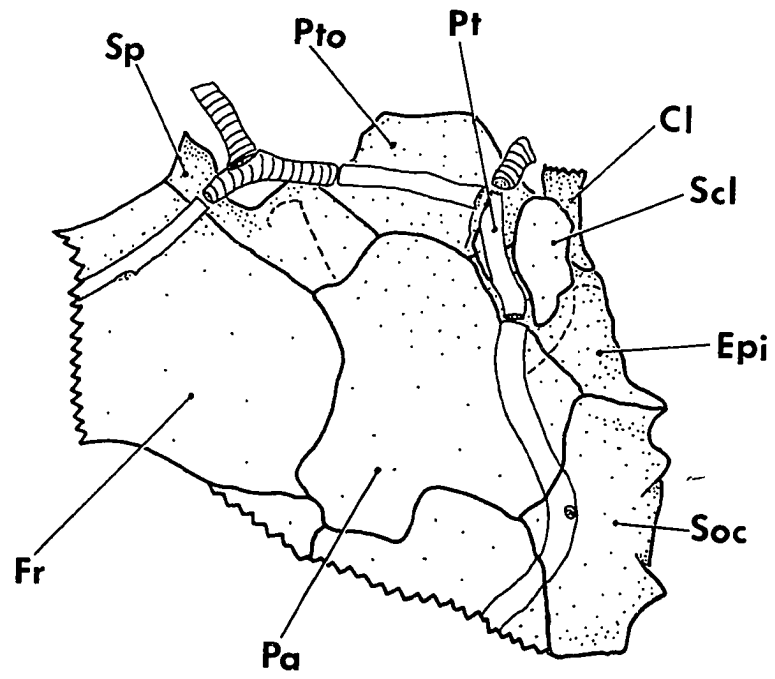


Figure 9

Fig. 10. Dorsal view of the left posterolateral region of the skull of Beaufortia zebroides AMNH 11054; anterior to the left. The posttemporal fossa is open directly from the rear and is entirely contained within the pterotic and epioccipital.

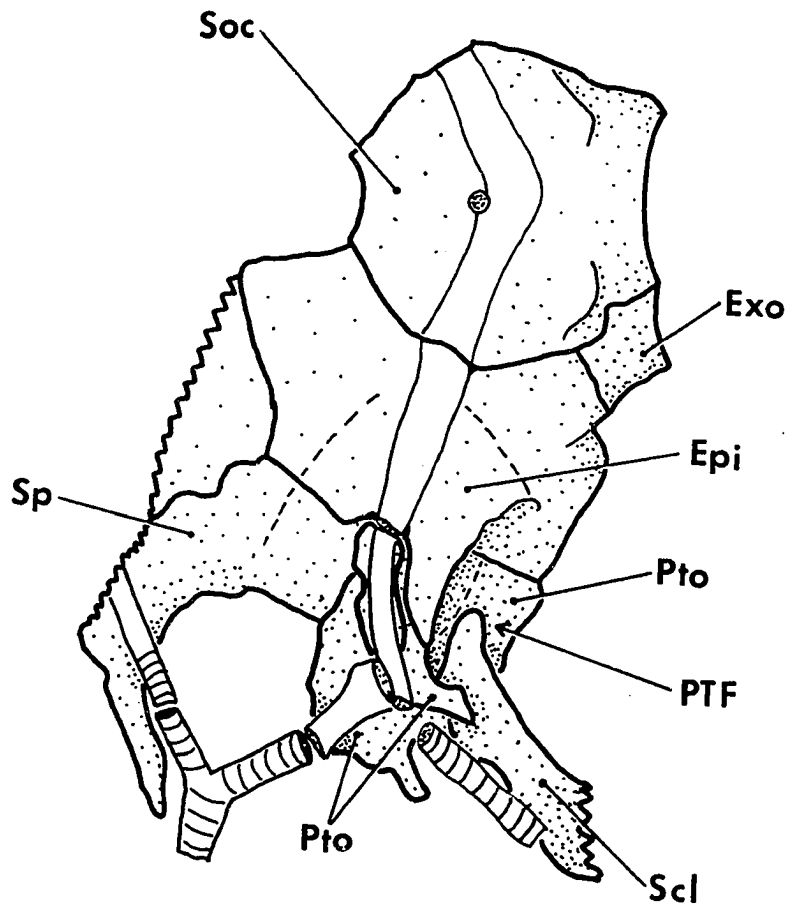


Figure 10

Fig. 11. Oblique dorsal view of the left posterolateral region of the skull of Gyrinocheilus aymonieri AMNH 77898SW; anterior to the left. Dotted lines delimit the course of the anterior and posterior semicircular canals and the limits of the sphenotic, supraoccipital, epioccipital and pterotic.

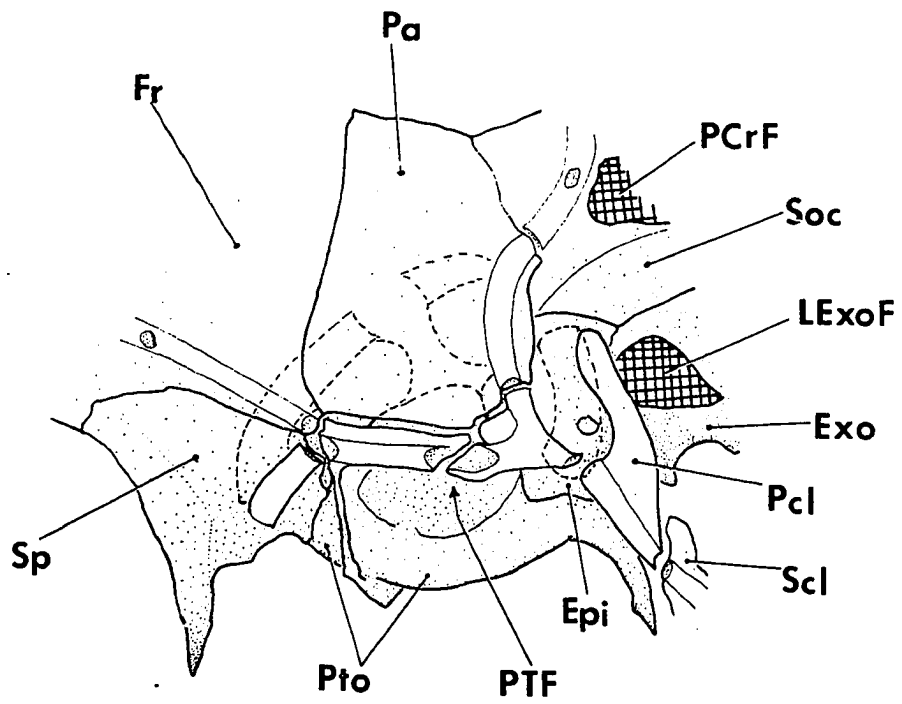


Figure 11

Fig. 12. Sharply oblique dorsal view of the posterolateral region of the skull of Carpionodes sp. AMNH 21694; anterior to the left and with the posttemporal bone and supracleithrum removed. The posttemporal fossa extends beneath the parietal and is filled by the levator operculi.

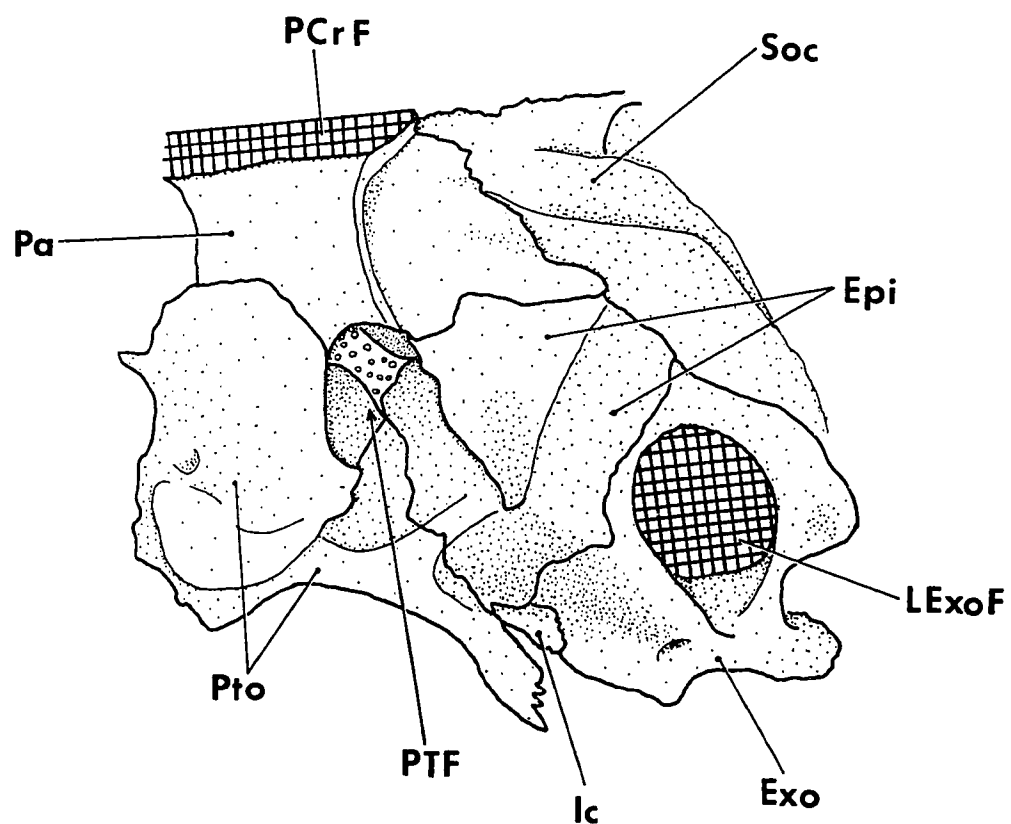
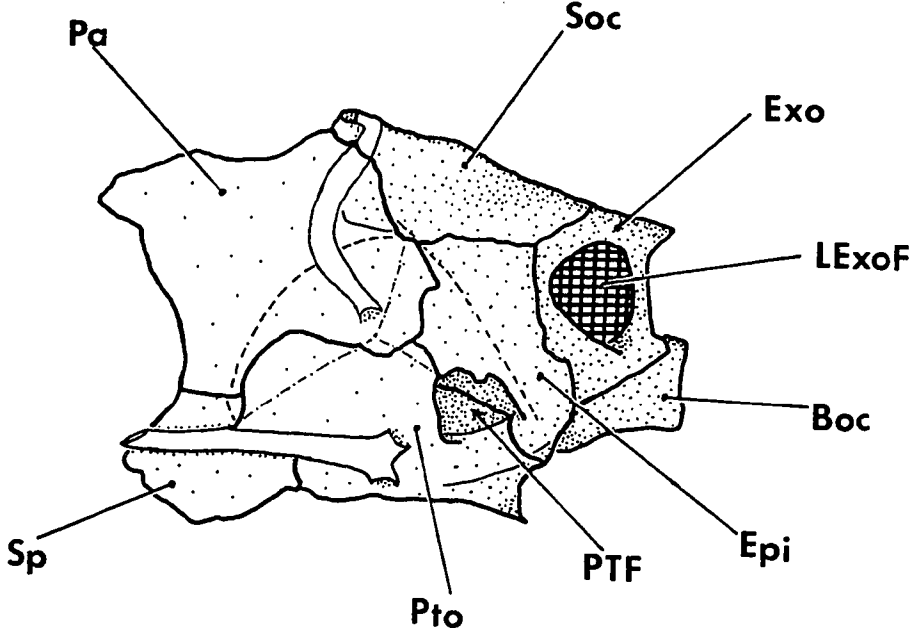


Figure 12

Fig. 13. A. Somewhat oblique dorsal view of the posterolateral region of the skull of Botia purpurea AMNH 10419; anterior to the left. The posttemporal bone has been removed to expose the opening into the posttemporal fossa. Dashed lines delimit the interior limits of the anterior and posterior semicircular canals; dash-dot-dash lines outline the approximate internal positions of the vertical medial corner and the anterior and posterior horizontal corners where the pterotic floor meets the vertical walls of the sphenotic and epioccipital, respectively. B. Dorsal view of the left posterolateral region of the skull of Vaillantella euepiptera AMNH 48938; anterior to the left. Dotted lines delimit the interiors of the arches of the anterior and posterior semicircular canals and the unossified laterosensory canal in the posttemporal and extrascapular region. The large canals of the cephalic laterosensory system block the posttemporal fossa opening found in other botiines (see fig. 6A). "Extrascapular" and "Posttemporal" canal ossifications are mere sheets of bone wrapped around the back side of the laterosensory canal.

A



B

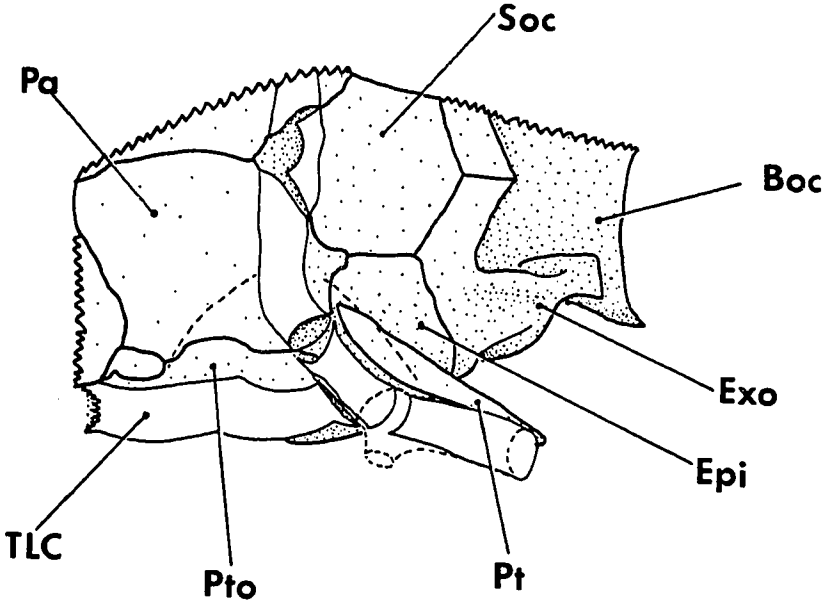


Figure 13

Fig. 14. Dorsal view of the posterolateral region of the skull of Noemacheilus barbatulus AMNH 37608; anterior to the left. The parietal forms a shallow shelf over the medial edge of the posttemporal fossa, leaving it chiefly unroofed. Epaxial muscle fibers run beneath the posttemporal bone to insert in the fossa.

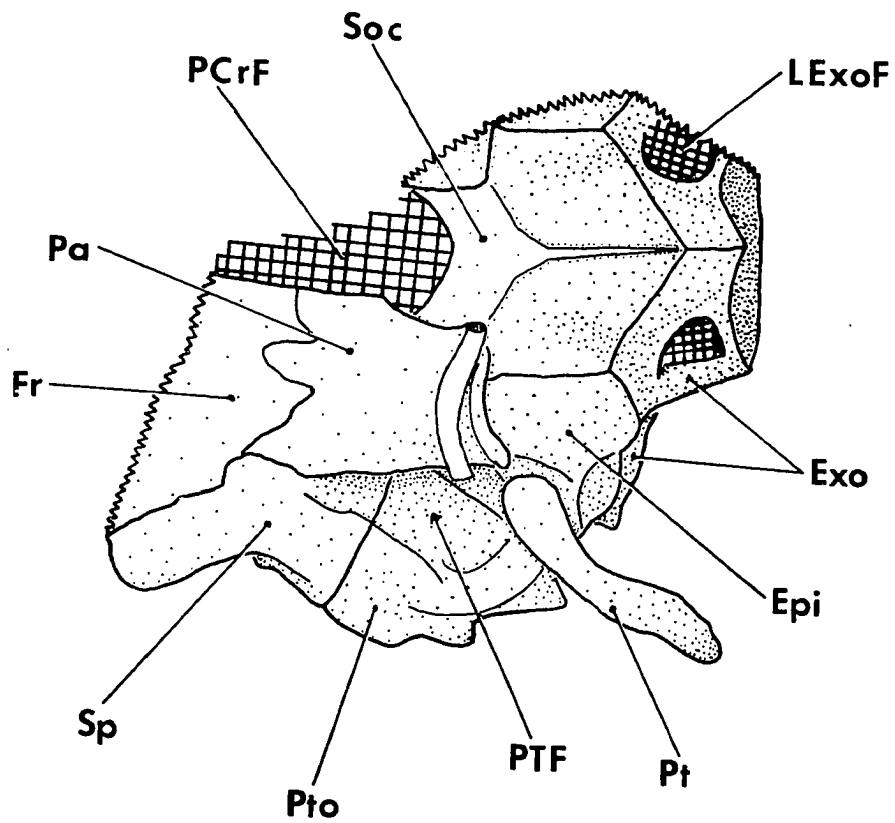


Figure 14

Fig. 15. Oblique dorsal view of the posterolateral region of the skull of Acanthopsis choirorhynchos FMNH 68142; anterior to the left. Dotted lines delimit the course of the anterior and posterior semicircular canals. A pterotic roof over the posttemporal fossa is absent but a shallow shelf of sphenotic, parietal and epioccipital composition overhangs the anterior, medial, and posterior edges of the fossa. Epaxial musculature enters directly from the rear. The laterosensory canals of the parietal and supraoccipital are deeply buried and epaxial muscle fibers advance anterior to them and cover the parietal. Note the epioccipital border of the lateral exoccipital fenestra.

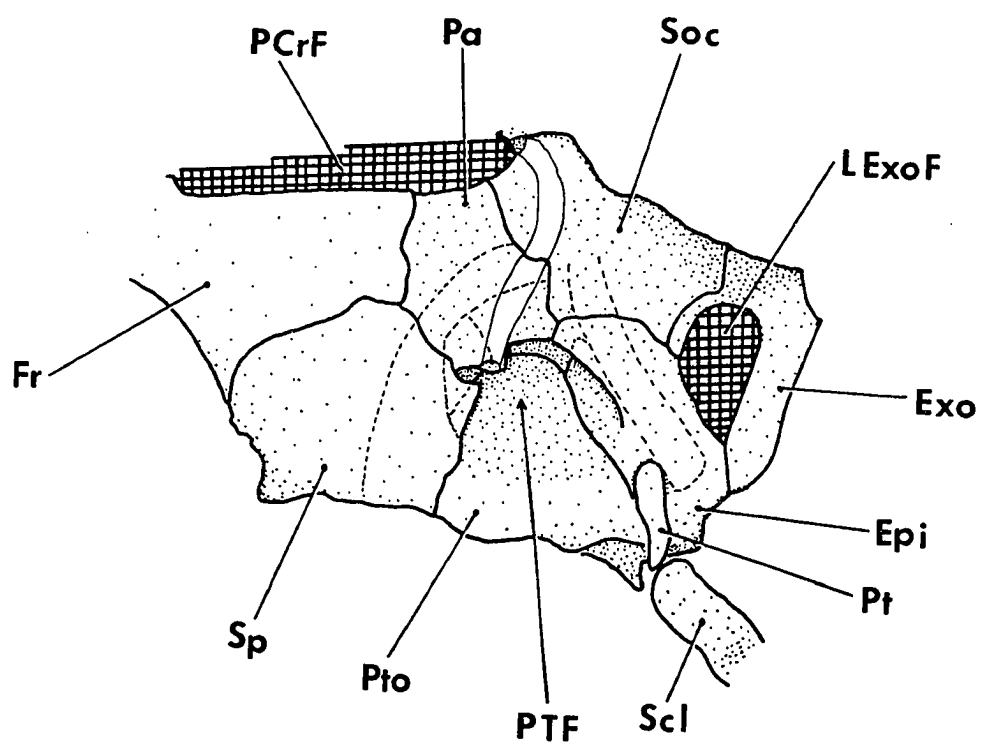


Figure 15

Fig. 16. Dorsally oblique lateral view of the skull of Chela oxygastroides AMNH 36368; anterior to the left. Epaxial musculature invades forward onto the skull, covering the frontals as far forward as the lateral ethmoid. The supratemporal commissure of the laterosensory system has been pushed ahead of the musculature. Instead of crossing the back of the skull it turns anteriorly on the parietal and angles forward on the frontal to where it meets its fellow anterior to the orbit.

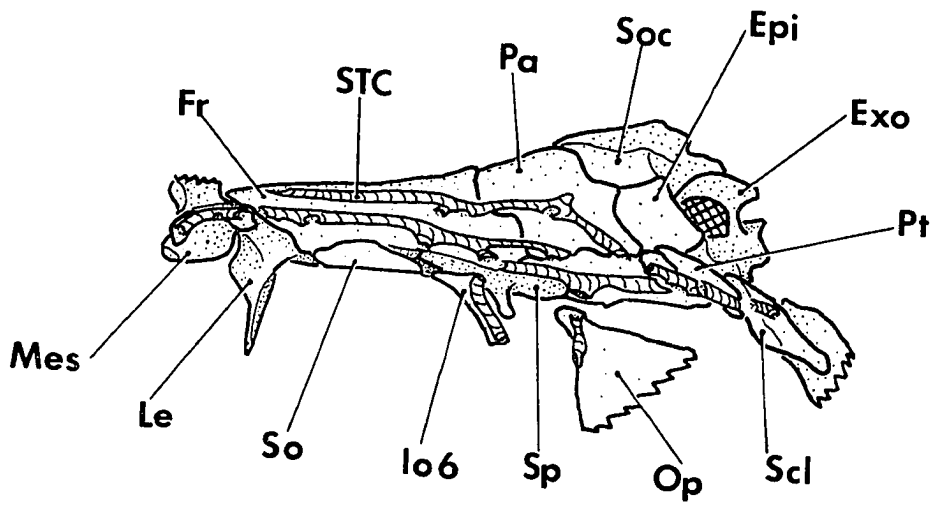


Figure 16

Fig. 17. Ventral view of the right posterolateral region of the skull of Ptychocheilus grandis AMNH 46007SD-C; posterior to the bottom of the page. The subtemporal fossa is large and deep. Its lateral edge is determined by the horizontal semicircular canal and a large part of its ceiling consists of the epioccipital. The basioccipital masticatory process extends posteriorly well beyond the basioccipital condyle and contains an arterial canal.

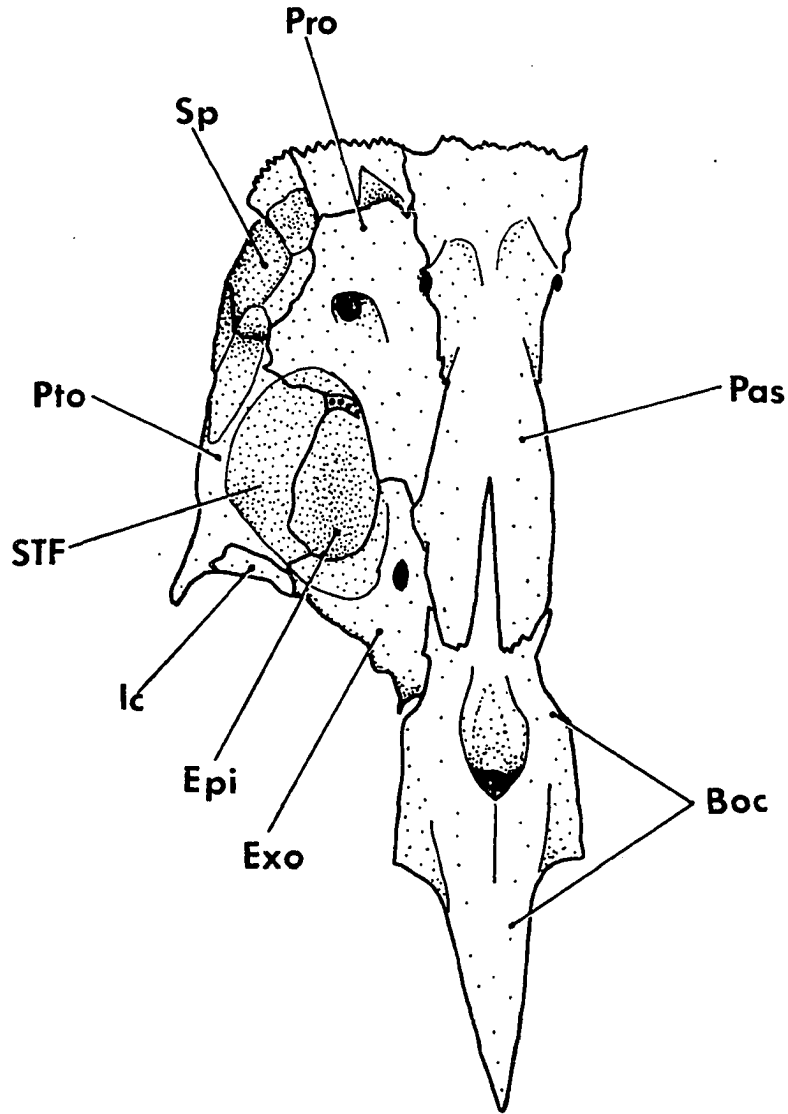


Figure 17

Fig. 18. Ventral view of the right posterolateral region of the skull of Gyrinocheilus aymonieri AMNH 77898; posterior to the bottom of the page. The subtemporal fossa is a mere indentation of the area where the prootic, pterotic and exoccipital meet. There is no basioccipital masticatory process (Gyrinocheilus is completely toothless) and the posterior myodome is open to the rear.

