MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, THE UNIVERSITY OF MICHIGAN NO. 171

Phylogenetic Interrelationships of the Stomiid Fishes (Teleostei: Stomiiformes)

by
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Errata for Fink's "Phylogenetic Interrelationships of the Stomiid Fishes (Teleostei: Stomiiformes)" (Misc. Publ. Mus. Zool. Univ. Michigan, No. 171, 1985)

page 2, insert "*Trigonolampa* Regan and Trewavas, 1930" below "*Thysanactis* Regan and Trewavas, 1930"

page 10, line five in the Results section should show 8 trees rather than six.

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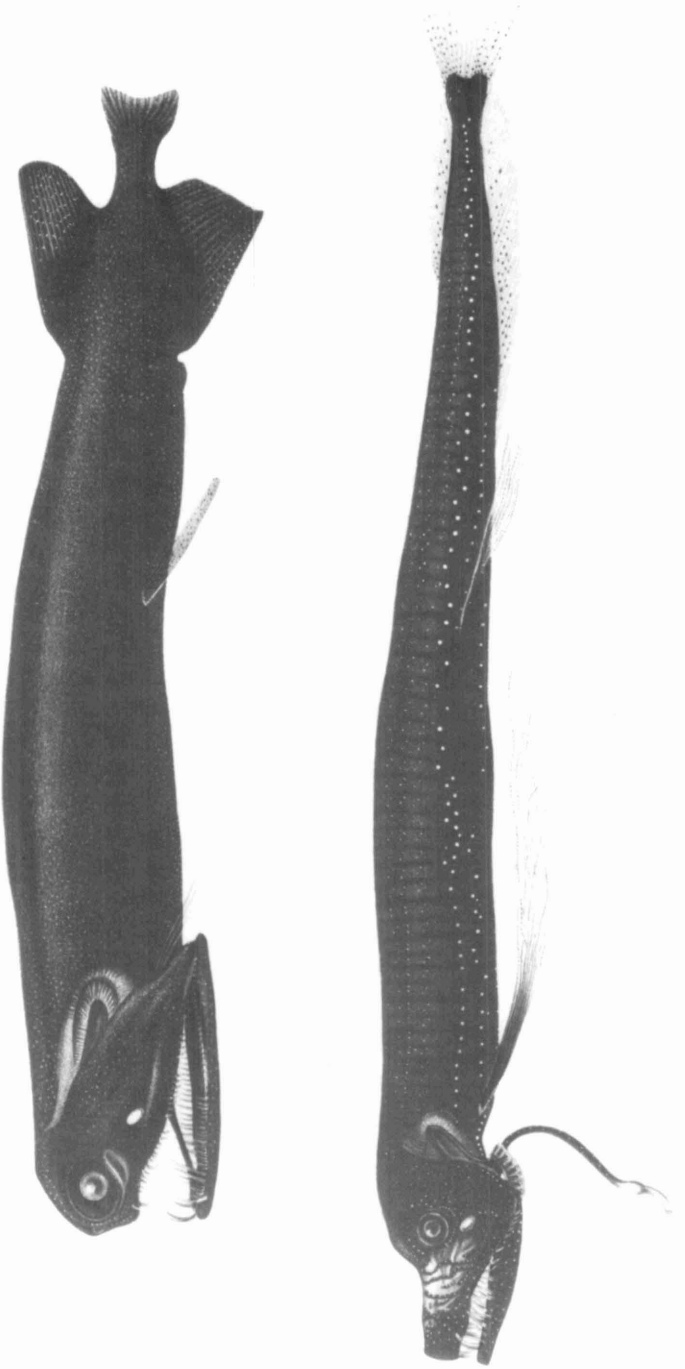

ABSTRACT

Fink, William L. 1985. Phylogenetic Interrelationships of the Stomiid Fishes (Teleostei: Stomiiformes). Misc. Publ. Mus. Zool. Univ. Michigan, 171:1–127, frontis., figs. 1–70. A phylogenetic analysis of the interrelationships of the twenty-five stomiiform genera formerly classified in the superfamily Stomiatoidea is presented. Previously comprising the families Astronesthidae, Chauliodontidae, Idiacanthidae, Malacosteidae, Melanostomiatidae