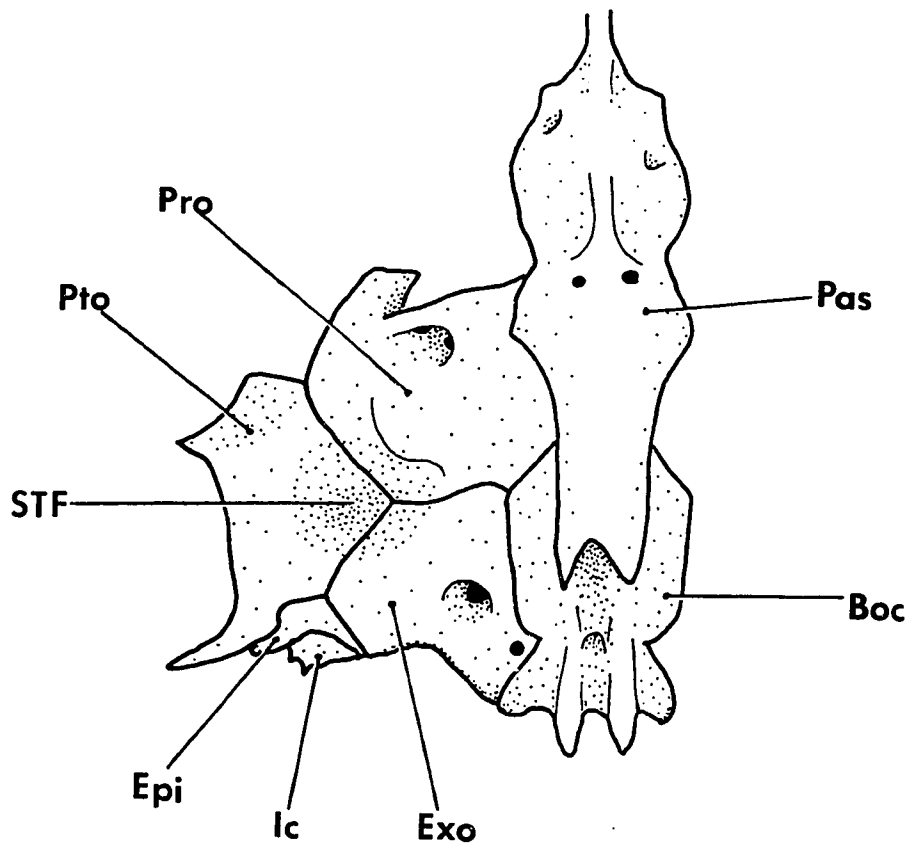


Figure 18

Fig. 19. Oblique ventral view of the right posterolateral region of the skull of Botia macracantha AMNH 56394SD; posterior to the bottom of the page. The subtemporal fossa is quite deep and large. There is no basioccipital masticatory process.

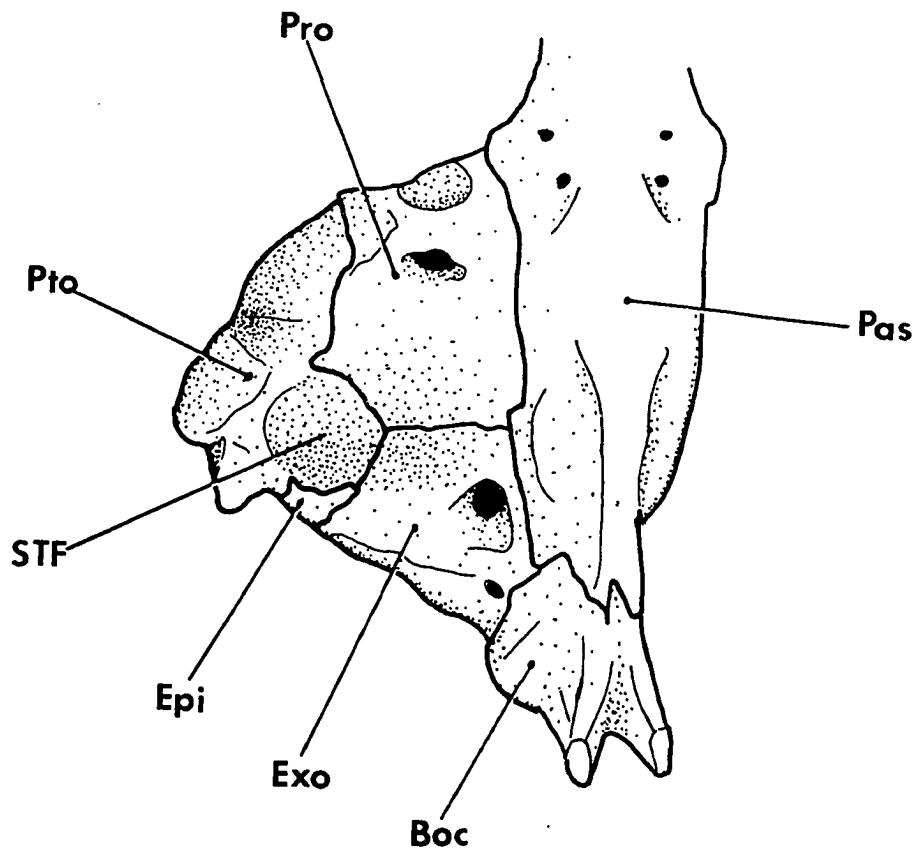


Figure 19

Fig. 20. Ventral view of the left posterolateral region of the skull of Misgurnus mizolepis AMNH 10362; posterior to the bottom of the page. No subtemporal fossa is identifiable and there is no basioccipital masticatory process.

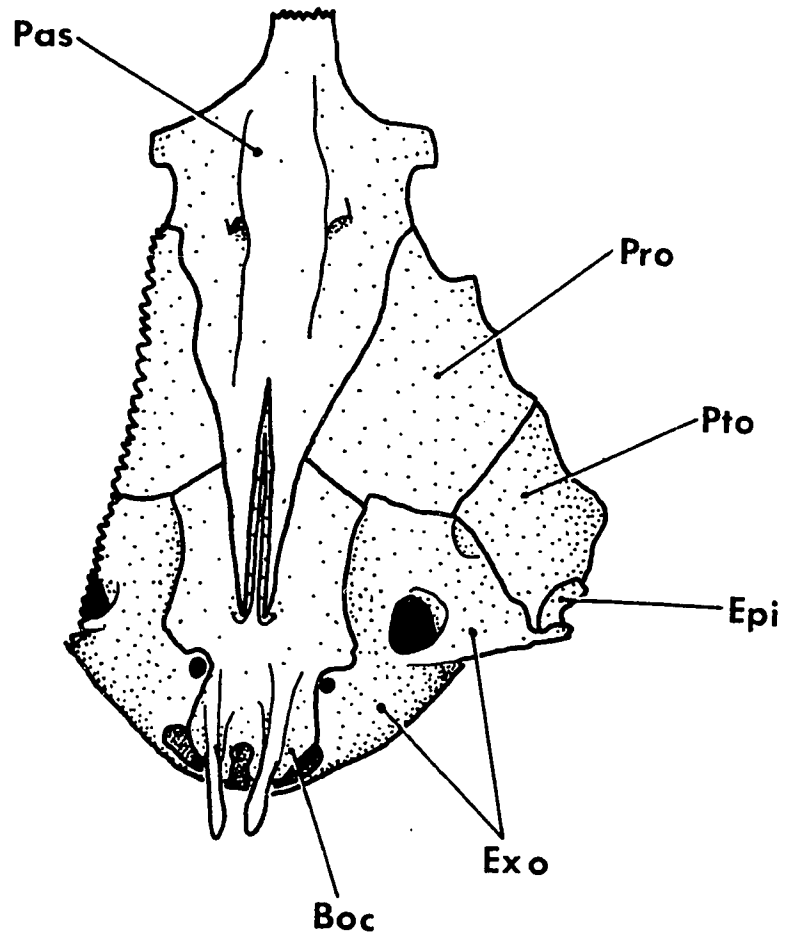


Figure 20

Fig. 21. Ventral view of the right posterolateral region of the skull of Lepturichthys fimbriata AMNH 10335; posterior to the bottom of the page. The subtemporal fossa is well defined and deep. The epioccipital contributes to its ceiling and its lateral edge is determined by the horizontal semicircular canal. There is no basioccipital masticatory process.

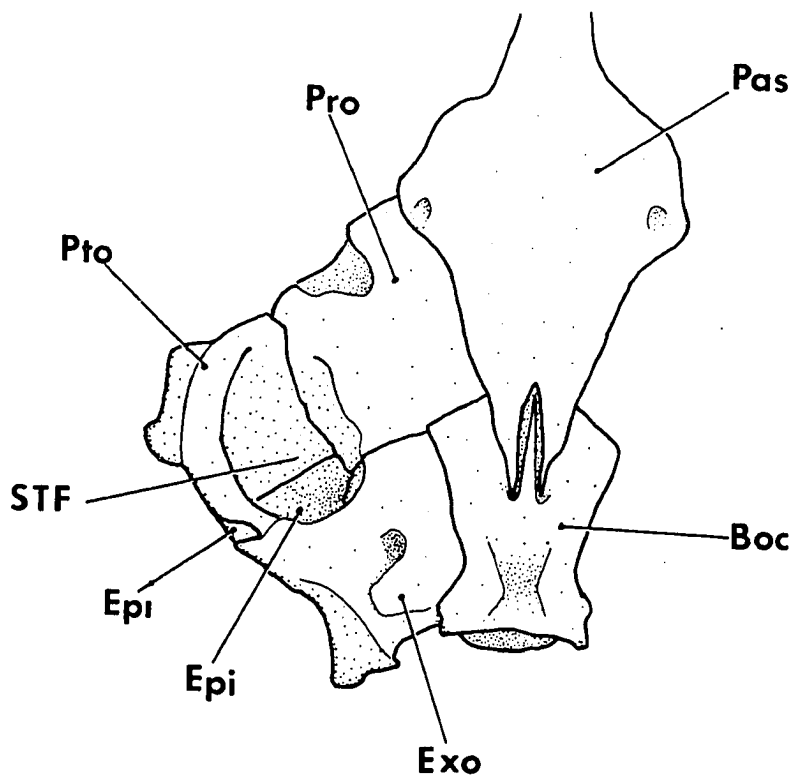


Figure 21

Fig. 22. Dorsal view of the left side dorsal gill arch elements of Chanos chanos AMNH 77918; anterior to the top of the page. The epibranchials are not fully illustrated and the medial pharyngobranchial is not illustrated at all. Chanos exhibits nearly all of the relationships among its dorsal elements considered general for teleosts. Three exceptions are notable: 1) Chanos possesses an accessory cartilage anterior to its Eb I; 2) its Eb III and IV uncinata processes are not associated with one another; and 3) Eb IV is hypertrophied in support of an epibranchial organ.

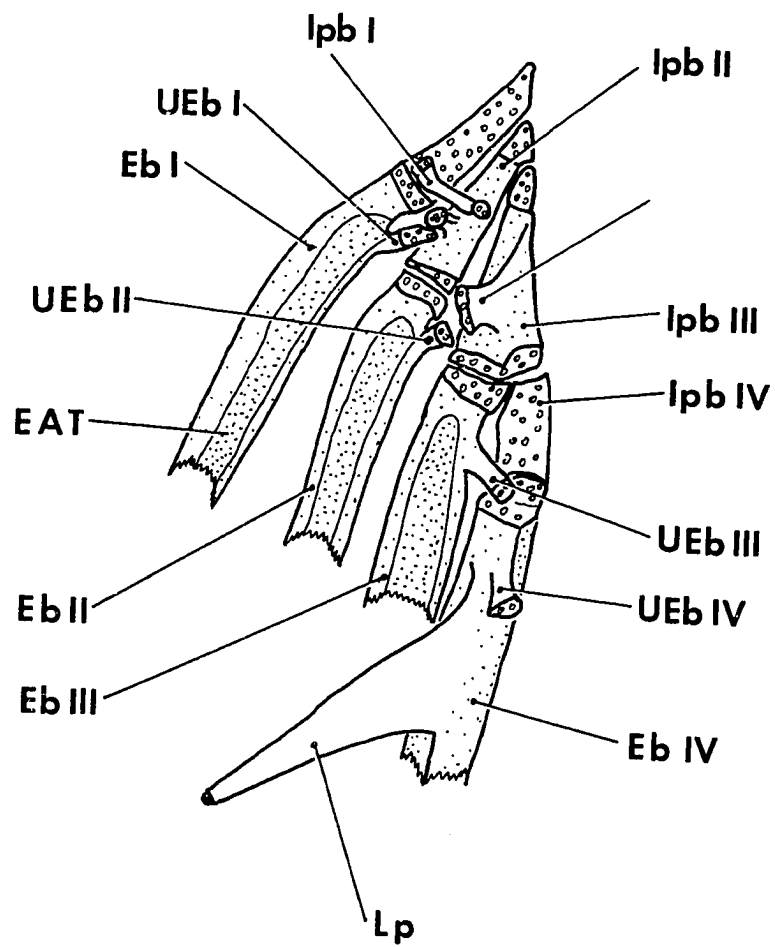


Figure 22

Fig. 23. Dorsal view of the right side dorsal gill arch elements of Diplomystes chilensis AMNH 55318SW; anterior to the top of the page. Though recognized as the "most primitive" siluroid by many workers, many features of its dorsal gill arch elements are highly derived. However, note the decrease in size of the epibranchials from anterior to posterior.

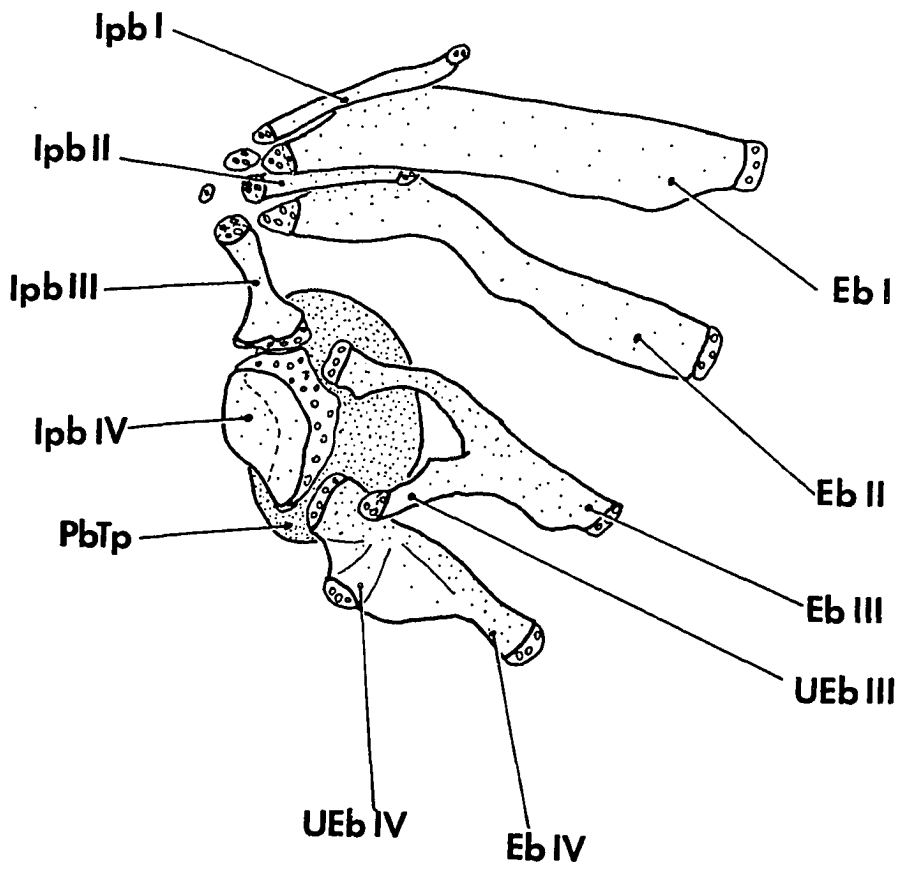


Figure 23

Fig. 24. Dorsal view of the right side dorsal gill arch elements of Gyrinocheilus sp. USNM 272884; anterior to the top of the page. Gyrinocheilid epibranchials are very short. Most unusually, Ipb II and III are the largest of all dorsal elements. Ipb I is rod-like, though bent, and oriented posterodorsally as is general among teleosts. An independent Ipb IV could not be identified with certainty.

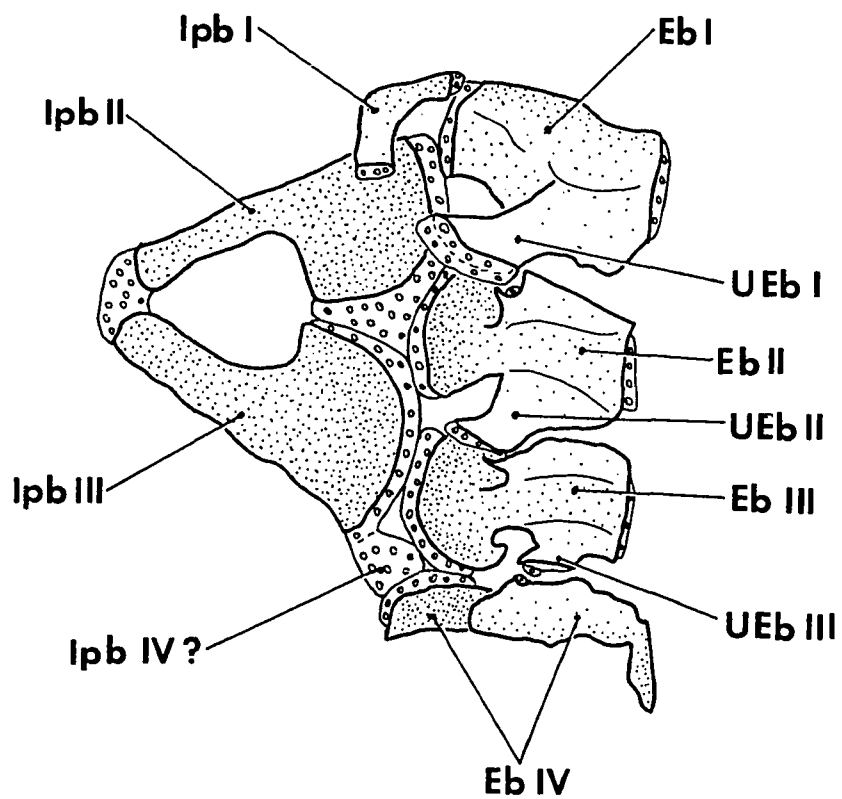


Figure 24

Fig. 25 Dorsal view of the right side dorsal gill arch elements of Minytrema melanops AMNH 49057; anterior to the top of page. Ipb II and III are the only ossified elements in the infrapharyngobranchial series. The catostomid Ipb I is a small cartilaginous nodule medial to the head of Eb I. Their epibranchials are deeply arched with expansive heads that help support a large palatal organ.

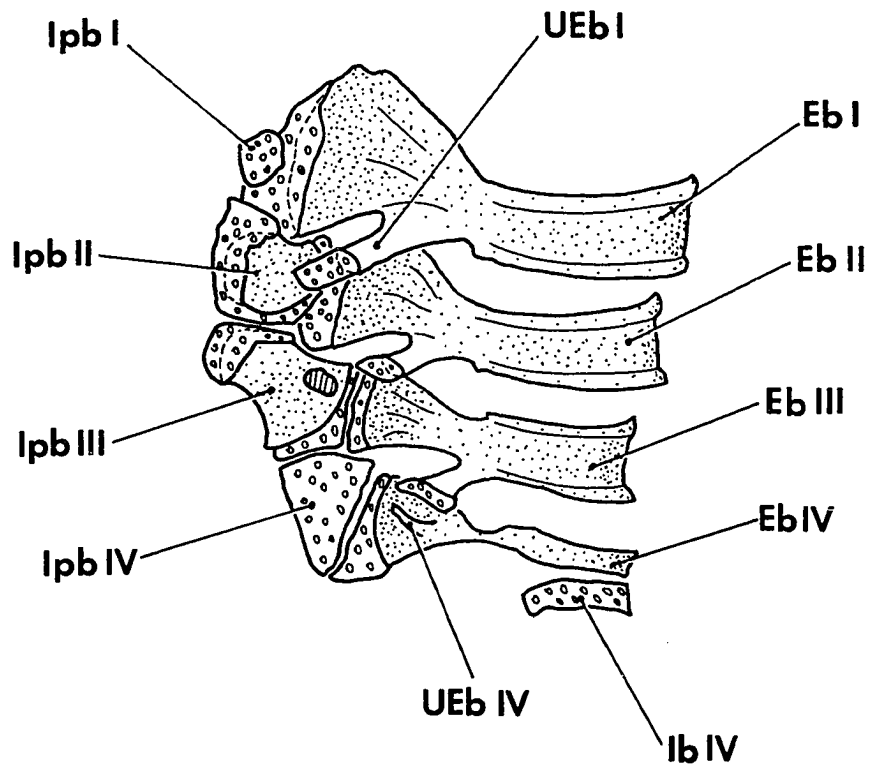


Figure 25

Fig. 26. A diagrammatic representation of the pattern of relationships between efferent arteries and the skeletal elements that underlie them. This pattern seems to be common among non-cyprinid cypriniforms but information concerning variation of it among them and of the pattern between efferent arteries and underlying skeletal elements of outgroups is too sketchy for a statement of its implication for cypriniform systematics. An EA runs atop Eb I-III (usually in a groove) and along the posterior side of Eb IV. EA IV passes through a canal formed by the Eb IV levator process and interbranchial IV.

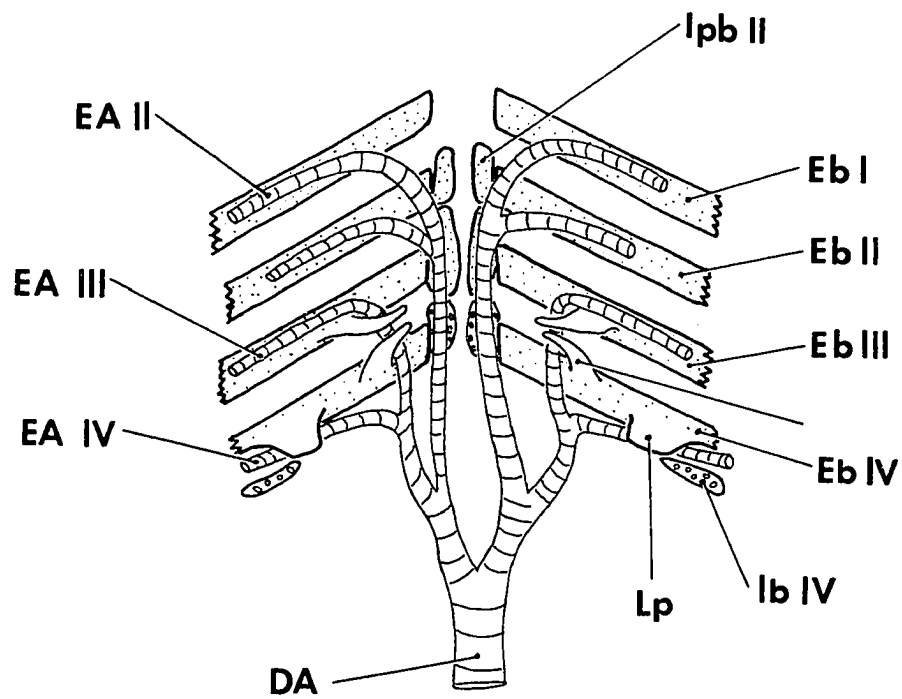


Figure 26

Fig. 27. Dorsal view of the right side dorsal gill arch elements of Leptobotia fasciata AMNH 10298SW; anterior to the top of the page. An Ipb I is absent and Ipb III overlaps Ipb II (and Eb II). The x's in Ipb IV are intended to represent mineralized particles. The anterior corner of Eb I's medial tip is deflected ventrad, twisting it around Ipb II. The levator process of Eb IV is expansive and separate from the Eb IV unciniate process. Obliquus dorsalis fibers originate from Eb III and IV unciniate processes to insert on Ipb III.

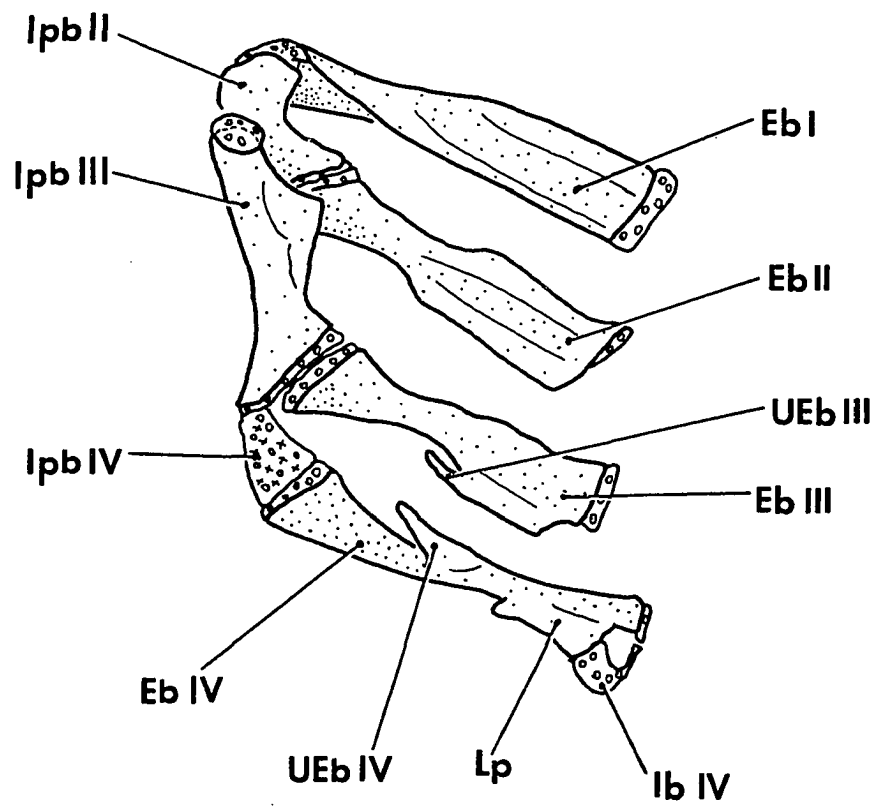


Figure 27

Fig. 28A,B. A. Dorsal view of the right side dorsal gill arch elements of Acanthopsis choirorhynchus FMNH 68146; anterior to the top of the page. Ipb I is absent, Ipb II is small and Ipb III is a waisted element with a dorsally turned anterior end. Eb II and III are distinctly shorter than Eb I and IV and the uncinata and levator processes of Eb IV are confluent. Note the large head of Eb IV.
B. Lateral view of the infrapharyngobranchial series of A. choirorhynchus illustrated to show the upward bend of the anterior end of Ipb III and the close association between Ipb II and III.

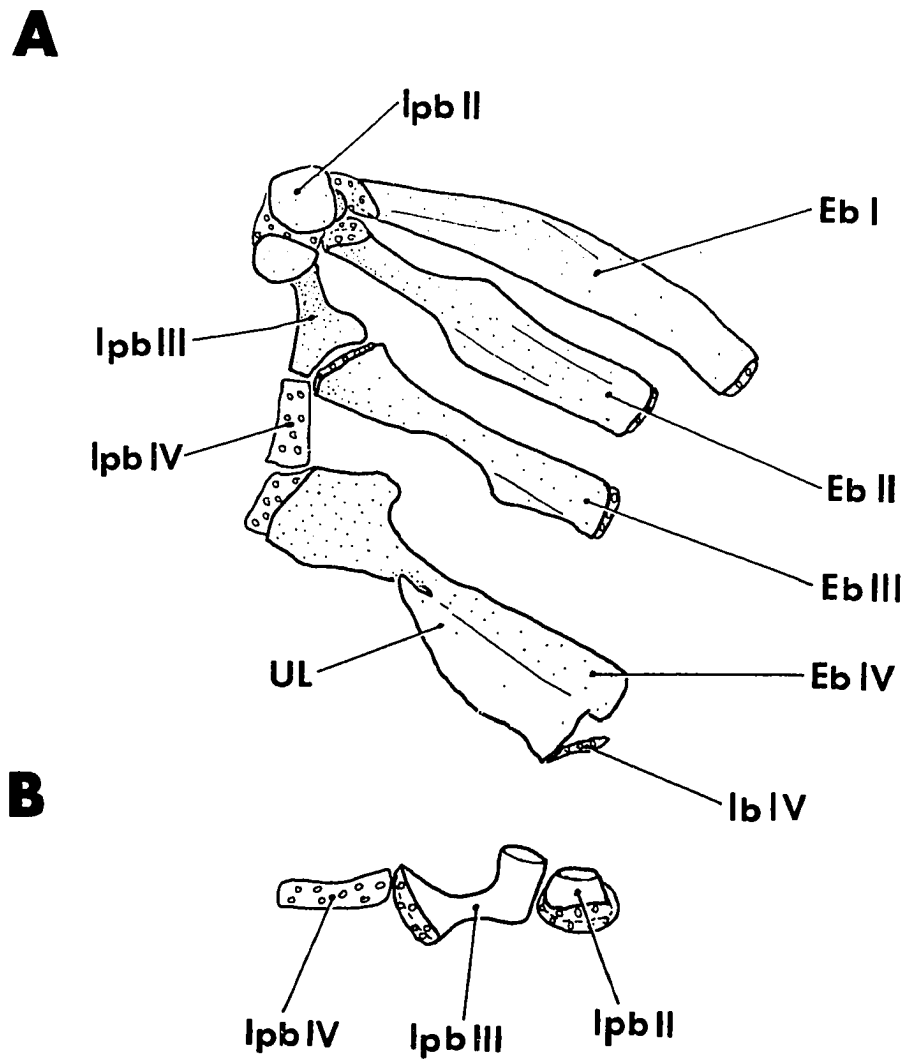


Figure 28

Fig. 29. Dorsal view of the relationship between the efferent arteries and underlying skeletal elements of Lepidocephalis thermalis AMNH 40956; anterior to the top of the page. Note EA I slips to the anterior side of Eb I, following the twist of that bone. Ipb III is waisted below the EA I and II union and the large head of Eb IV lies beneath EA III. The confluent Eb IV uncinata and levator processes overlie EA IV.

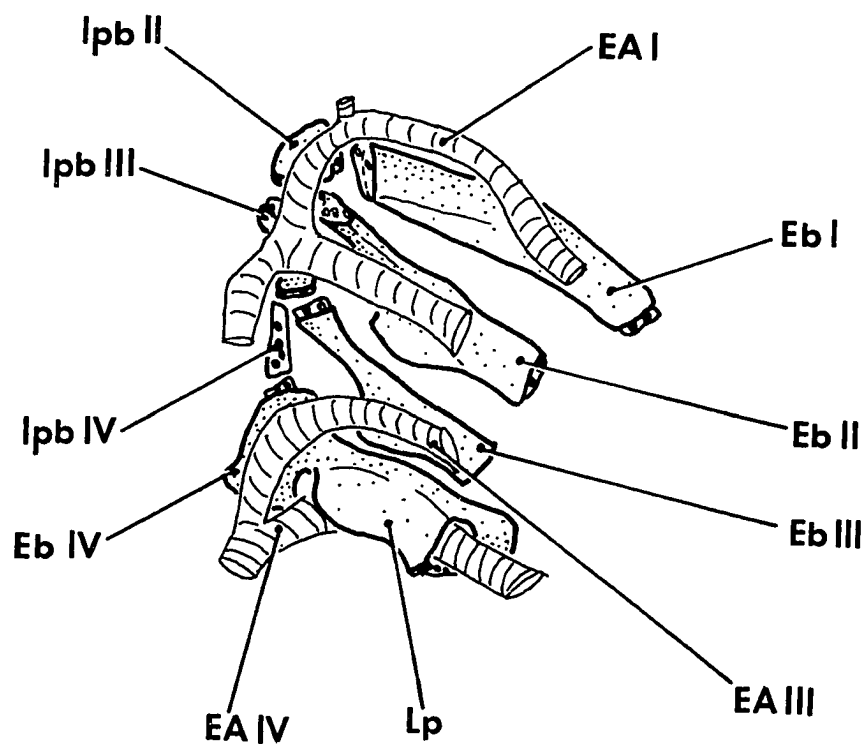


Figure 29

Fig. 30A-D. Dorsal views of the right side dorsal gill arch elements of: A. Noemacheilus barbatulus AMNH 37608, B. N. pulcher AMNH 10347, C. N. stoliczkai AMNH 10350SW, and D. Lefua echigonia AMNH 37356; anterior to the top of the page. Among them, note absence of Ipb I, lack of an identifiable separate Ipb IV, absence of an Eb III unciniate process (except for N. pulcher), the consolidation of the infrapharyngobranchial series with the end-to-end relationship between Ipb II and Ipb III, and that Eb II and III are shorter than Eb I and Eb IV. Note the modification of the medial ends of Eb I and II of L. echigonia into rod-like elements.

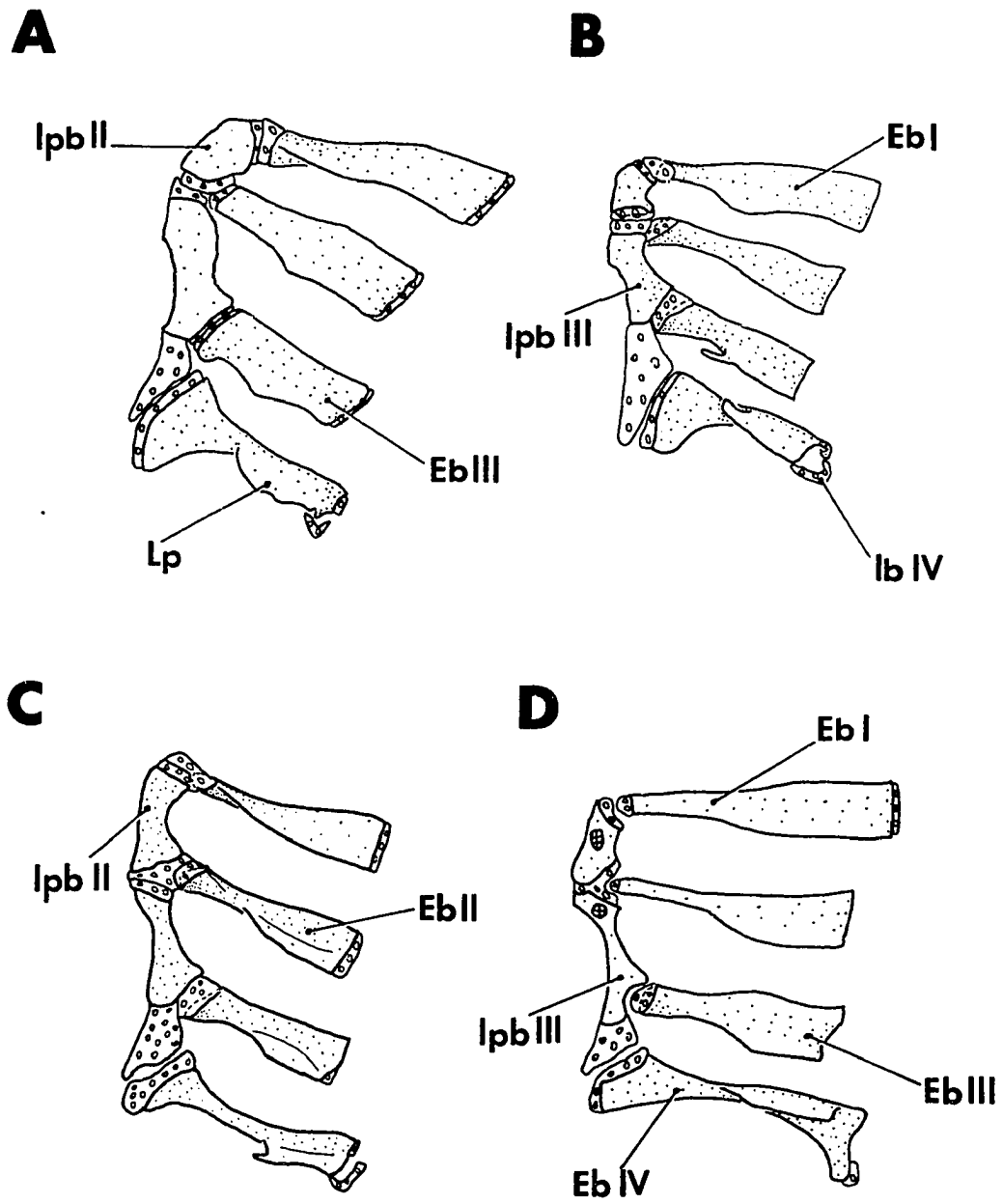
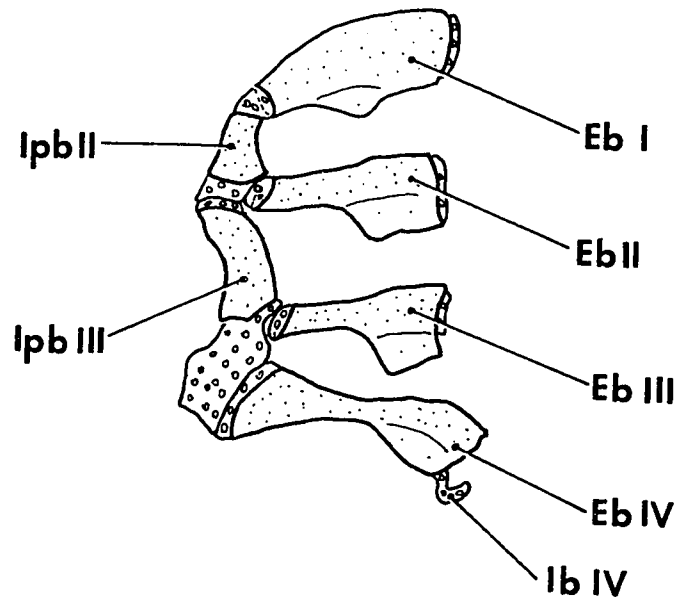


Figure 30

Fig. 31A,B. Dorsal views of the dorsal gill arch elements of: A. Crossostoma davidi AMNH 10282, a gastromyzontin, and B. Homaloptera orthogoniata AMNH 77899, a homalopterin; anterior to the top of the page. Note between them the lack of Ipb I, the end-to-end arrangement of Ipb II and III, lack of an Ipb IV unciniate process, shortness of Eb I-III, and the posteromesial orientation of Eb I. Note the posterior elongation of the Ipb III of H. orthogoniata.

A



B

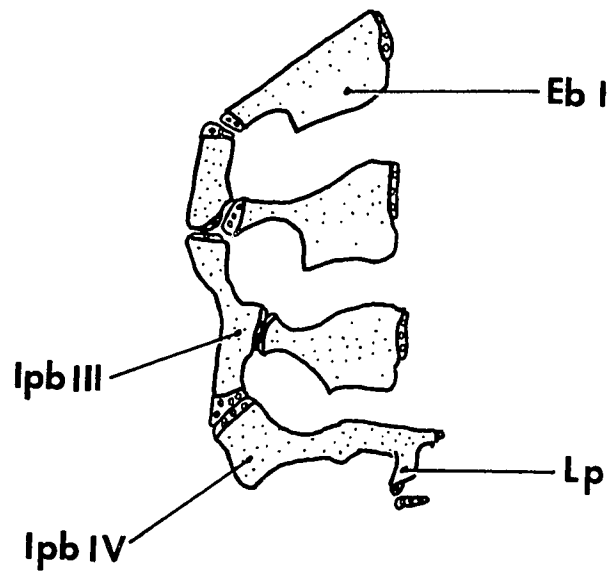


Figure 31

Fig. 32. Dorsal view of right side dorsal gill arch elements of Ellopostoma sp. AMNH 55110; anterior to the top of the page. It lacks an Ipb I and its Eb I extends anterior to Ipb II. Eb II and III are shortest, only Eb III has an uncinat process and there is a cartilaginous upgrowth of CB IV in the position of IB IV.

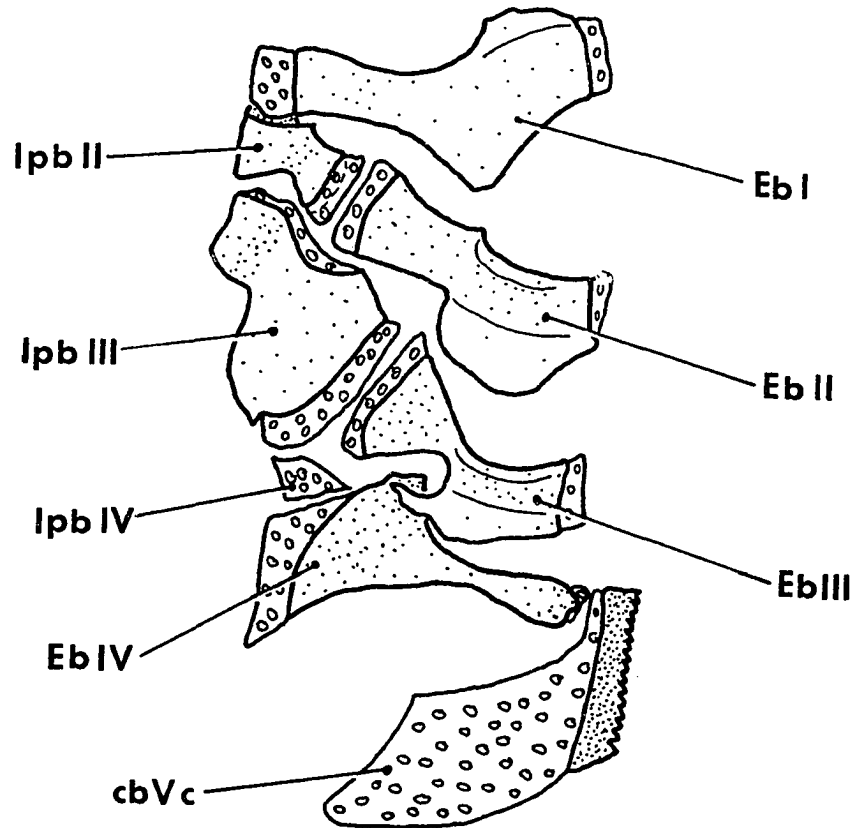
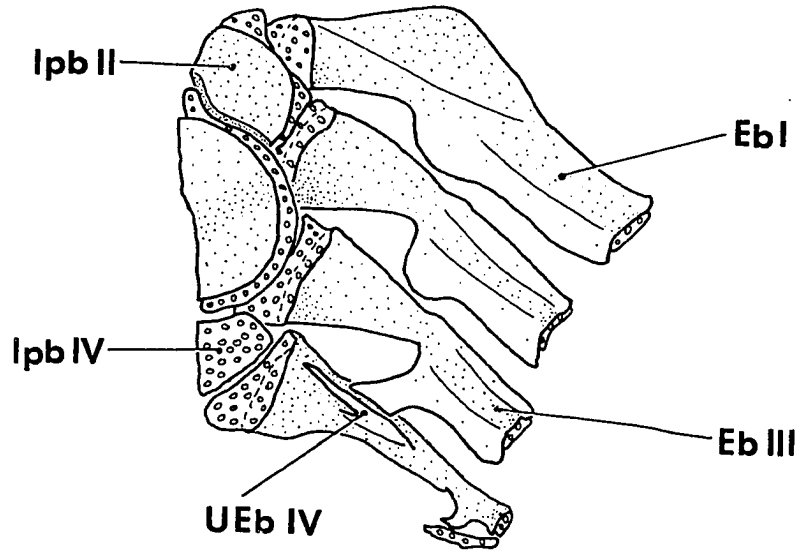


Figure 32

Fig. 33A,B. Dorsal view of the dorsal gill arch elements of: A. Abramis brama AMNH 37594 (right side elements), and B. Acrocheilus alutaceus AMNH 54631 (left side elements); anterior to the top of page. An Ipb I is absent, Ipb II is modified to accommodate overlap by Ipb III and an Ipb IV is identifiable as a separate cartilage. Eb I jogs posteriorly to extend beneath Ipb II, Eb I and II lack uncinat processes and those of Eb III and IV associate closely with each other. An IB IV is present and with the levator process of Eb IV forms an EA canal.

A



B

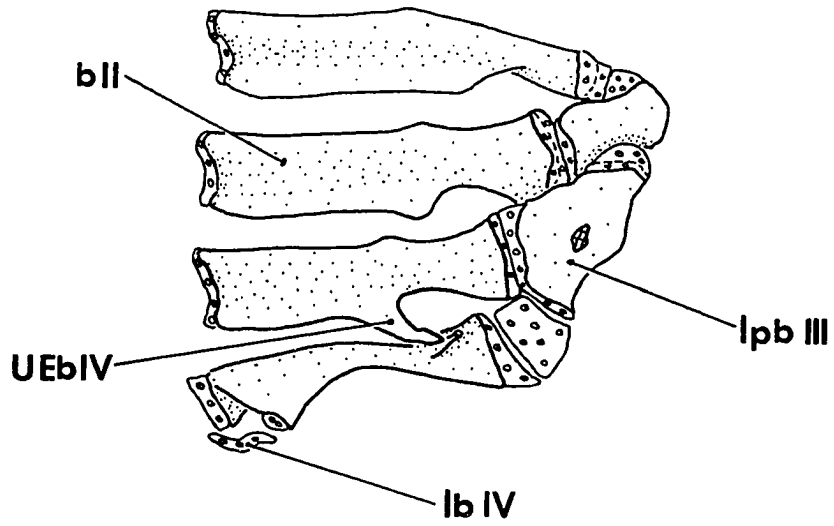


Figure 33A,B

Fig. 33C,D. Dorsal view of the right side dorsal gill arch elements of: C. Cyclocheilichthys armatus AMNH 48918, and D. Cyprinis carpio AMNH 49088; anterior to the top of the page. General features are as described for fig. 33A,B. Note the waisted shape of Ipb III of Cyclocheilichthys and its relationship to the arterial trunk formed by the union of EA I and II.

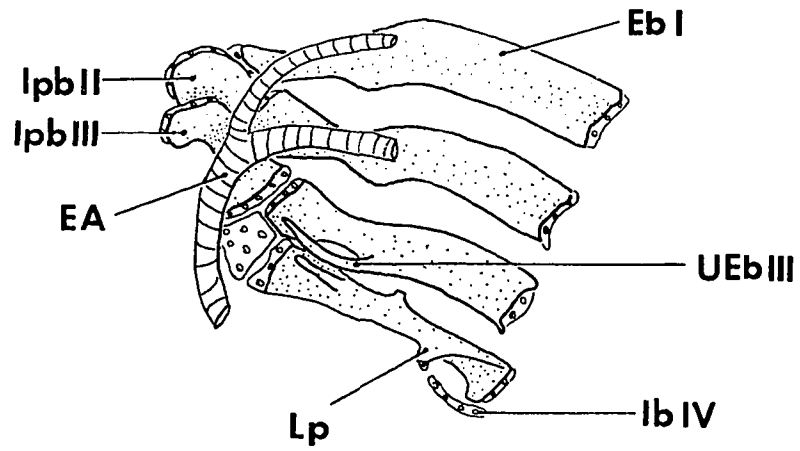
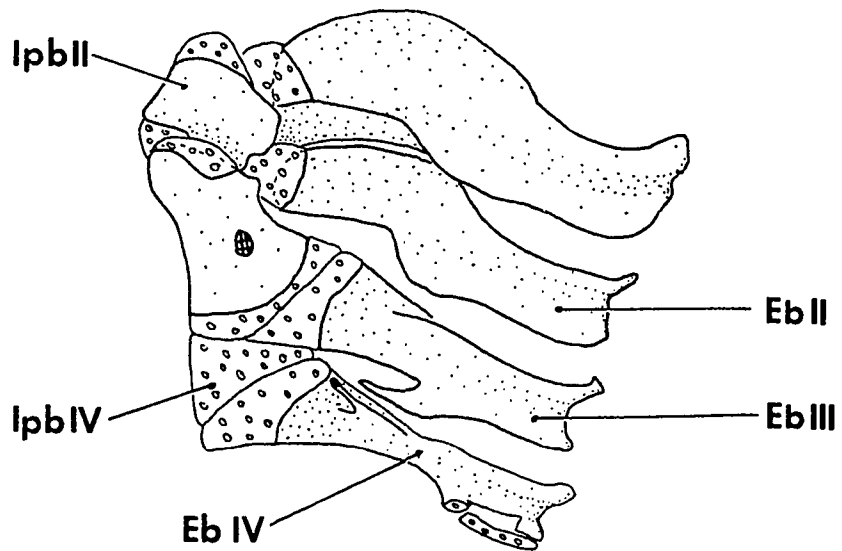
C**D**

Figure 33C,D

Fig. 33E. Aboral view (top) and oral view (bottom) of the right side dorsal gill arch elements of Dangila festiva AMNH 77919; anterior of the aboral view to the top of the page and anterior of the oral view to the bottom of the page. General aspects are as described for fig. 33A,B. Note the large laminar flanges extending from the anterior edges of Eb I-III.

E

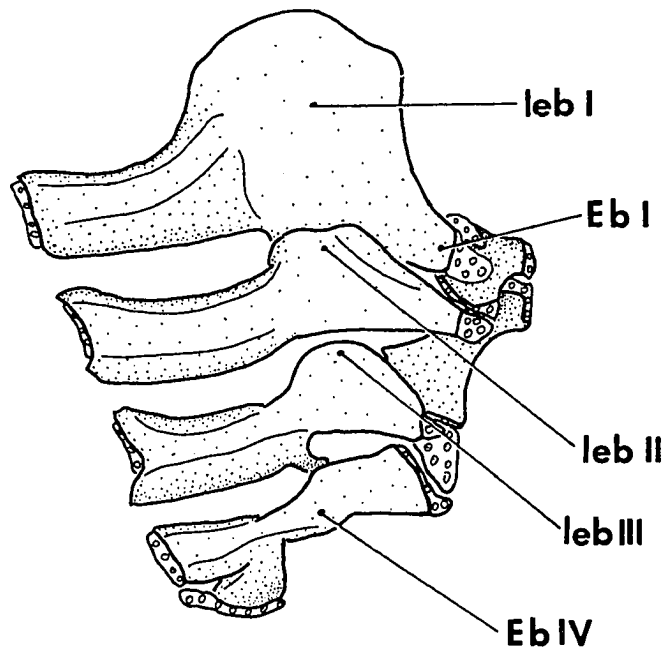
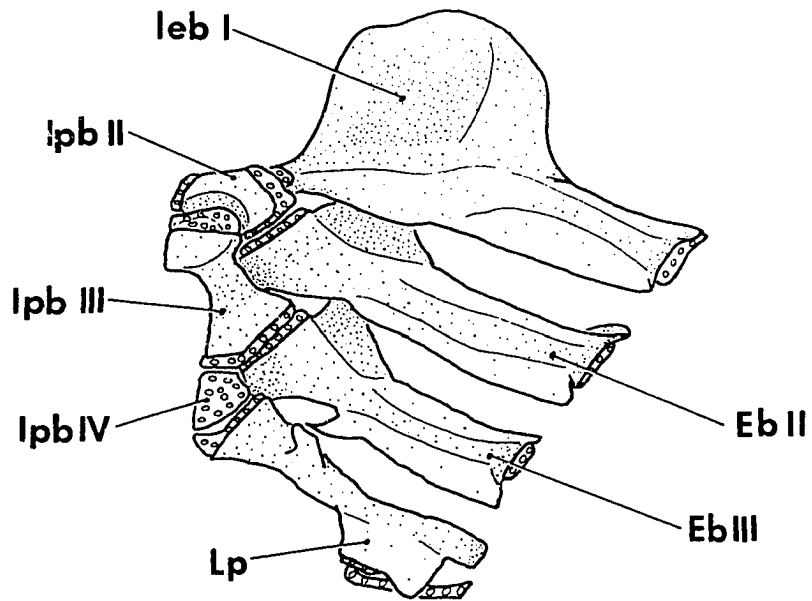


Figure 33E

Fig. 33F. Dorsal view of the right side dorsal gill arch elements of Elopichthys bambusa USNM 130383; anterior to the top of the page. General features of the skeletal elements are as described for fig. 33A,B except no separate Ipb IV is identifiable. Efferent arteries are figured to illustrate the relationship between them and the underlying skeletal elements. EA I to III run atop Eb I-III, EA IV courses posteriorly to Eb IV. Whether the union of the EA I and II trunk from the right and left sides to form a common vessel before joining the EA III-IV vessels is a pattern characteristic of cyprinids is not known, but is clearly different from the pattern illustrated in fig. 26 for non-cyprinid cypriniforms.

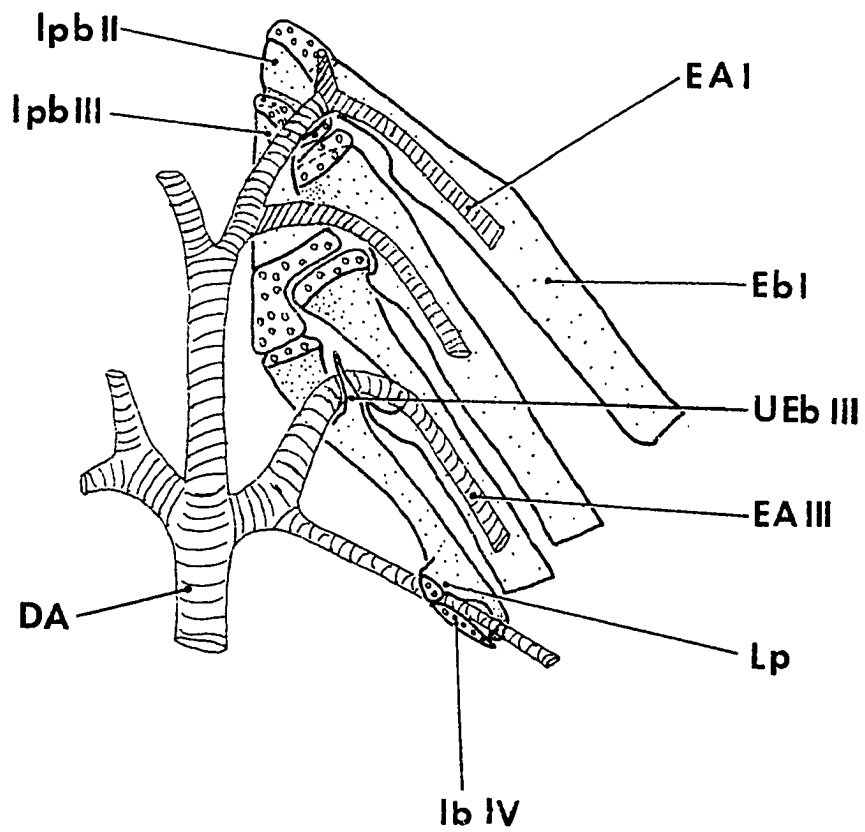
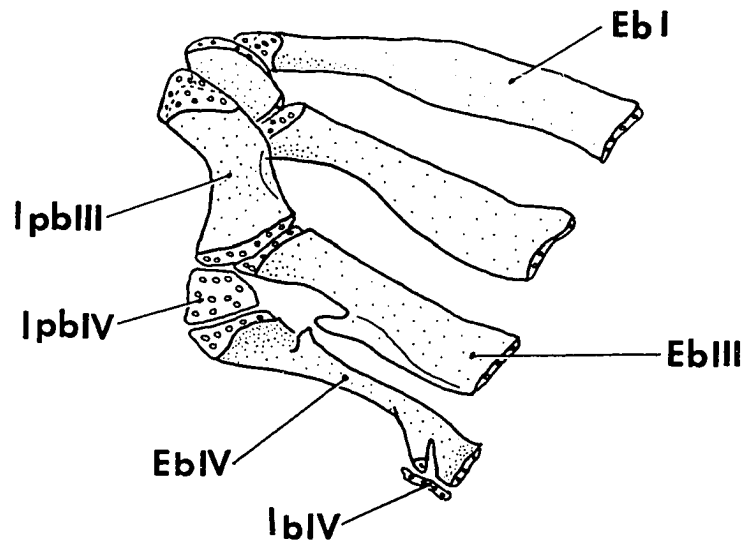
F

Figure 33F

Fig. 33G,H. Dorsal view of the dorsal gill arch elements of: G. Gobio gobio AMNH 37609 (right side elements), and H. Labeo niloticus AMNH 9548 (left side elements); anterior to the top of the page. General aspects are as for fig. 12A,B. Labeo possesses a large flange on the anterior edge of Eb I as does Dangila (fig. 33E).

G



H

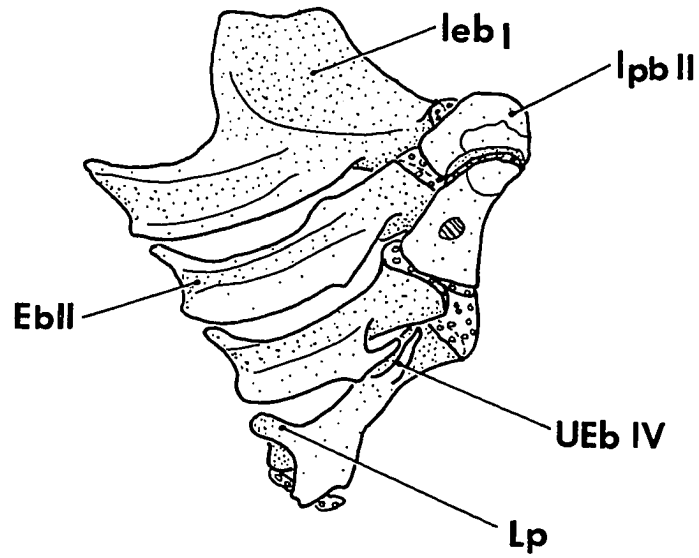


Figure 33G,H

Fig. 33I,J,K. Dorsal view of the dorsal gill arch elements of: I. Notropis atherinoides AMNH 41051 (right side elements), J. Rasbora pauciperforta AMNH 48933 (left side elements), and K. Zacco spilurus AMNH 10932 (right side elements); anterior to the top of the page. General aspects are as described for fig. 33A,B. Note, however, none of these species possess a separate Ipb IV.

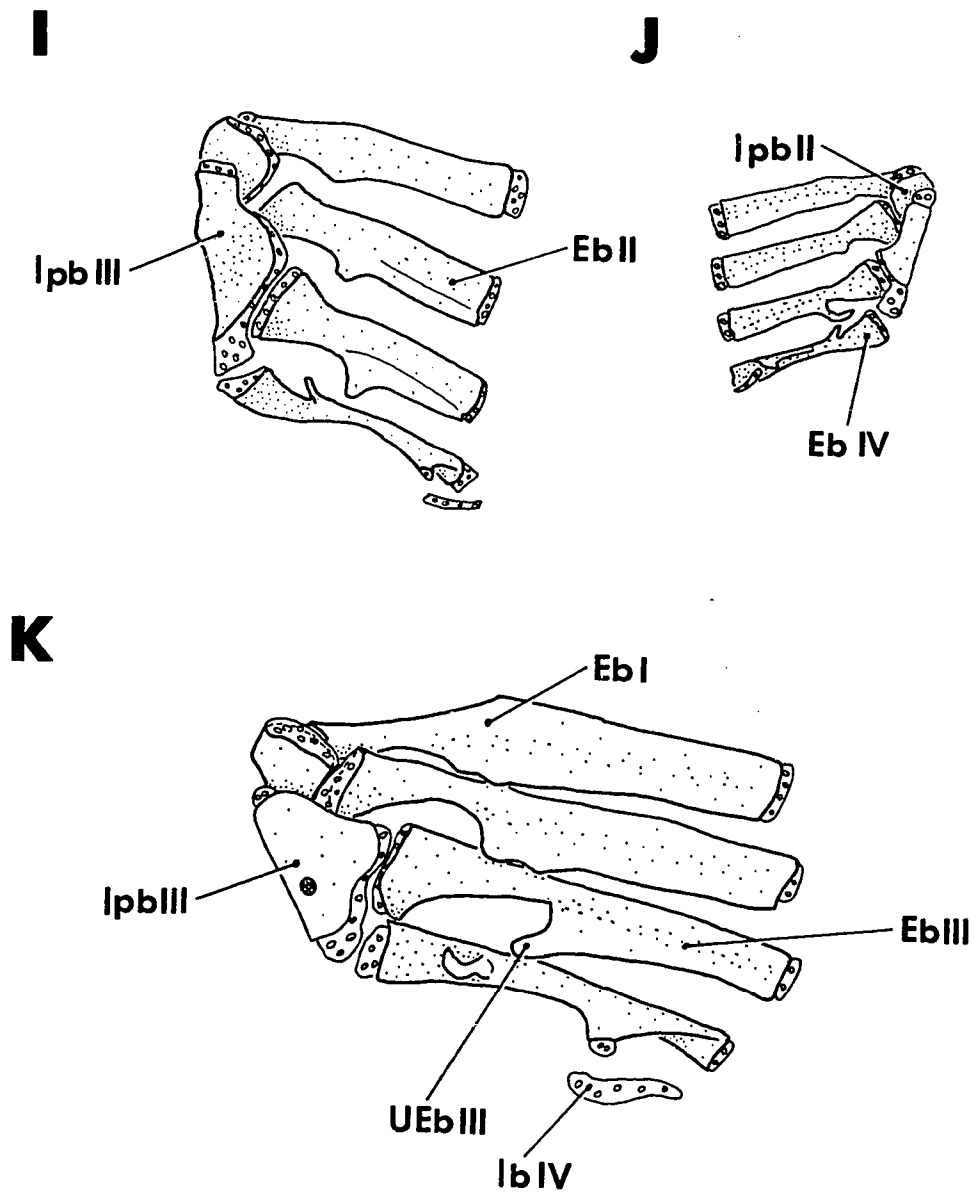


Figure 33I,J,K

Fig. 34. Oral view of the ventral gill arch elements of Chanos chanos AMNH 77918; anterior to the top of page. Left side paired elements of the hyoid and first four branchial arches are not illustrated. The median series consists of a basihyal, basibranchials 1-3, and copula 3. Dermal plates are found on the Bh, Bb 3, and C 3. Paired elements consist of 3 pairs of hypobranchials of which Hb I and II are long, and 5 pairs of ceratobranchials, the last of which is modified in support of an epibranchial organ.

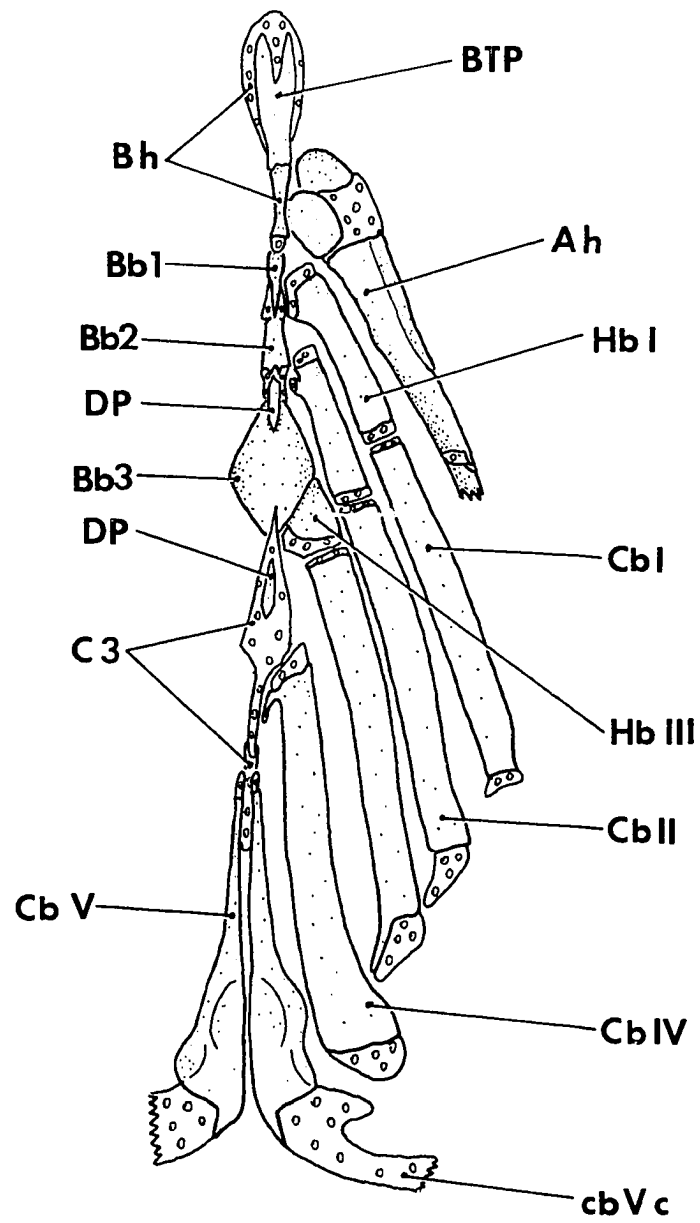


Figure 34

Fig. 35. Lateral view of the median series of ventral gill arch elements from a variety of actinopterygians with a diagram of their interrelationships. Note that among teleosts the anterior end of C 3 is positioned superiorly to the posterior end of C 2 (Bb 3).

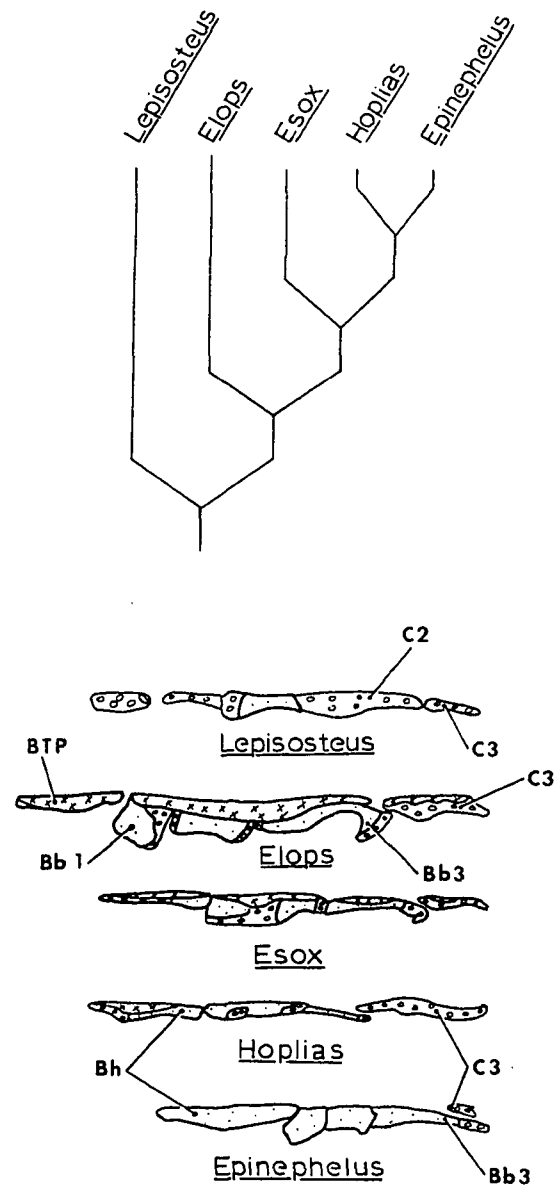
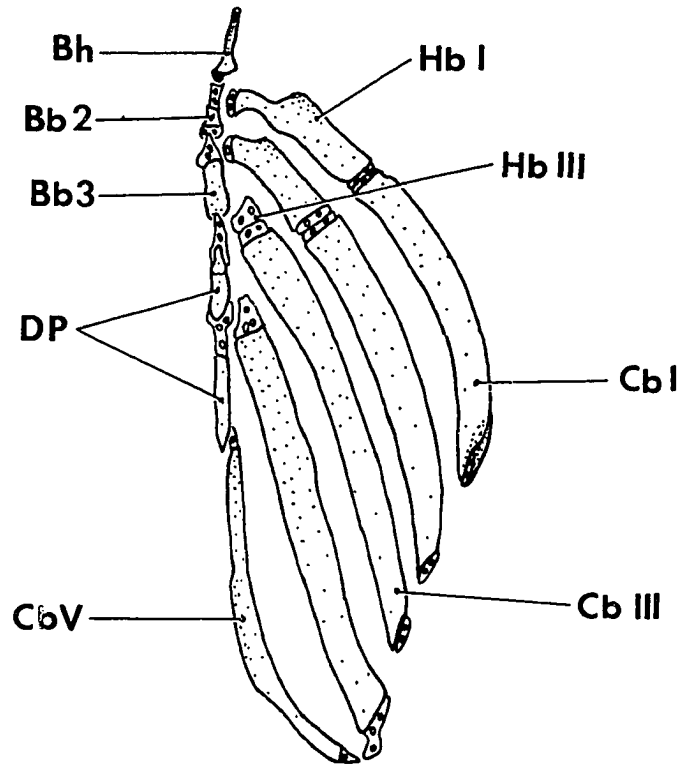


Figure 35

Fig. 36A,B. A. Oral view of the median series and right side paired elements of the ventral gill arch elements of Gyrinocheilus sp. USNM 272884; anterior to the top of the page. Bb 1 is absent and there are two dermal plates associated with C 3. Hb I and II are long; Hb 3 is short and cartilagenous. The toothless ceratobranchial V is the smallest of the ceratobranchial series.

B. Lateral view of the C 2 and C 3 elements of the median series of ventral gill arch elements of Gyrinocheilus sp. Note C 3 dermal plates and its anterior tip positioned dorsal to the posterior end of Bb 3.

A



B

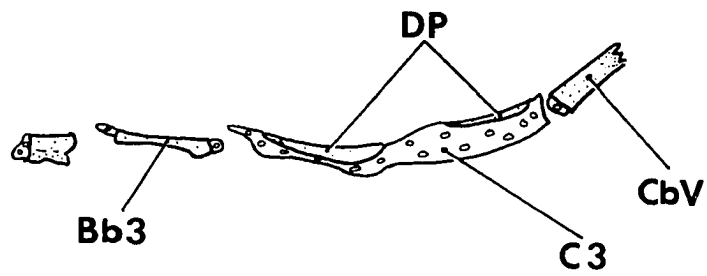
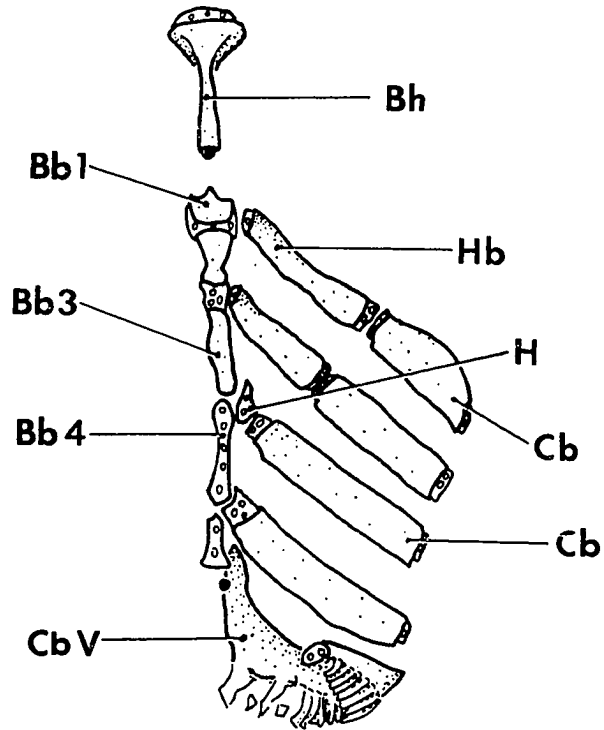


Figure 36

Fig. 37A,B. A. Oral view of the median series and right side paired elements of the ventral gill arch elements of Moxostoma cervinum AMNH 70819; anterior to the top of the page. Copula 3 of the median series is segmented into Bb 4 and 5, both of which remain cartilaginous. Hb III is small and cartilaginous. Cb V is toothed and arches far dorsally, up to the bottom of the braincase. B. Lateral view of the median series of the ventral gill arch elements of Catostomus commersoni AMNH ; anterior to the left. Note the presence of a sublingual ossification beneath the basihyal and that C 3 is segmented into Bb 4-6. Note also the positional relationships and shape of Bb 4.

A



B

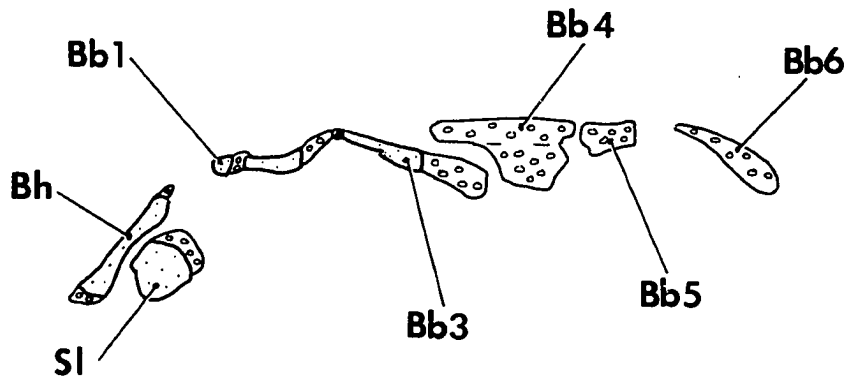


Figure 37

Fig. 38. Ceratobranchial V of Catostomus wigginsi
AMNH 77911. A single row of specialized teeth lines
its posteromedial edge. C. wigginsi is among those
catostomids with the fewest Cb V teeth. Most
catostomids possess at least forty teeth per arch,
but some ictiobines possess more than 150 teeth per
arch.



Figure 38

Fig. 39A,B. A. Oral view of the median series and right side paired elements of the ventral gill arch elements of Cobitis taenia AMNH 20366; anterior to the top of the page. Bb 1 is absent from the median series (see text), Bb 2 is fan-shaped in oral view, and copula 3 is segmented into Bb 4 and 5 of which Bb 4 is ossified. Hb I and II are short, and with anteroventrally directed prongs. That of Hb I is the attachment site of the rectus I muscle. Cb I is long, slender and deeply arched. Cb V bears a single row of conical teeth.

B. Lateral view of the median series of ventral gill arch elements of Misgurnus mizolepis AMNH 17928; anterior to the left. Note the sublingual ossification, the positional relationships of Bb 4 relative to Bb 3, and the rectus I prong on Hb I.

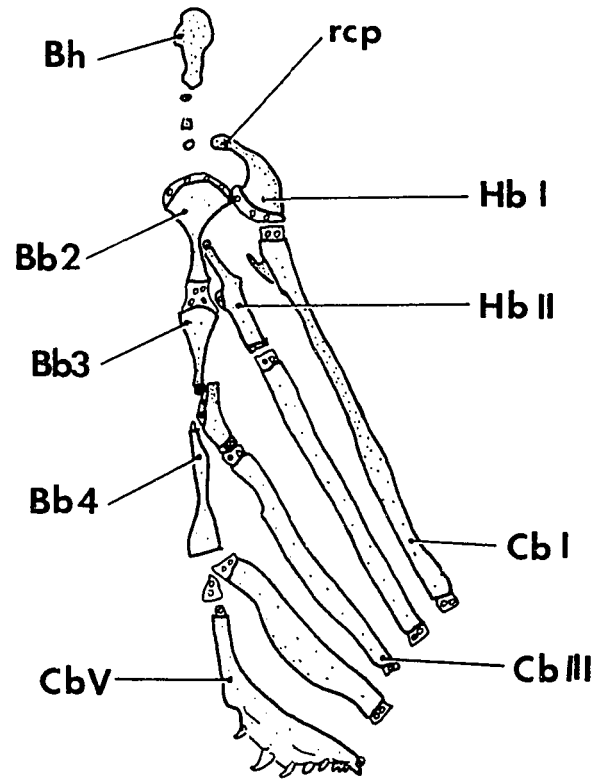
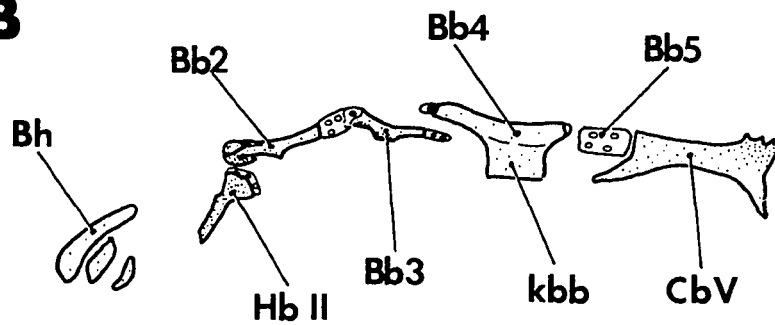
A**B**

Figure 39

Fig. 40A-C. Ventral view of Cb V of: A. Cobitis taenia AMNH 20366, B. Misgurnus mizolepis AMNH 17928, and C. Acanthopthalmus kuhli AMNH 77902. Note all possess a ventrally directed spike for the attachment of the transversus ventralis V muscle.

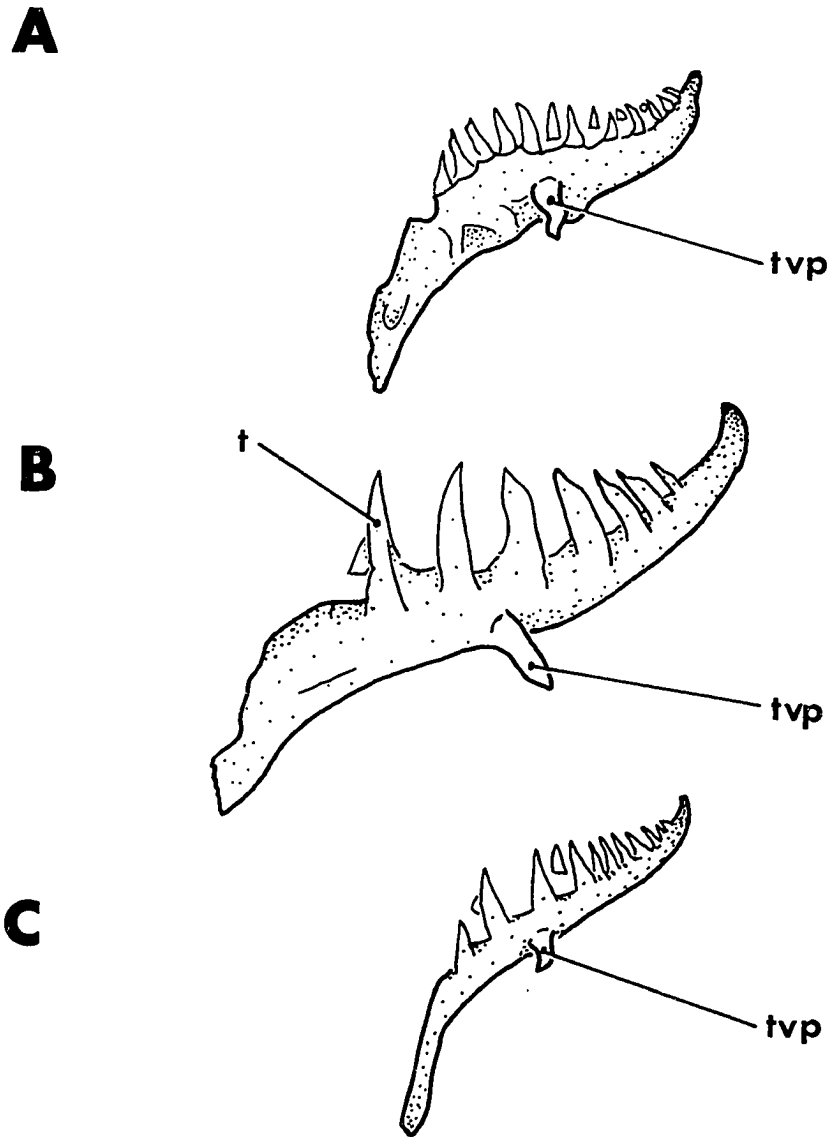
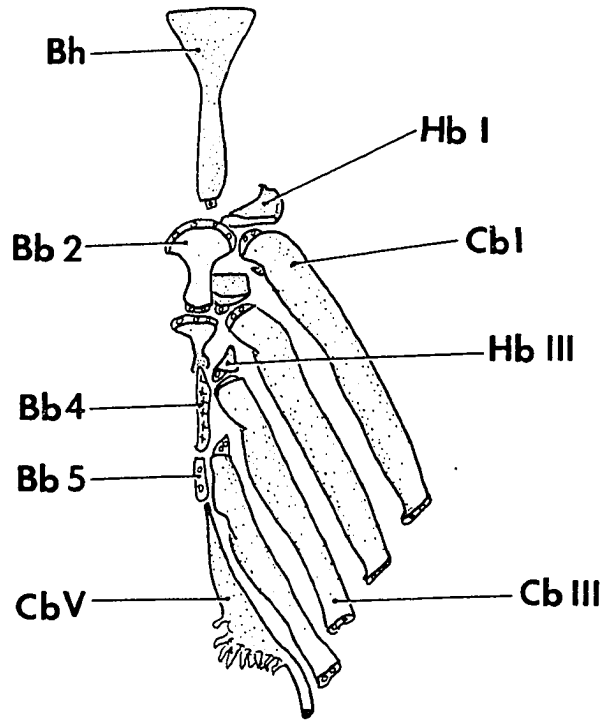


Figure 40

Fig. 41A,B. A. Oral view of the median series and right side paired elements of the ventral gill arch elements of Botia macracantha AMNH 77904; anterior to the top of page. Bb 1 is absent and both Bb 2 and 3 are fan-shaped anteriorly in oral view. Hb I possess a rectus I process.

B. Lateral view of the median series of elements of the ventral gill arch elements of B. macracantha, anterior to the left. Sublingual ossifications are present, Hb I appears as in Cobitis (fig. 39A), and Bb 4 is unossified. Bb 4 is, however, mineralized.

A



B

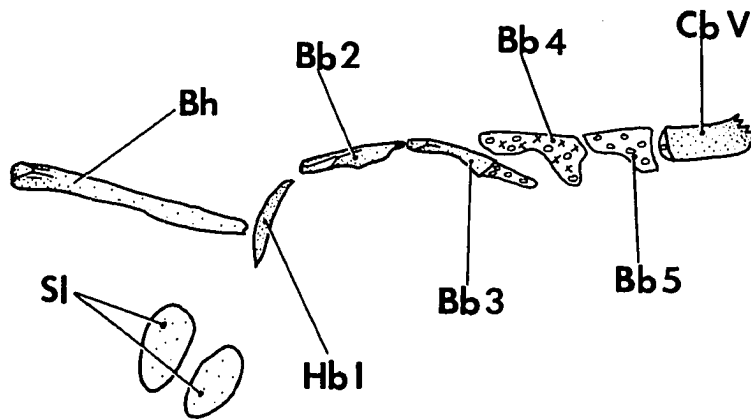
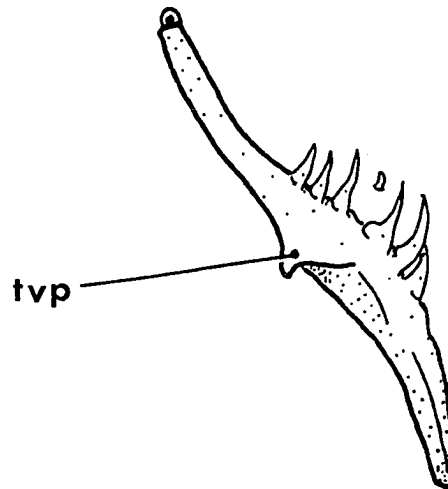


Figure 41

Fig. 42A,B. Ventral view of Cb V of: A. Botia purpurea AMNH 10419SW, and B. Leptobotia fasciata AMNH 10298SW. Both possess the transversus ventralis V prong and a single row of conical teeth.

A



B

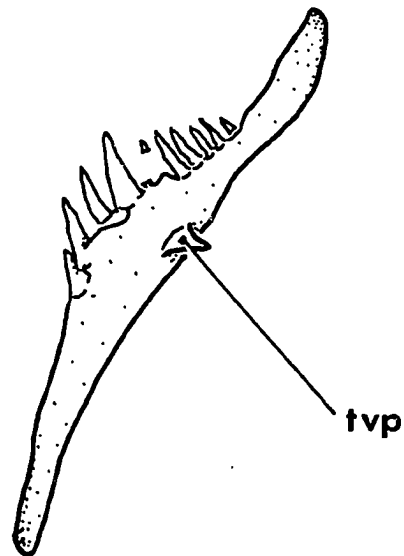


Figure 42

Fig. 43A,B. Oral view of the median series and right side paired elements of the ventral gill arches of: A. Noemacheilus barbatulus AMNH 37608, and B. Lefua echigonia AMNH 37356; anterior to the top of the page. The basihyal of this N. barbatulus specimen is damaged but is expanded anteriorly and Bb 2 of Lefua is somewhat cross-shaped like that of homalopterines. Both lack Bb 1.

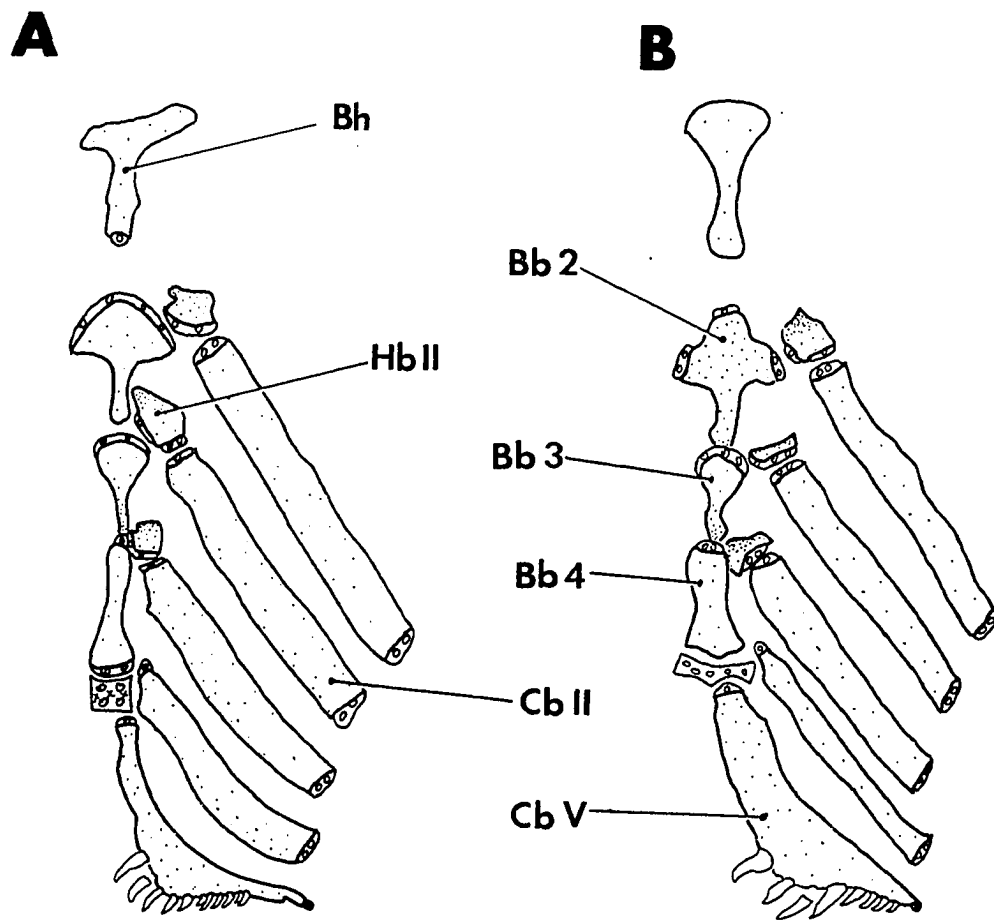


Figure 43

Fig. 44. Lateral view of the median series of the ventral gill arch elements of Noemacheilus posteroventralis AMNH 29706; anterior to the left. A sublingual ossification is present and Bb 1 is absent. Bb 4 is ossified and has a strong ventral keel. Behind it is an ossified Hb IV, an element present in all examined material of N. posteroventralis (see also Nelson, 1969a).

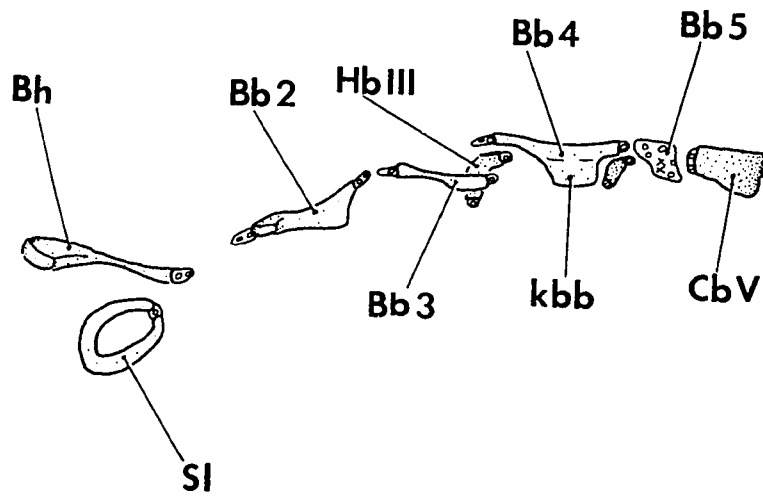


Figure 44

Fig. 45A,B. Oral view of the median series and the right side paired elements of the ventral gill arches of: A. Homaloptera orthogoniata AMNH 77899, and B. Lepturichtys fimbriata AMNH 10335; anterior to the top of page. Note the Y-shaped basihyal and cross-shaped Bb 2 (Bb 1 is absent).

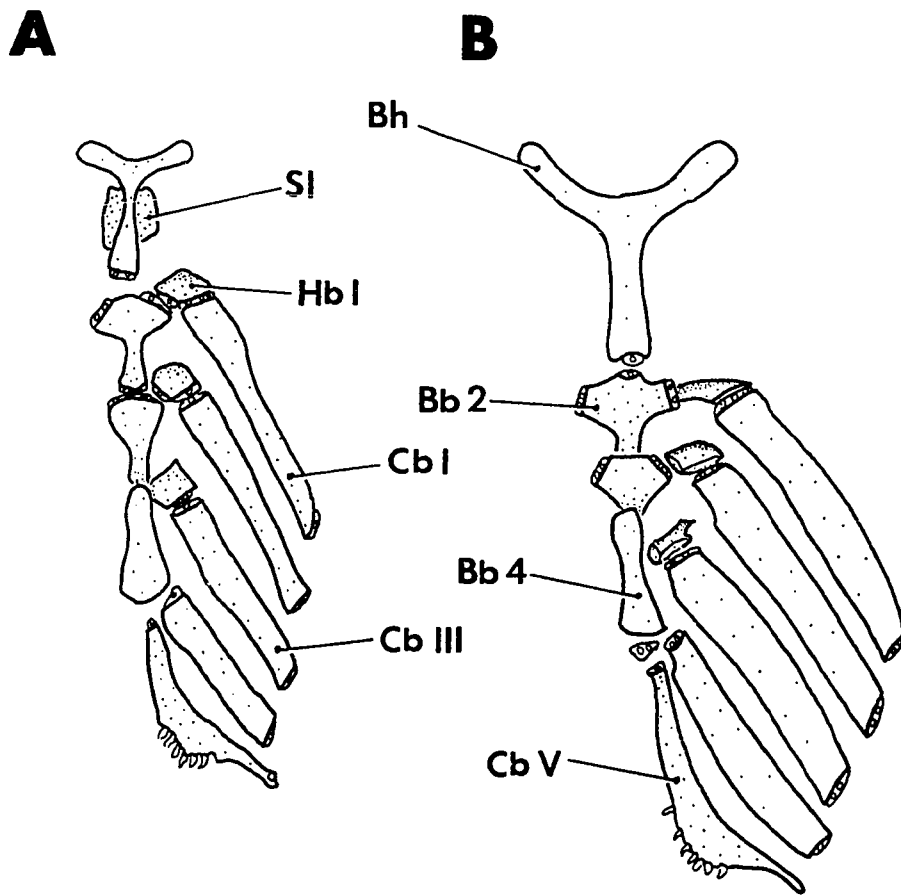


Figure 45A,B

Fig. 45C. Oral view of the median series and right side paired elements of the ventral gill arches of Gastromyzon borneensis AMNH 77900; anterior to the top of the page. The basihyal is not illustrated but it is large and Y-shaped. Bb 1 is absent and Bb 2 is modified into a transversely lying bar in the floor of the mouth.

C

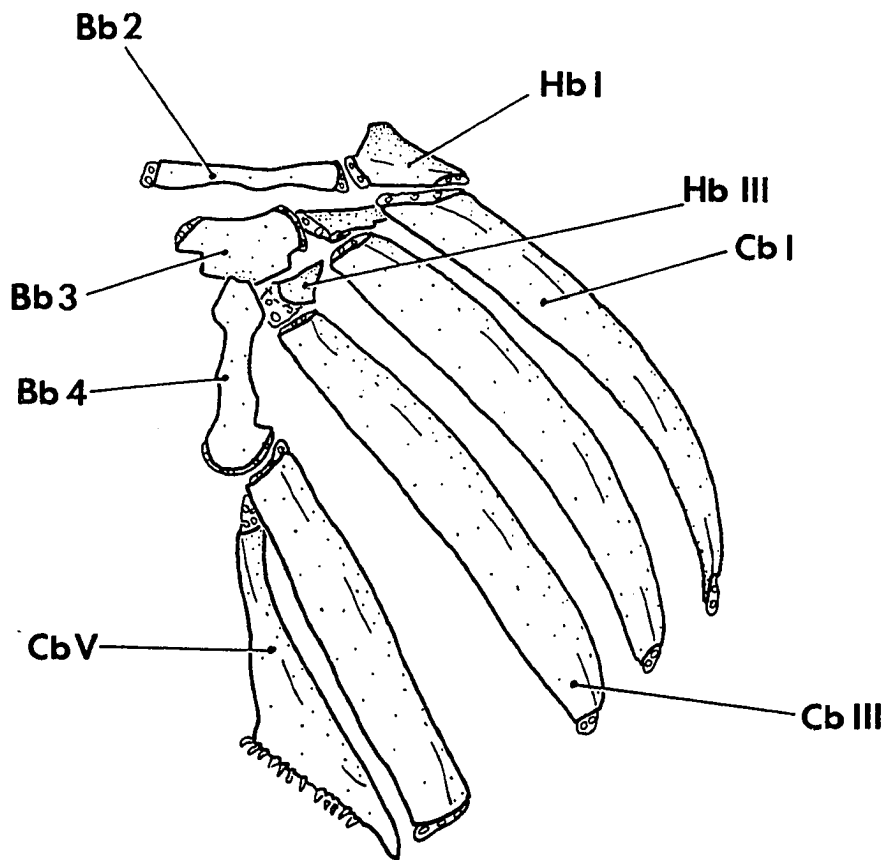


Figure 45C

Fig. 46. Oral view of the median series and right side paired elements of the ventral gill arch elements of Ellopostoma sp. AMNH 55110; anterior to the top of page. The basihyal is y-shaped, Bb 1 is absent, and Bb 2 is T-shaped. Ceratobranchial V bears a single row of numerous conical teeth.

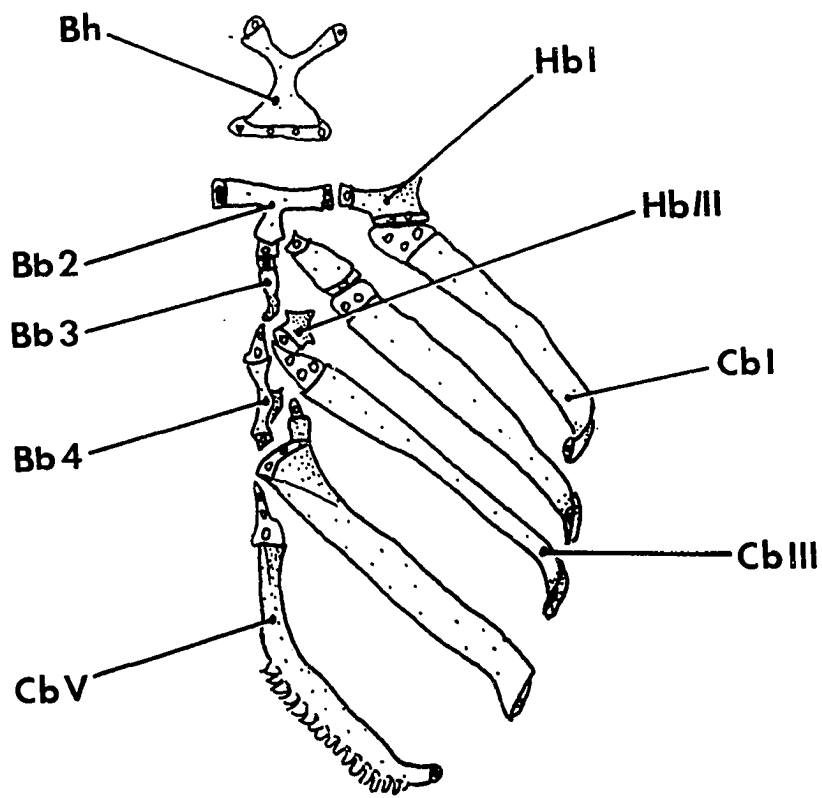


Figure 46

Fig. 47. Lateral view of the median series of the ventral gill arch elements of Vanmanenia caldwelli AMNH 11138; anterior to the left. Bb 1 is absent and Bb 4 is ossified and keeled. Its shape and position are like those found among other homalopterines.

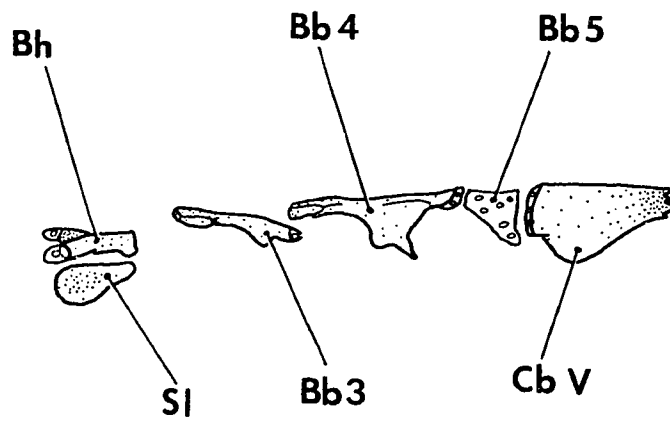
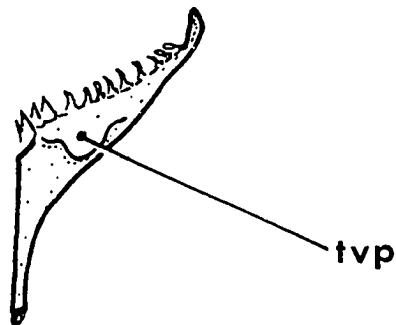


Figure 47

Fig. 48A,B. Ventral view of Cb V of: A. Homaloptera orthogoniata AMNH 77899, and B. Ellopostoma sp. AMNH 55110. Both possess the transversus ventralis V process characteristic of cobitidids and homalopterids.

A



B

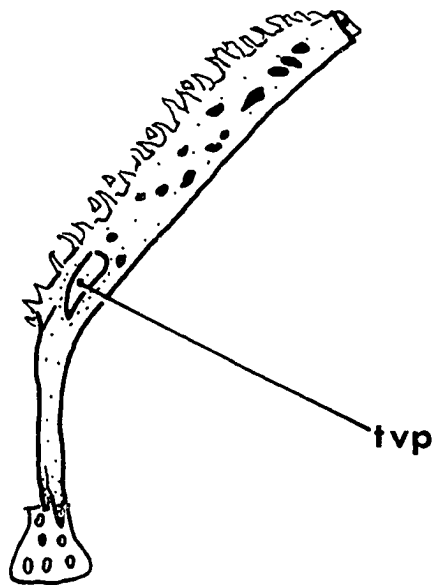


Figure 48

Fig. 49A,B. Oral view of the median series and right side paired elements of the ventral gill arch elements of: A. Barbus barbus AMNH 54635, and B. Cyprinus carpio AMNH 48088; anterior to the top of the page. A basihyal, three basibranchials, and an unsegmented C 3 are present in the median series. Hb I-III are present and ossified. Their orientation is such that in oral view all that is seen of them are their cartilaginous Hb-Cb articular surfaces. Cb V is a huge falcate element with three rows of teeth.

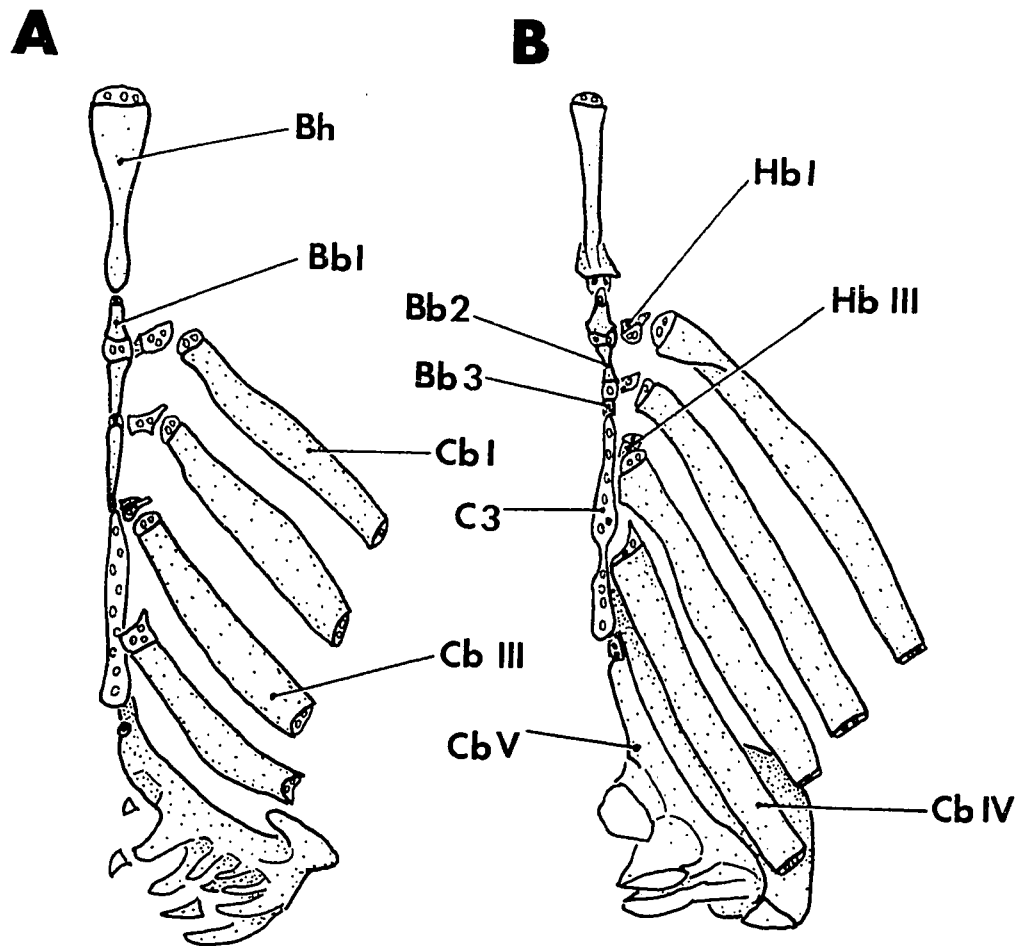


Figure 49A,B

Fig. 49C,D. Oral view of the median series and paired elements of one side of: C. Labeo niloticus AMNH 9548, and D. Notropis atherinoides AMNH 48088; anterior to the top of page. Bb 1 is absent from Labeo, its Bb 2 is cross-shaped, and its C 3 is very long with Cb V consequently removed posteriorly from its anterior neighbors. The median series of elements of Notropis consists of elements, at least in oral view, that are rather slender.

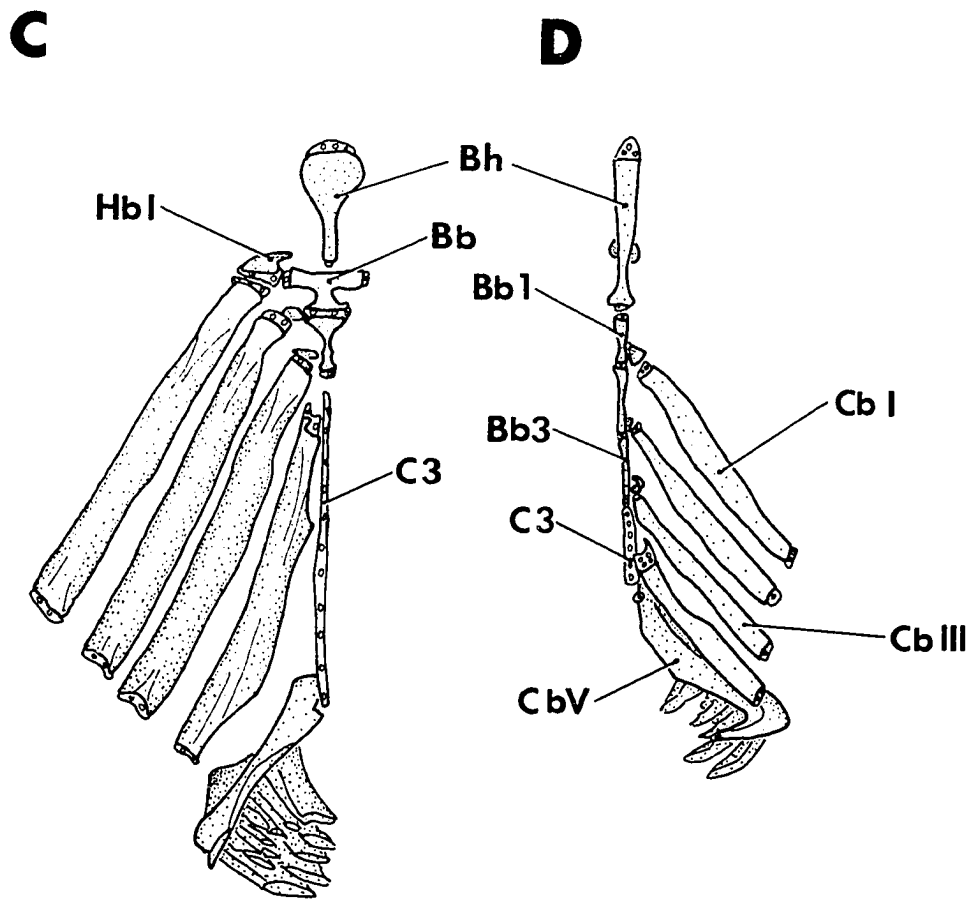


Figure 49C,D

Fig. 49E,F. Oral view of the median series and paired elements of one side of the ventral gill arches of: E. Opsariichthys bidens AMNH 10955, and F. Saurogobio dumerilli USNM 130296; anterior to the top of page. The median series of Opsariichthys is slender like that of Notropis (fig. gvl6D). Hb I of these taxa is as large as seen among cyprinids. Fig. 49E illustrates the relationships between some afferent blood vessels and lower gill arch elements. Hb III is a curved, ventrally oriented spike that forms a canal in which both afferent arteries and Bb 3 reside.

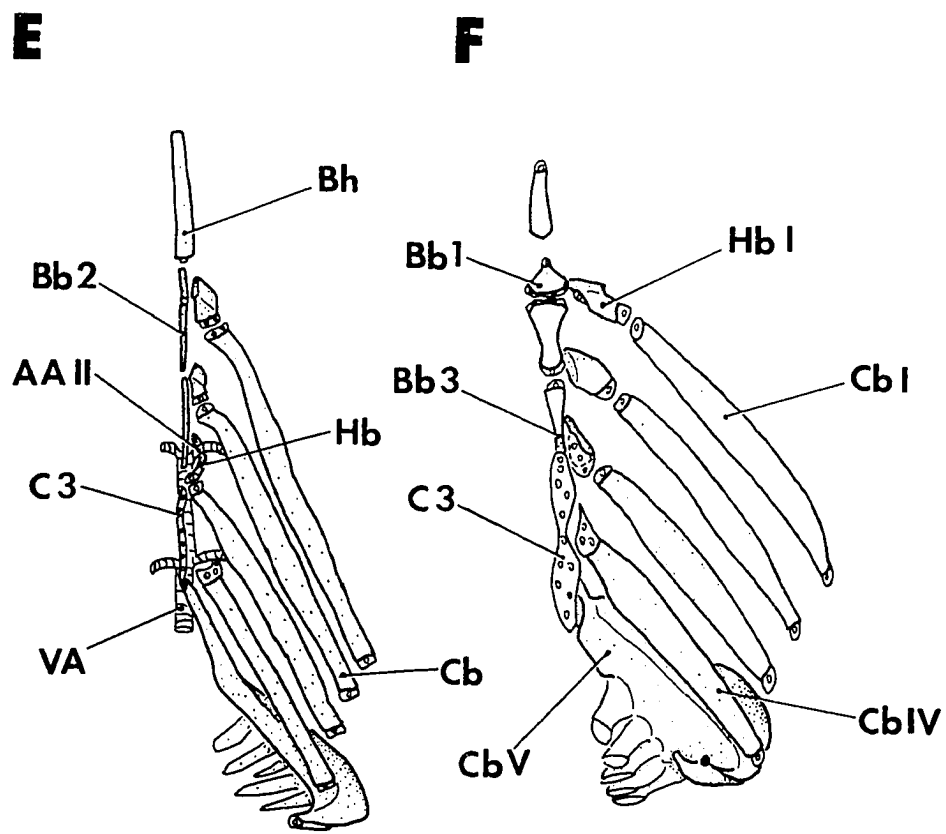


Figure 49E,F

Fig. 50A-D. Lateral views of the median series of the ventral gill arch elements of: A. Gobio gobio AMNH 37609, B. Notropis atherinoides AMNH 41051, C. Phoxinus phoxinus AMNH 36873, and D. Zacco spilurus AMNH 10932; anterior to the left. A sublingual ossification is present in Gobio (A). Note the vertical orientation of Hb III in all taxa. In Phoxinus and especially in Zacco it forms a canal in which both the afferent arterial trunk and Bb 3 reside. Note also the relationship between the anterior end of C 3 and the posterior end of Bb 3 in all taxa.

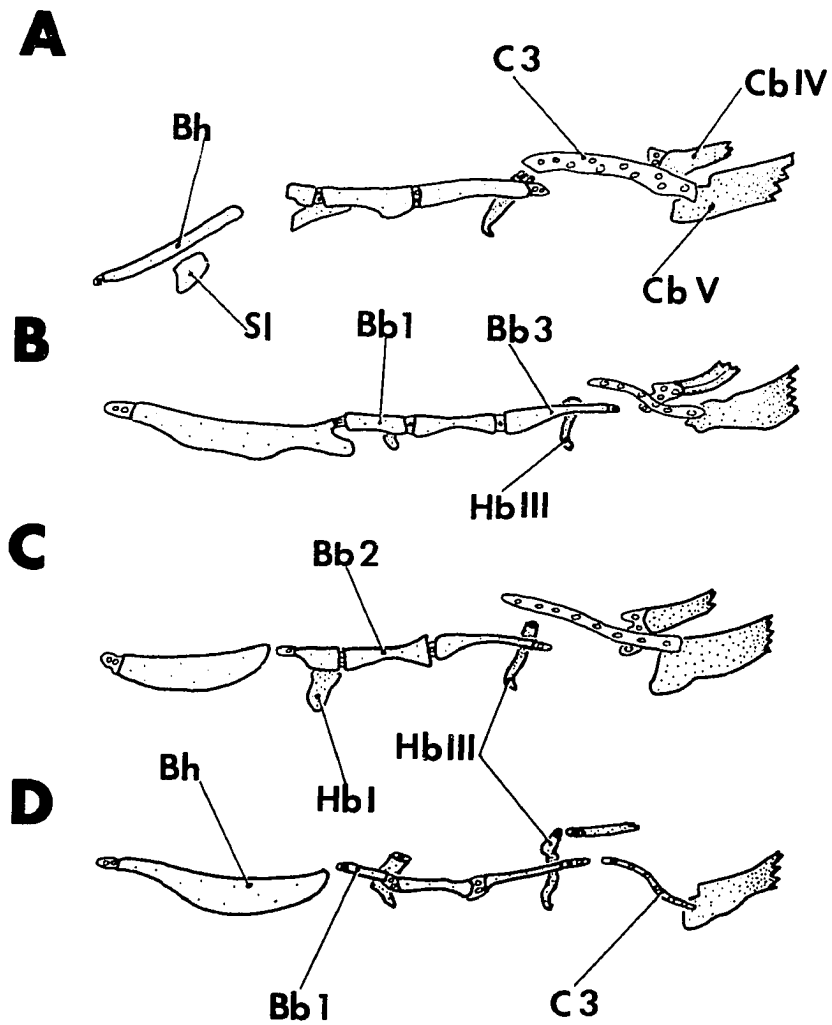


Figure 50

Fig. 51A,B. Lateral view of the median series of the ventral gill arch elements and its relationship to the afferent blood supply of: A. Misgurnus mizolepis AMNH 10362, and B. Catostomus commersoni AMNH 43638, anterior to the left. A common AA 3-4 trunk rises from the ventral aorta ahead of the Bb 4 keel. AA 4 courses back alongside the keel before turning laterally to run beneath Cb IV.

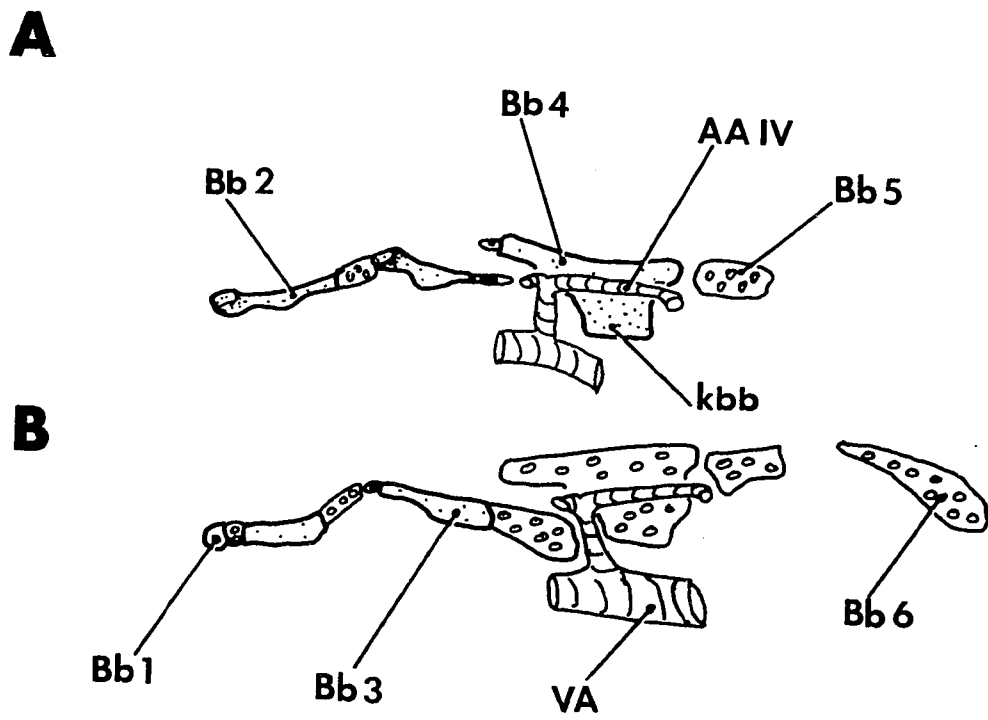


Figure 51

Fig. 52A,B. Dorsal (A; anterior to the top of the page) and lateral (B; anterior to the right) views of the ethmoid region of Balanteocheilus melanopterus AMNH 77920. Cyprinid lateral ethmoids are generalized. The transverse wing of it separates the orbital and nasal regions.

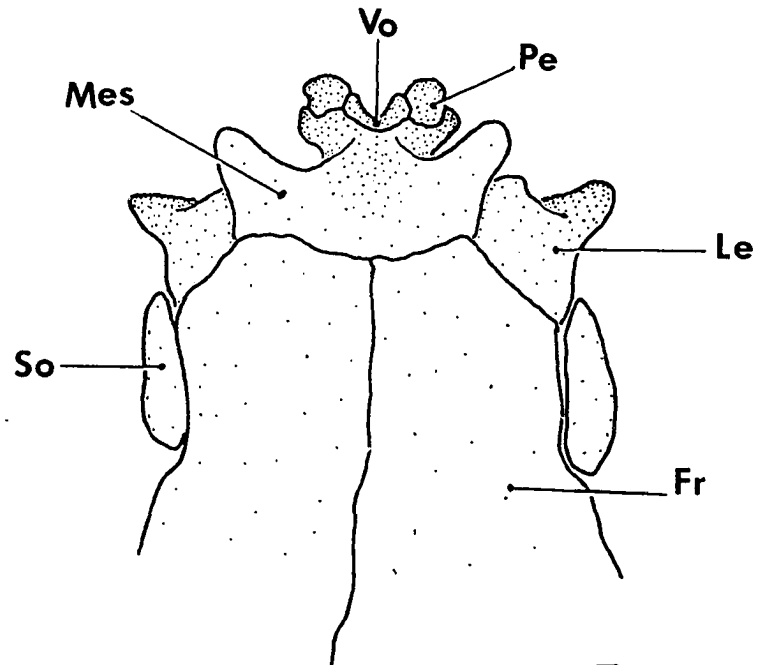
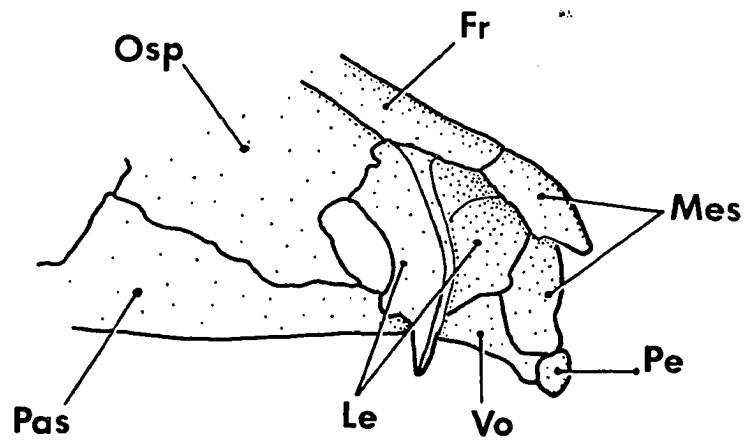
A**B**

Figure 52

Fig. 53. Dorsal view of the right side ethmoid region of Gyrinocheilus aymonieri AMNH 77898; anterior to the top of the page. The lateral ethmoid of gyrinocheilids has an anteriorly directed lateral process (anterolateral process) that cups the nasal capsule (the nasal capsule lies between the mesethmoid and the anterolateral process), and against which Io 1 lies. Note the position of the supraorbital over the anterior part of the orbit.

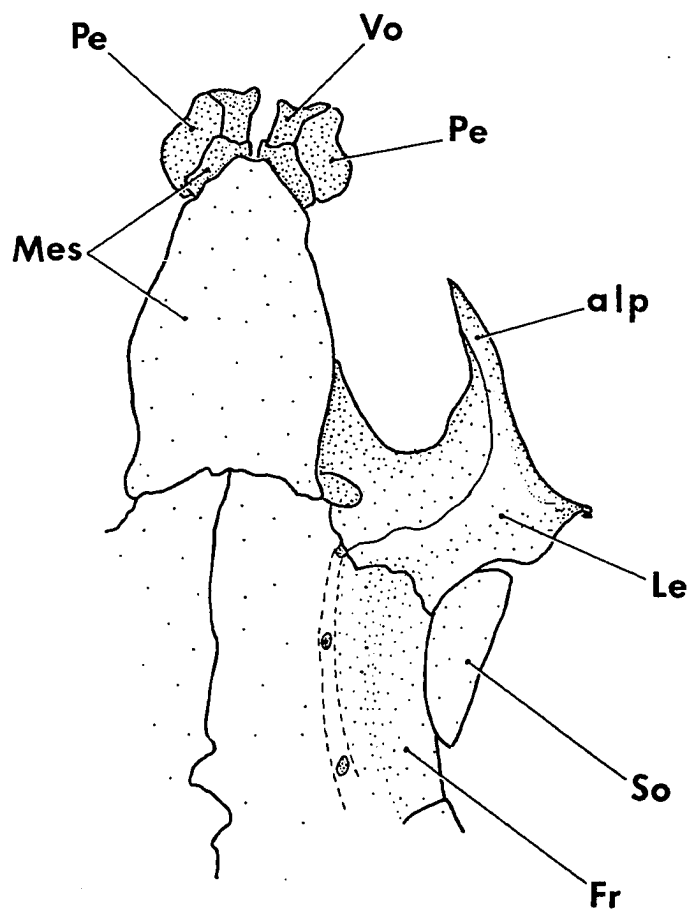


Figure 53

Fig. 54A,B. Dorsal (A; anterior to the top of the page) and lateral (B; anterior to the right) views of the ethmoid region of Minytrema melanops AMNH 22208SW. Catostomid lateral ethmoids possess an anterolateral process like gyri-nocheilids. It shelters the nasal capsule and Io 1 abuts it. Again, note the position of the supraorbital.

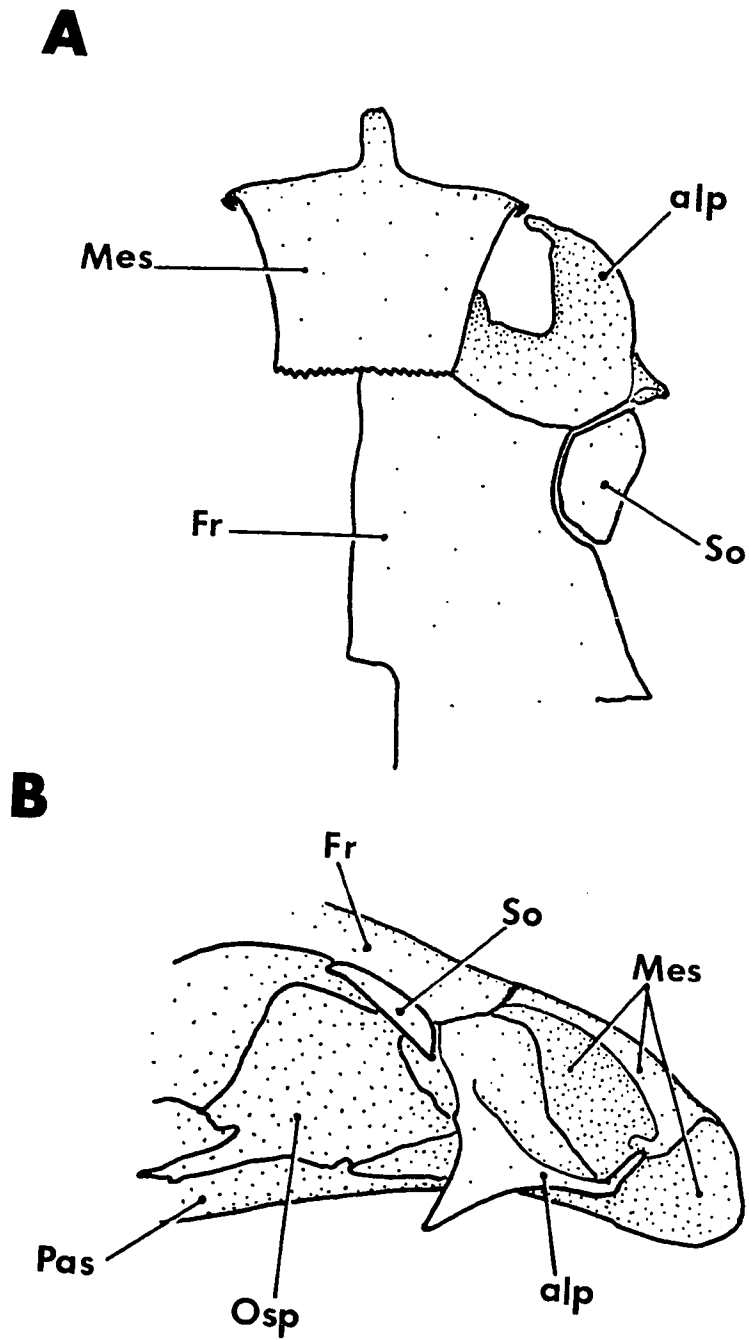
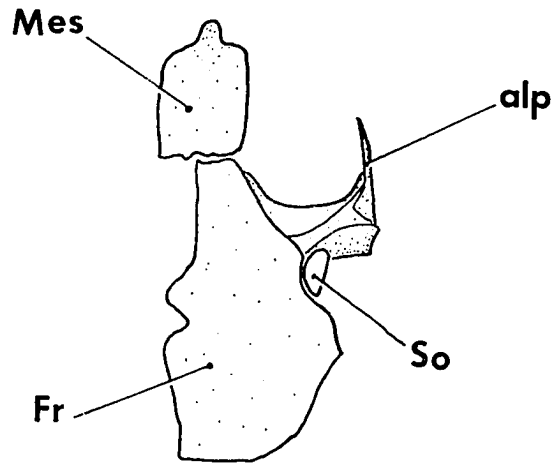


Figure 54

Fig. 55A,B. Dorsal view of the right side ethmoid region of: A. Homaloptera orthogoniata AMNH 77899, and B. Noemacheilus barbatulus AMNH 37608; anterior to the top of the page. Both possess an anterolateral process on their lateral ethmoids.

A



B

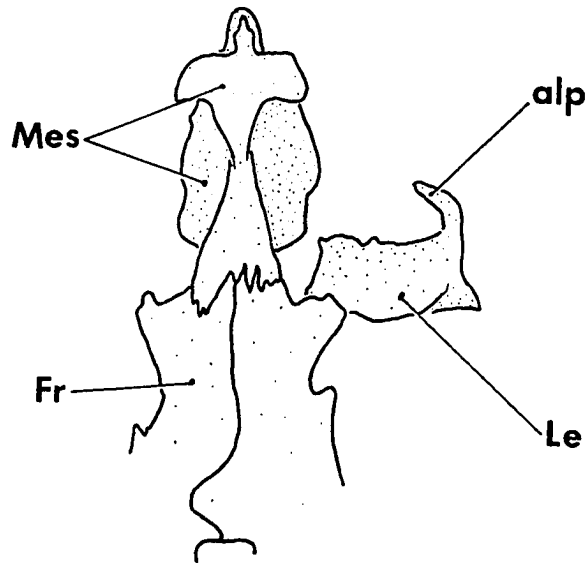
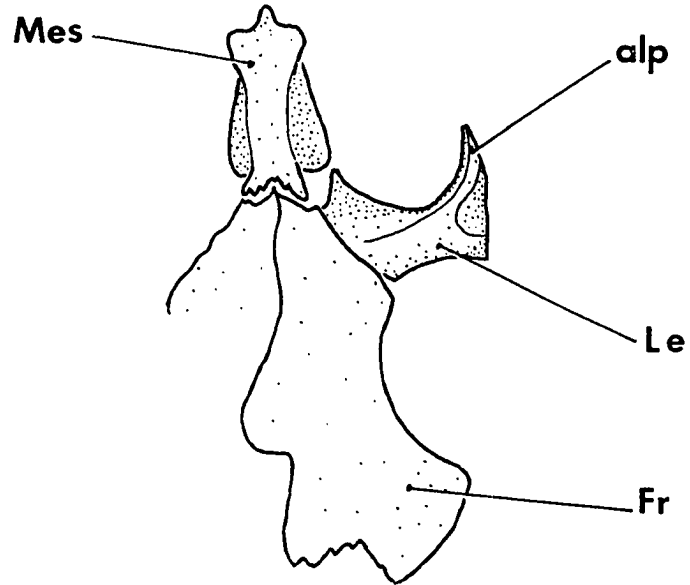


Figure 55A,B

Fig. 55C,D. Dorsal (C; anterior to the top of the page) and lateral (B; anterior to the left) of the ethmoid region of Noemacheilus posteroventralis AMNH 29706. All homalopterids possess an anterolateral process and in lateral view that of N. posteroventralis is a substantial plate-like element of the nasal region.

C



D

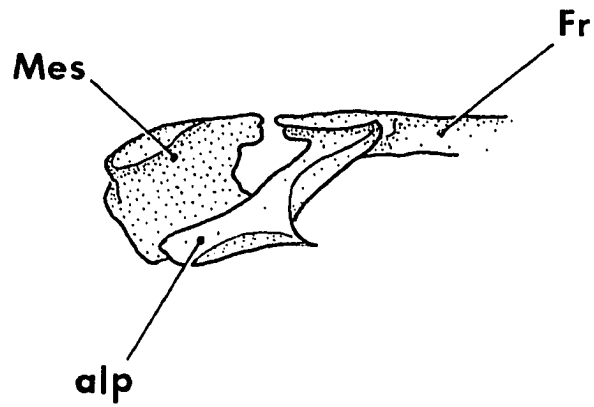


Figure 55C,D

Fig. 56. Dorsal view of the anterior of the cranium of Cobitis taenia AMNH 20366; anterior to the top of the page. Cobitidine lateral ethmoids are modified into an erectile suborbital spine. Structures herein called nasal ribbons curve around the anterolateral region of the nasal area.

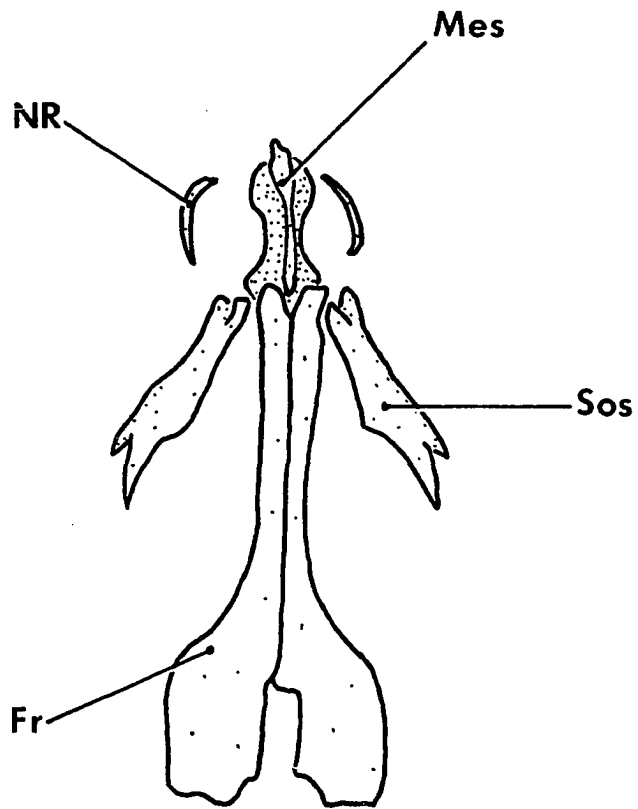


Figure 56

Fig. 57. Dorsal view of the ethmoid region of Leptobotia fasciata AMNH 10298SW; anterior to the top of the page. Its lateral ethmoids form prominent suborbital spines and its Io 1 is an elongate blade-like element stretching from the lateral ethmoid to far in front of the supraethmoid complex.

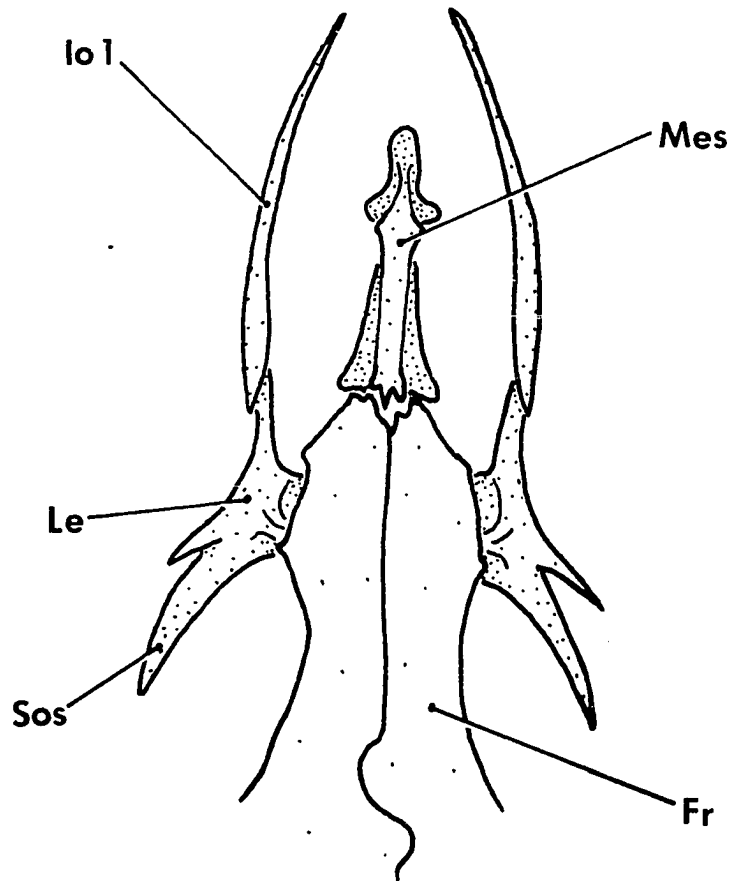


Figure 57

Fig. 58. Dorsal view of the ethmoid region of Vaillantella euepiptera AMNH 48938; anterior to the top of the page. Its lateral ethmoids are not suborbital spines and possess a long slender "anterolateral process". Associated with that anterolateral process is a peculiar Io 1. It is an ossified blade-like element in the region of the lateral ethmoid, a strand of fibrous connective tissue to the region behind the anterior part of the infraorbital laterosensory canal, and a weak sheet of ossification on the mesial side of the antermost portion of the IoC (the region marked by x's).

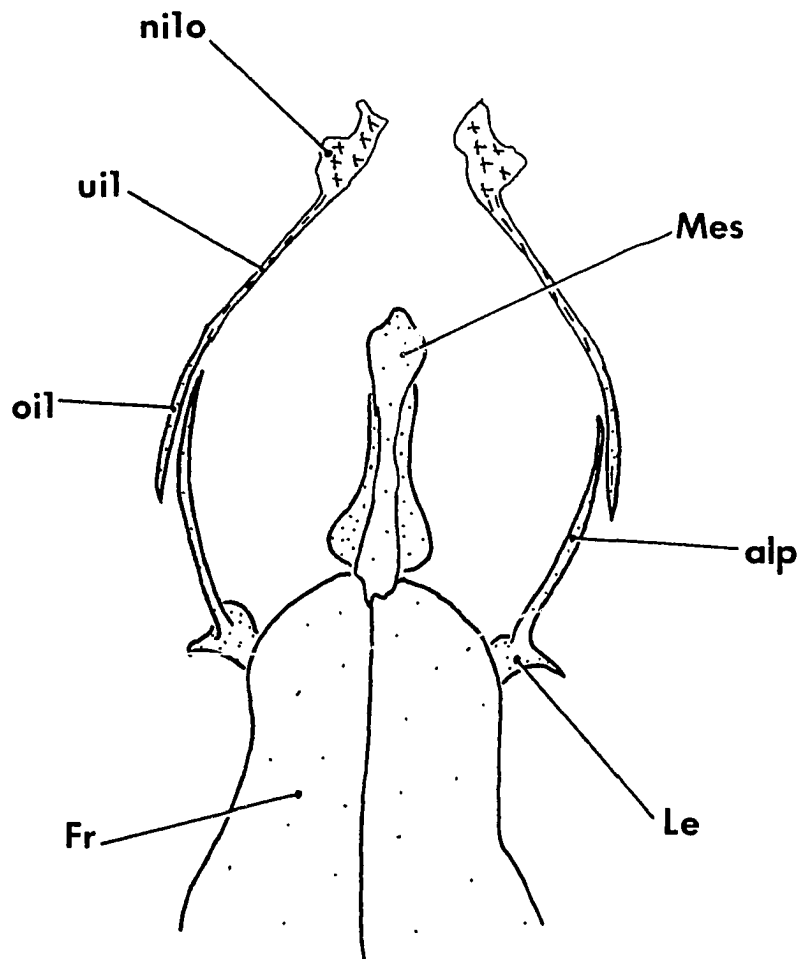


Figure 58

Fig. 59. Lateral view of the palatomaxillary area of Catostomus wigginsi AMNH 77911; anterior to the left. The prepalatine is a cartilaginous rod between the autopalatine and the maxilla, the 2nd pre-ethmoid is a similarly cartilaginous rod (sometimes mineralized) between the pre-ethmoid and the head of the dorsoposteriorly directed arm of the maxilla, and the mesioprepalatine is a cartilage between the kinethmoid and the palatine, lying medially to the prepalatine (hence its name) and dorsally to the second pre-ethmoid.

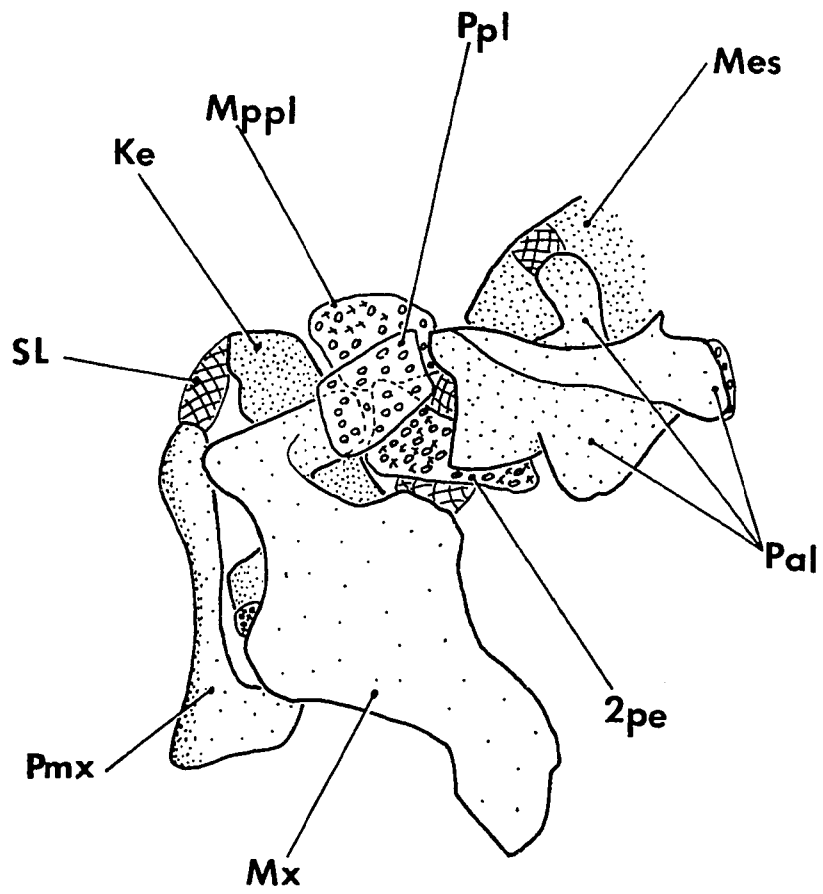


Figure 59

Fig. 60. Diagrammatic presentation of the interconnections of the cephalic laterosensory canals for a teleost fish Nelson (1969a) considered primitive, as well as the one herein considered primitive (interconnection of the suborbital and infraorbital canals).

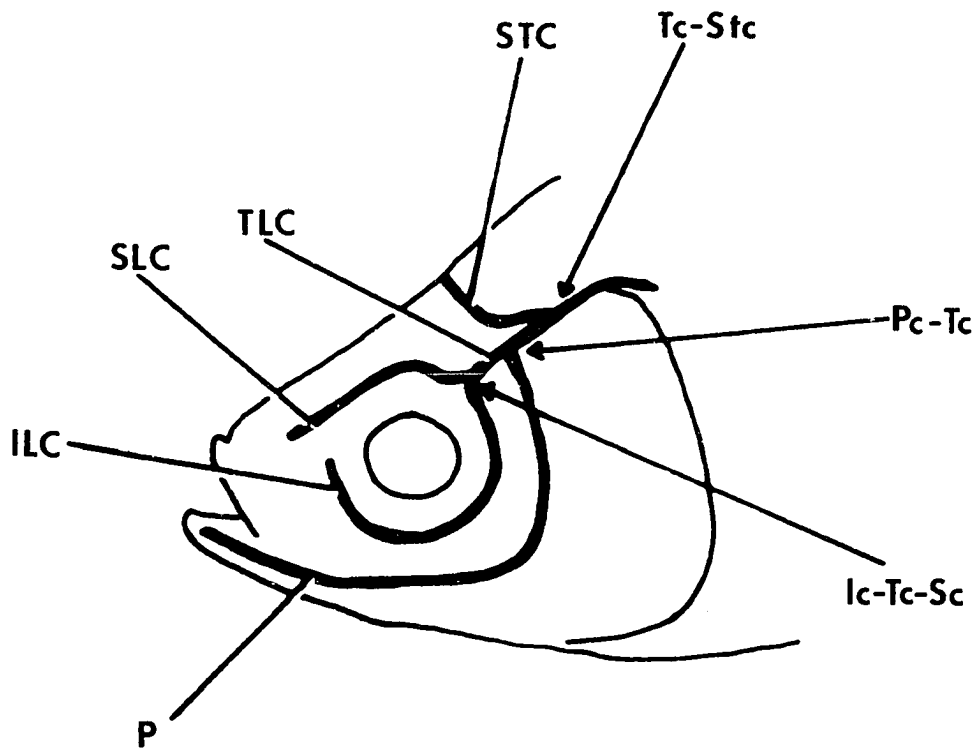


Figure 60

Fig. 61. Lateral view of the orbital region of Hemiculter leucisculus AMNH 10846; anterior to the left. Note there are only 5 infraorbital bones, the position of the supraorbital over the anterior part of the orbit, that the supraorbital and infraorbital canals are interconnected, and a suprapreoperculum fused to the dialator arm of the operculum.

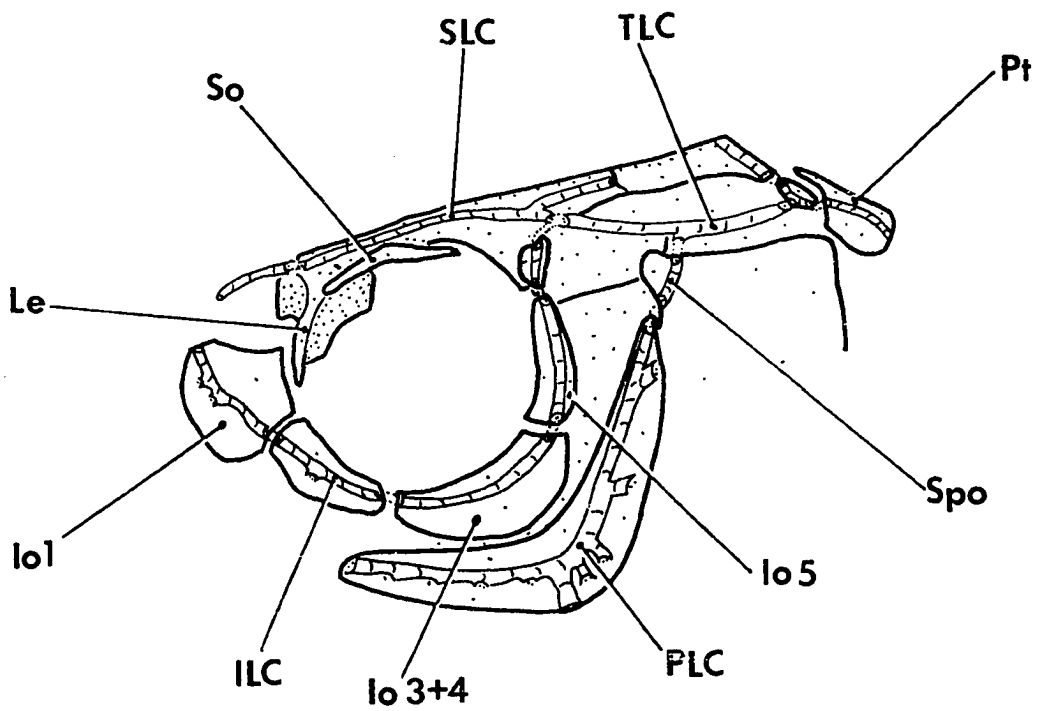


Figure 61

Fig. 62. Lateral view of the orbital region of Chelaethiops elongatus AMNH 6212; anterior to the left. Its supraorbital is posteriorly elongate, reaching backwards over the posterior part of the orbit. Note also the absence of a supraorbital-infraorbital canal connection.

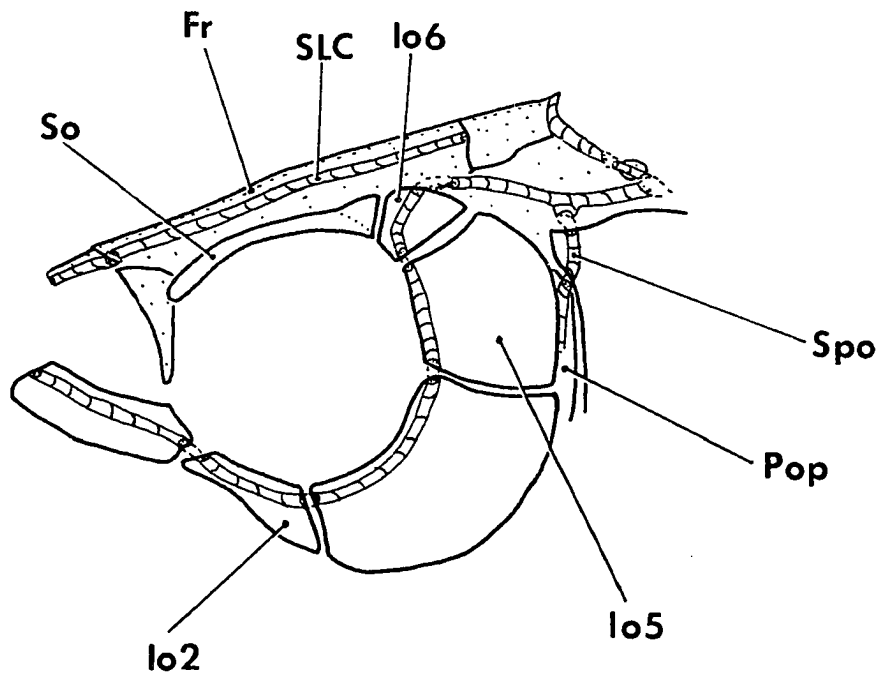


Figure 62

Fig. 63. Lateral view of the head of Gila ditaenia AMNH 27263; anterior to the left. The supraorbital and infraorbital canals do not interconnect and neither do the preopercular and temporal canals. The preopercular canal ends blindly before crossing the operculum, consequently a suprapreoperculum is absent.

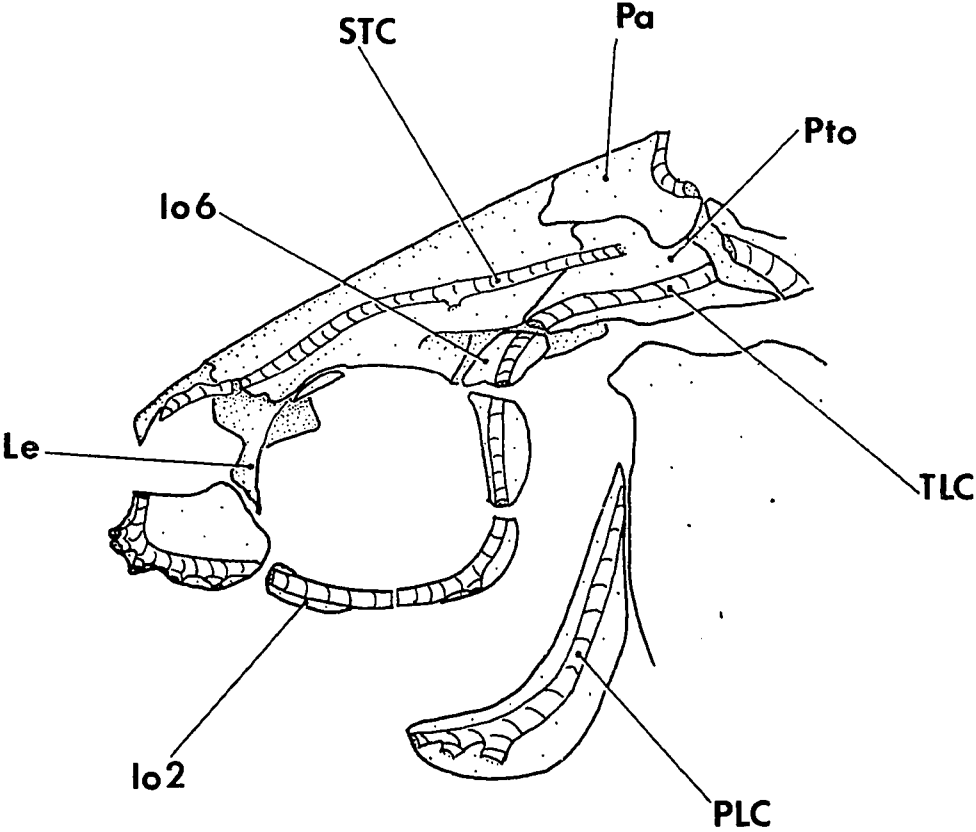


Figure 63

Fig. 64. Lateral view of the suborbital region of Gyrinocheilus aymonieri AMNH 77898; anterior to the left. Io 1 is the largest element of the infraorbital series and Io 2 and 3 are much reduced. The preopercular canal joins the infraorbital canal between what are possibly Io 4 and 5.

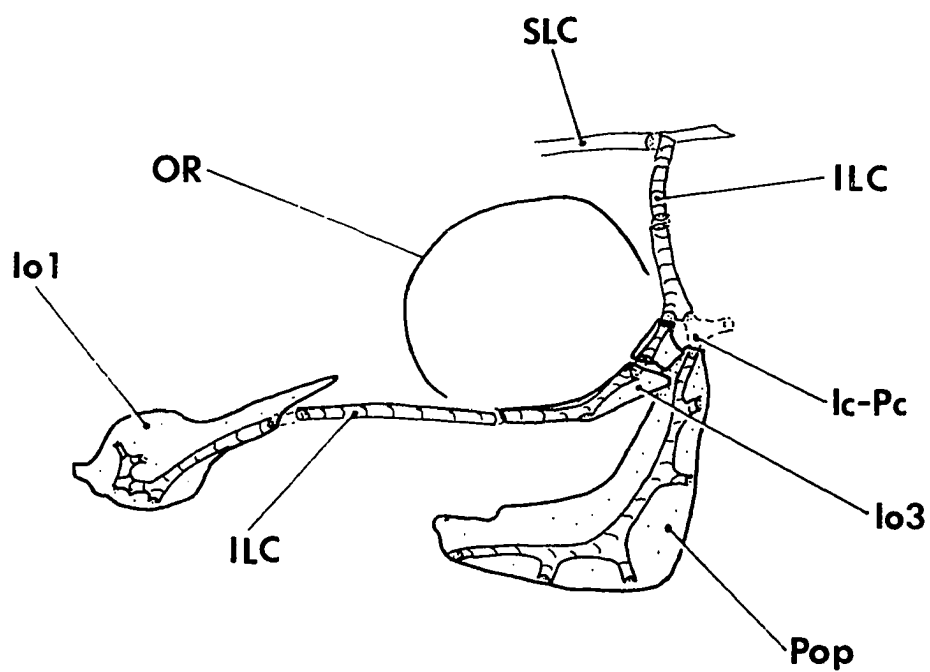
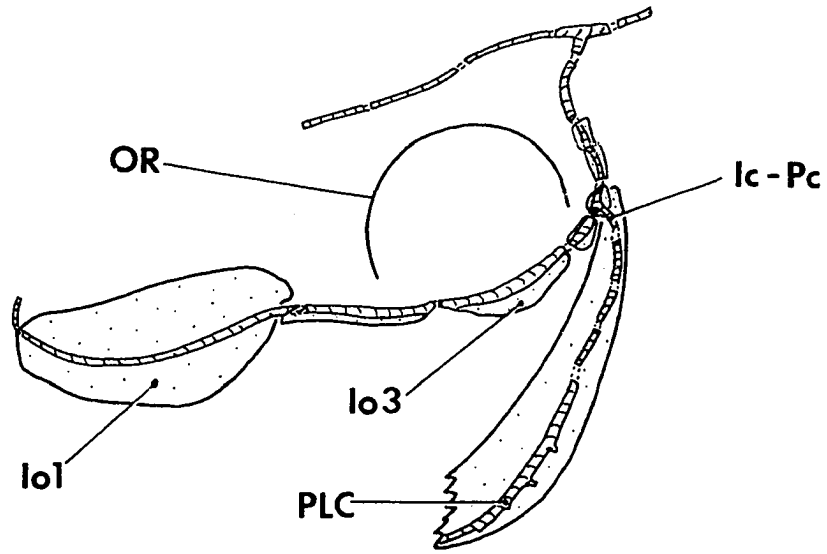


Figure 64

Fig. 65A,B. Lateral view of the suborbital region of:
A. Cycleptus elongatus AMNH uncat., and B. Ictiobus labiosus UMMZ 189565; anterior to the left. Io 1 of Cycleptus is large and Io 3 and 4 are much reduced. The preopercular canal joins the infraorbital canal. Dorsal to the PoC-IoC connections lies a series of "drainpipe" bones. Io 1-3 of Ictiobus are fairly conventional infraorbital bones. Posterior to Io 3 though, the circumorbital series of Ictiobus resembles that of Cycleptus.

A



B

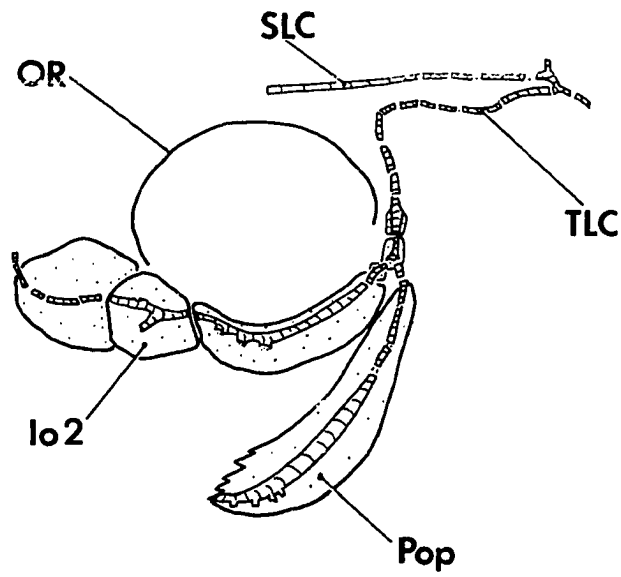
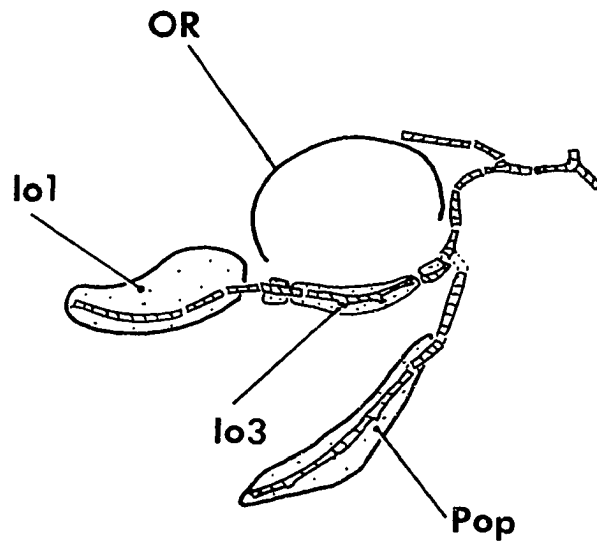


Figure 65A,B

Fig. 65C,D. Lateral view of the suborbital region of:
C. Hypentelium nigricans AMNH 49057, and D. Moxostoma
erythrurum AMNH 45976; anterior to the left. Io 1 is
the largest of the infraorbital series and the
preopercular canal joins the infraorbital canal.
Dorsal to that union lie the "drainpipe" bones.

C



D

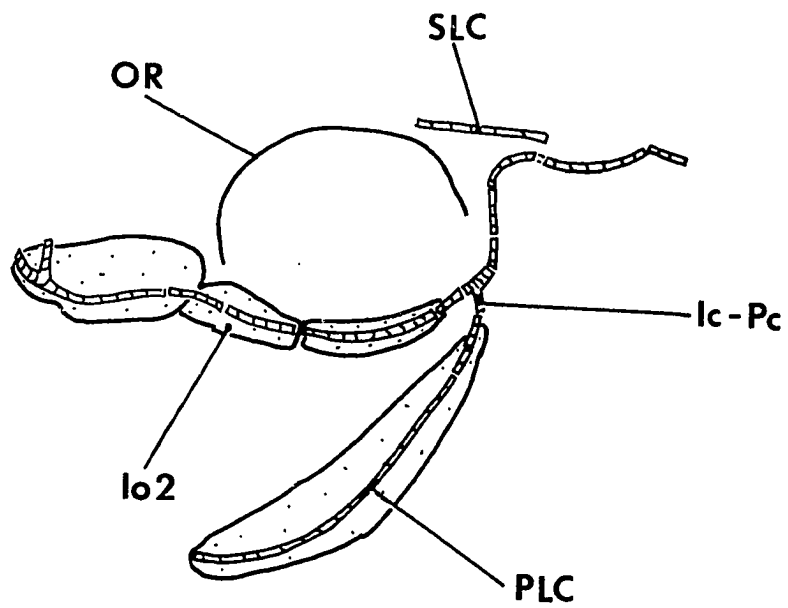


Figure 65C,D

Fig. 66. Diagrammatic representations of the patterns of cephalic laterosensory canal interconnections among catostomids. Only the infraorbital to temporal canal and the temporal to supratemporal canal interconnections are always made.

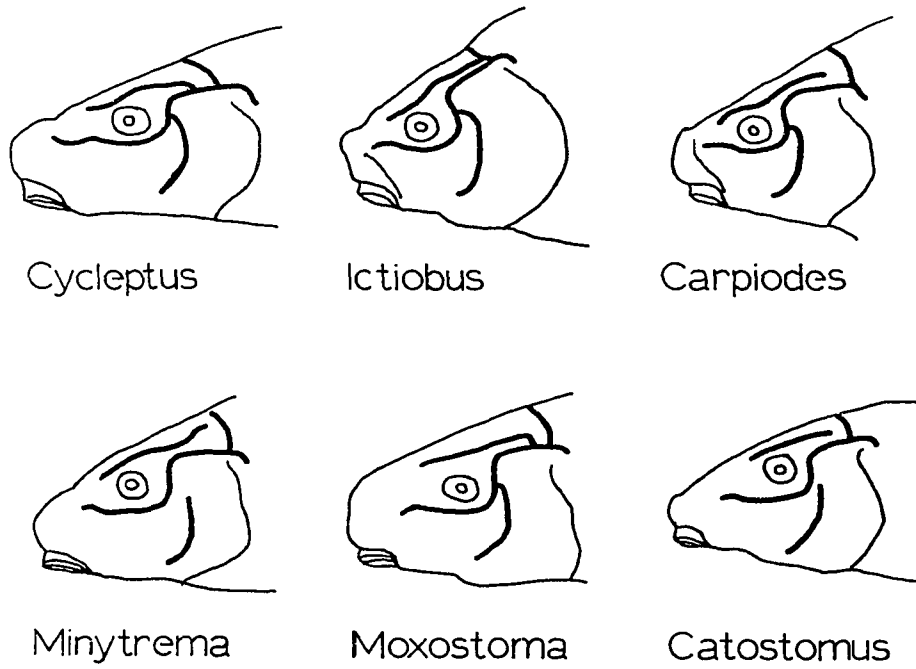


Figure 66

Fig. 67. Lateral view of the suborbital region of Botia macracantha AMNH 77904; anterior to the left. Io 1 is the only laminar element in the infraorbital series. Its posterior end is not ossified. Note the two long suprapreoperculars (neither fused to the operculum) and the preopercular-temporal canal interconnection.

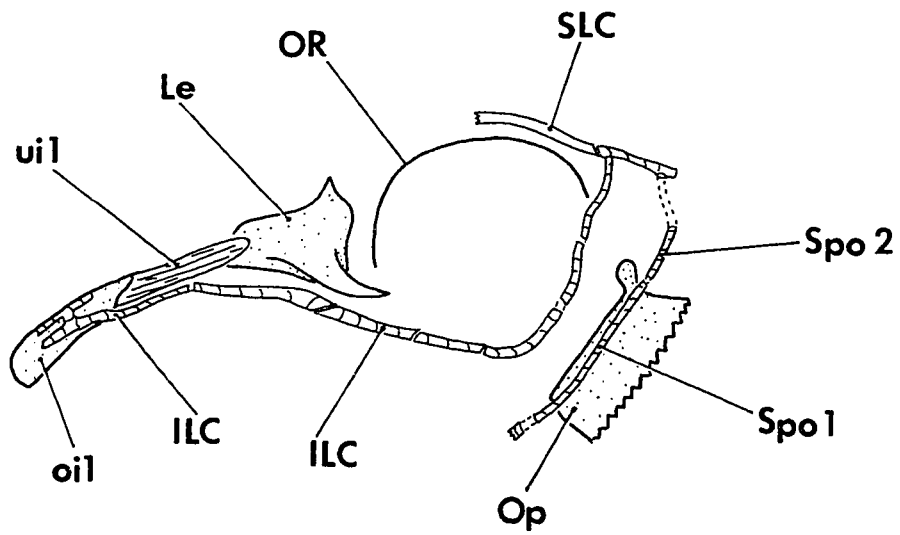


Figure 67

Fig. 68A,B. A. Dorsolateral view of the orbital region of Botia purpurea AMNH 10419SW (anterior to the left), and B. dorsal view of its ethmoid region (anterior to the top of the page). Io 1 is ossified only in the lateral ethmoid region. Its anterior end is unossified and associated with an ossification on the mesial side of the anterior end of the infraorbital laterosensory canal.

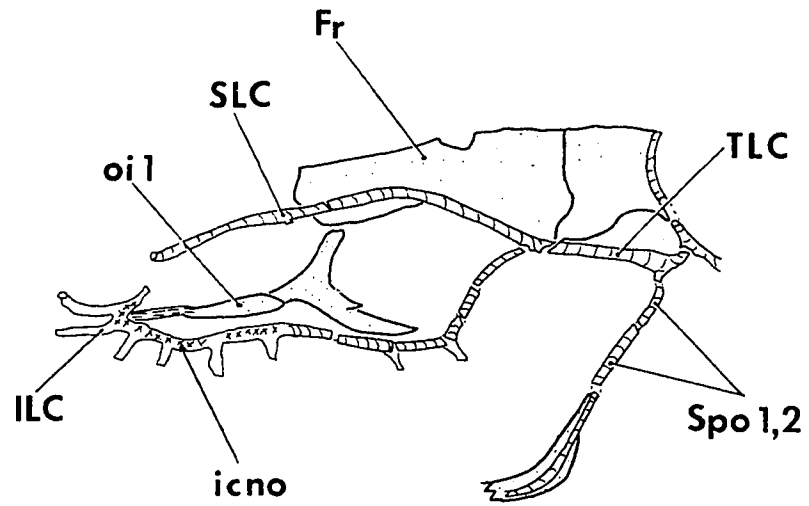
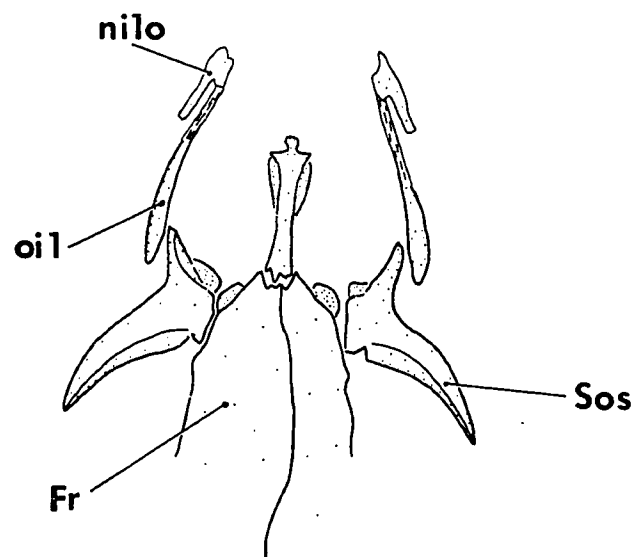
A**B**

Figure 68

Fig. 69. Lateral view of the orbital region of Leptobotia fasciata AMNH 10298SW; anterior to the left. Note Io 1 is not wholly ossified and that there are two suprapreoperculars, neither fused to the operculum.

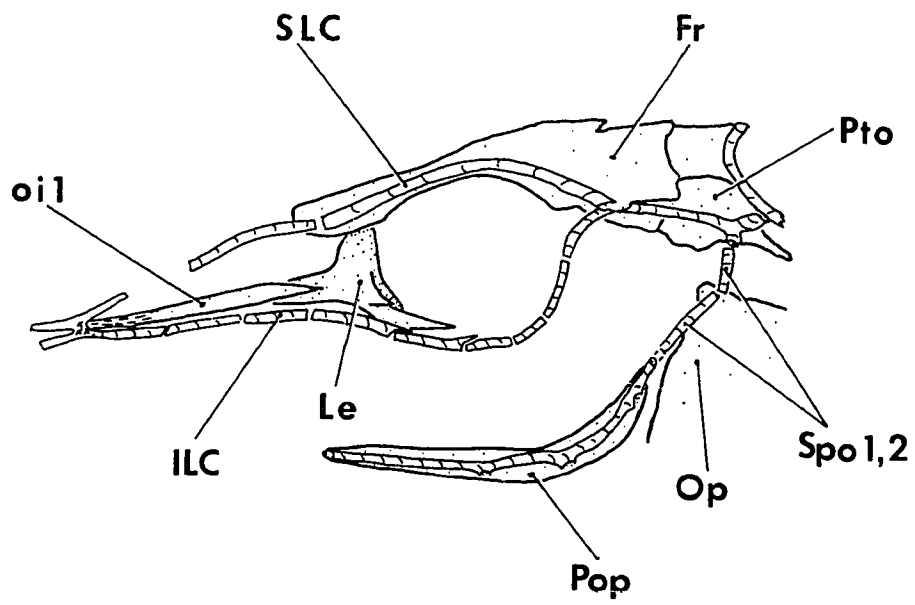


Figure 69

Fig. 70. Lateral view of the orbital region of Vaillantella euepiptera AMNH 48938; anterior to the left. Weak ossifications appear on the mesial side of the infraorbital canal in association with neuromasts.

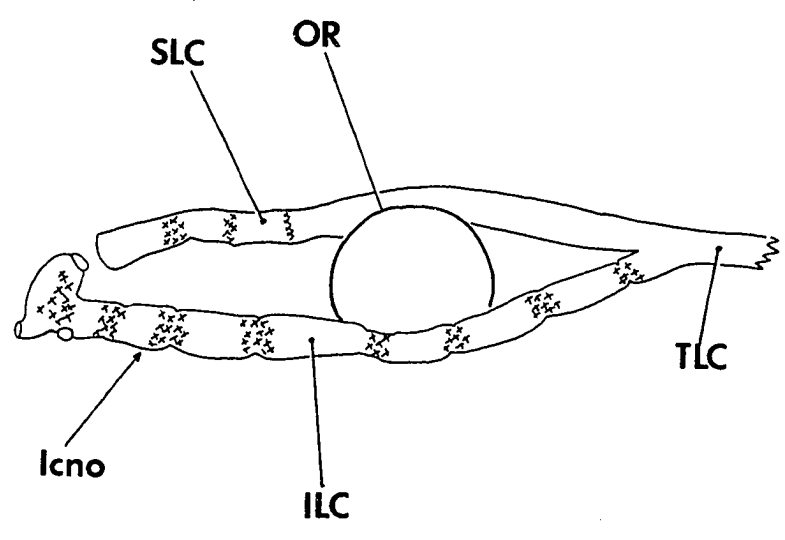


Figure 70

Fig. 71. Lateral view of Io 1 and the infraorbital laterosensory canal of Noemacheilus posteroventralis AMNH 10323; anterior to the left. The anterior part of Io I is unossified. The only other infraorbital ossifications are weakly ossified areas on the mesial side of the infraorbital laterosensory canal.

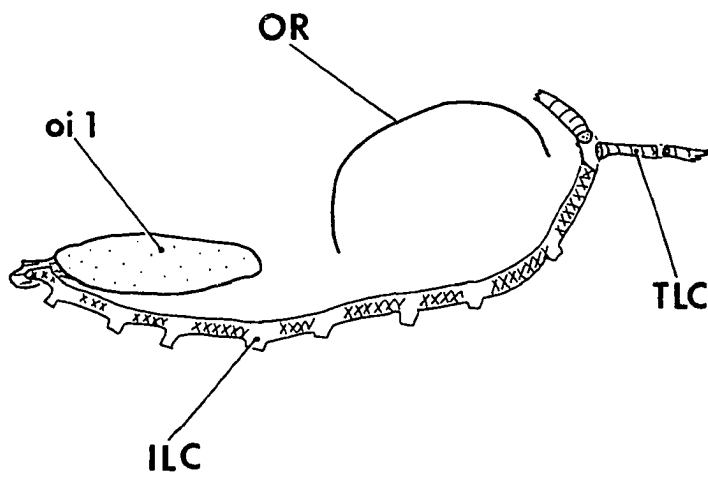


Figure 71

Fig. 72A,B. Lateral view of the suborbital region of:
A. Homaloptera amphisquamata AMNH 9257, and B.
Lepturichthys fimbriata AMNH 10335; anterior to the
left. Io 1, the only infraorbital element
identifiable, is not wholly ossified. Its unossified
anterior part is associated with the anterior part of
the infraorbital laterosensory canal.

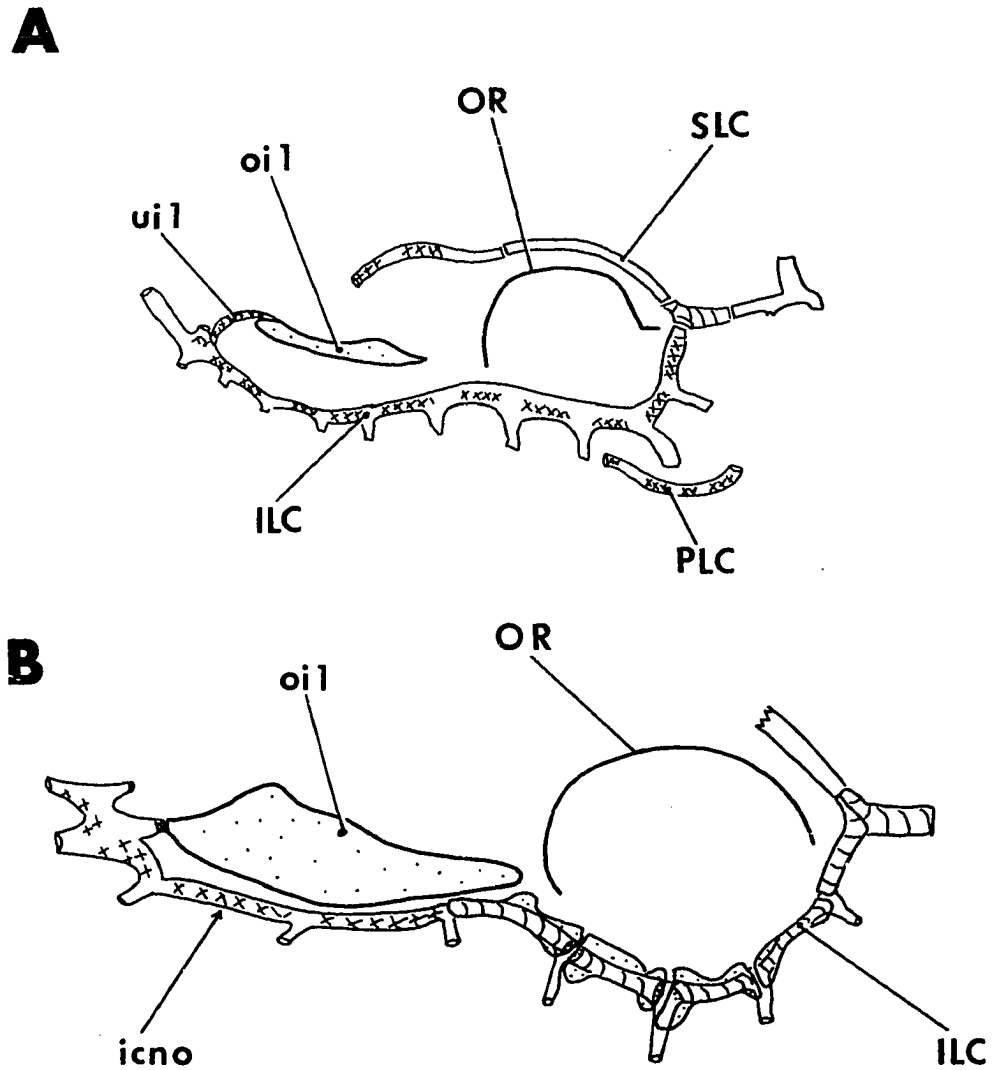


Figure 72

Fig. 73. Dorsal view of the ethmoid region of Homaloptera orthogoniata AMNH 77899; anterior to the top of the page. H. orthogoniata is illustrated to show the relationships of Io 1 to the anterior part of the IoC and to the lateral ethmoid.

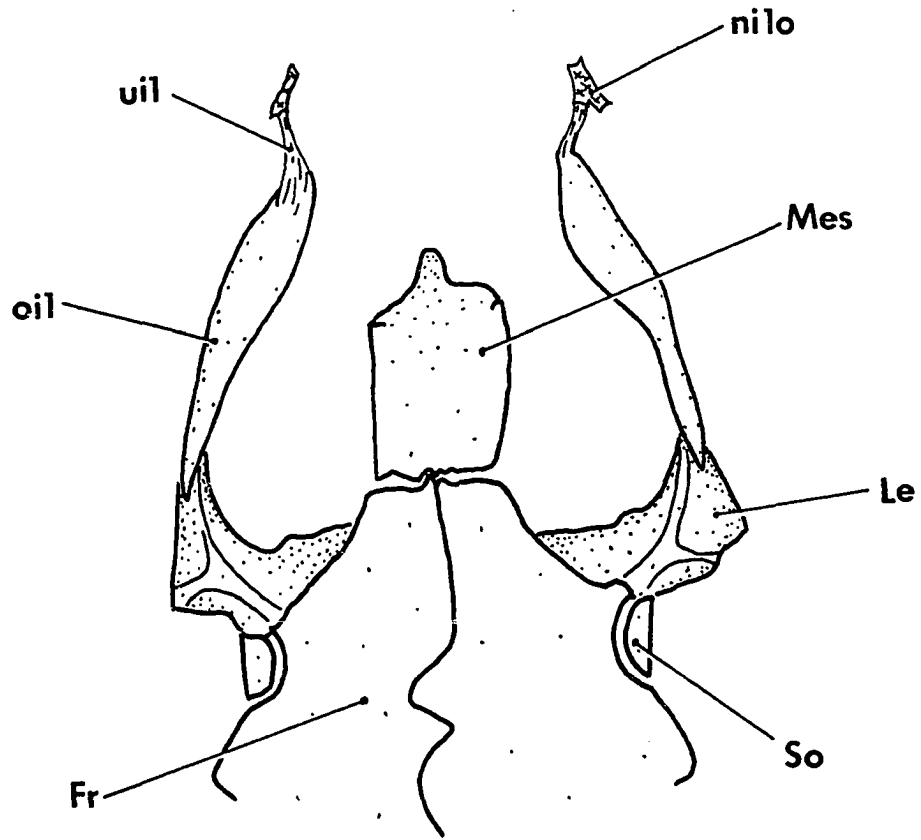


Figure 73

Fig. 74A,B. Dorsolateral view of the suborbital region of: A. Crossostoma davidi AMNH 10282, and B. Gastromyzon borneensis AMNH 77900; anterior to the left. Io 1 among gastromyzontins is not connected with the ILC and in many taxa is a huge element that extends in front of the upper jaw elements. The preopercular canal always joins the infraorbital canal among them and unlike other homalopterids, some laminar development of infraorbitals occurs posterior to the Io 1 region.

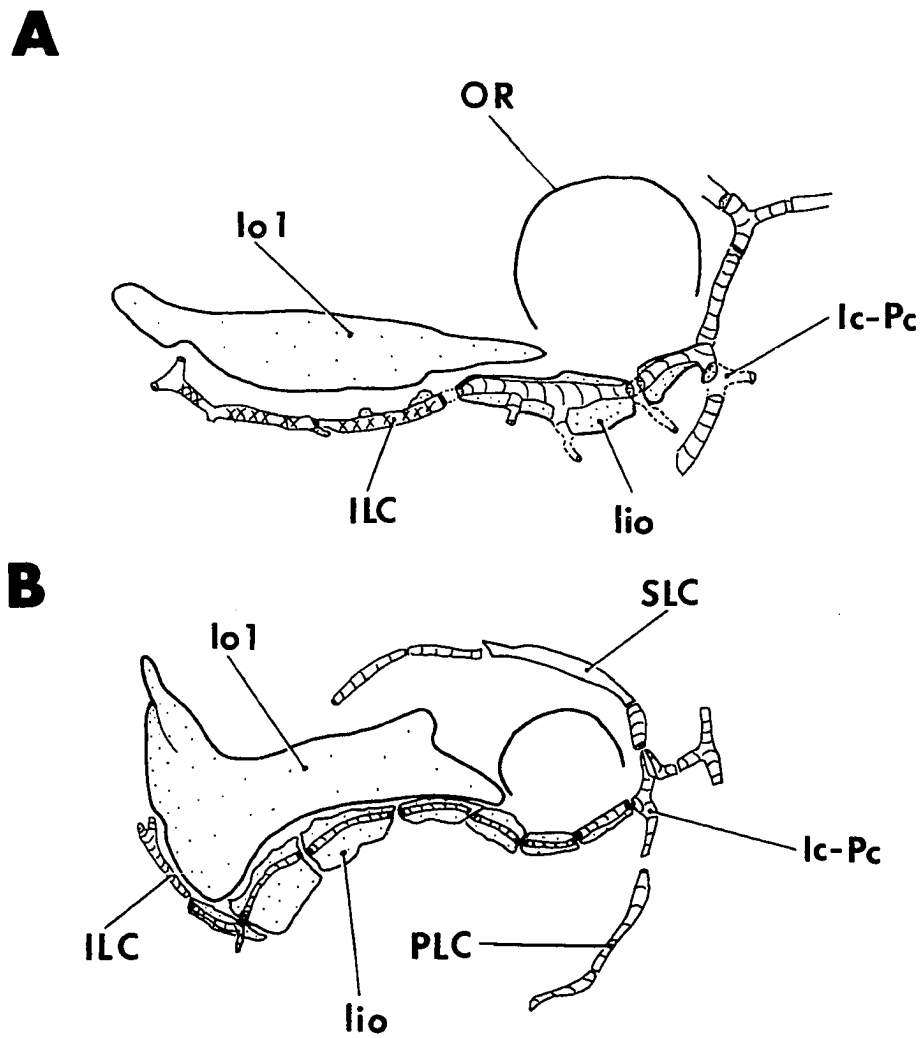


Figure 74

Fig. 75. Dorsal view of the anterior cranial skeleton of Acanthopsis choirorhynchos FMNH 68146; anterior to the top of the page. This was the only cobitidine found to possess any cephalic laterosensory canals (the supraorbital and preopercular canals are absent). No laminar ossifications are associated with the laterosensory canals that are present. Note the blade-like nasal ribbon ossifications.

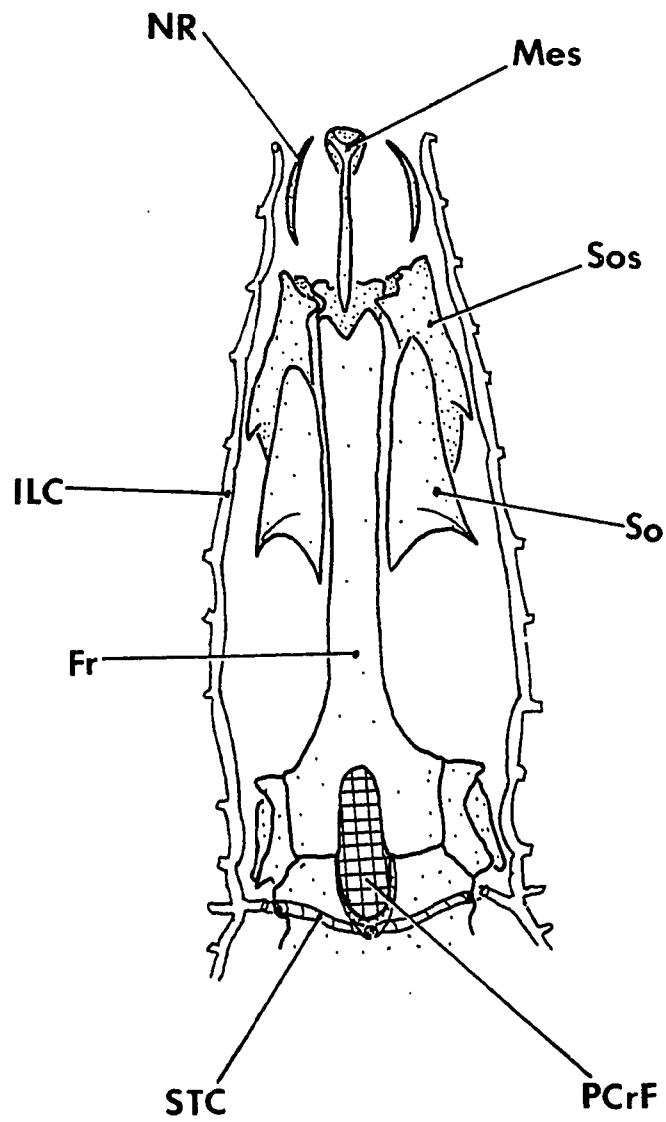


Figure 75

Fig. 76. Dorsal view of the ethmoid region of Misgurnus mizolepis AMNH 10362; anterior to the top of the page. Like all cobitidines except Acanthopsis (fig. C16), Misgurnus completely lacks laterosensory head canals. Nasal ribbons, interpreted as remnant Io 1's, are present around the nasal capsule, and are perforated by a foramen (see text; see also fig. 56 and 75).

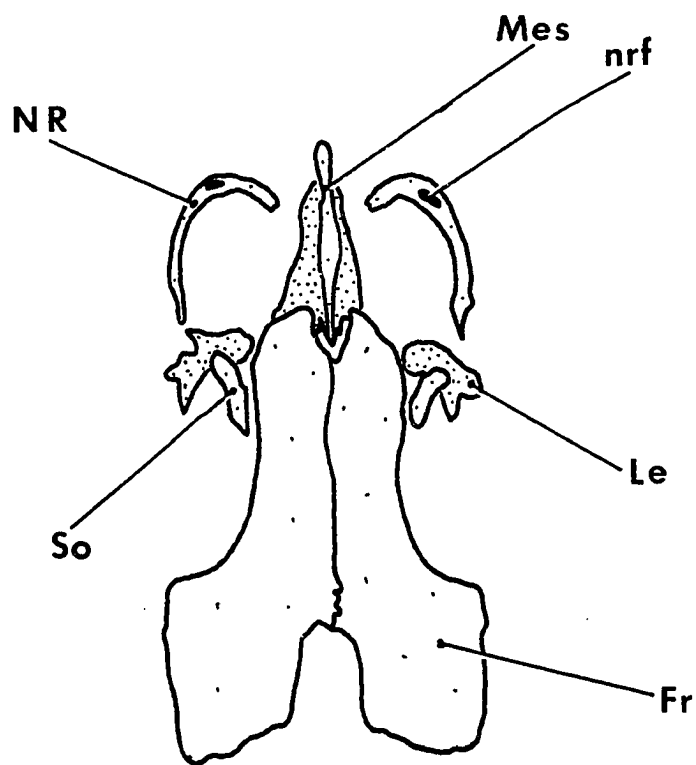


Figure 76

Fig. 77. Diagrammatic representation of the classification of the order Cypriniformes advocated herein with the character distribution, as determined by the branch-and-bound procedure of PAUP, noted on it (stars denote homoplasious features). The list of characters is as follows (for a full discussion of the characters see text): 1. absence of Ipb uncinatate processes; 2. absence of Eb I and II uncinatate processes; 3. absence of Ipb I; 4. consolidation of the Ipb series; 5. absence of Ipb IV; 6. medial tips of Eb I and II modified; 7. Eb I and IV largest of the Eb series; 8. anterior corner of the head of Eb I twisted ventrad; 9. overlap of Ipb II by Ipb III; 10. absence of Eb III uncinatate process; 11. EA flange on Eb IV; 12. directly medial orientation of Eb's; 13. absence of BhTp; 14. absence of Bb 1; 15. cartilaginous Hb III; 16. sublingual ossifications; 17. segmentation of C 3; 18. Bb 4 ossified; 19 Bb 4 keeled; 20. rectus communis I process on Hb I; 21. Y-shaped Bh; 22. T-shaped Bb 2; 23. single row of Cb V teeth; 24. transversus ventralis V process on Cb V; 25. anterolateral process of the lateral ethmoid; 26. suborbital spine; 27. 2nd pre-ethmoid; 28. prepalatine; 29. mesioprepalatine; 30. ossified palatomaxillary elements; 31. ILC-PLC connection; 32. Io 1 largest of the infraorbital series; 33. preopercular laterosensory canal free from the preoperculum; 34. reduction of Io 2 and 3; 35. enlarged pleural ribs (from Sawada, 1982); 36. gas bladder division (from Sawada, 1982); 37. Y-shaped tripus (from Sawada, 1982); 38. supraethmoid (from Sawada, 1982); 39. shoulder girdle (from Sawada, 1982); 40. transverse shelf on 2nd neural arch; and 41. subtemporal fossa discrete.

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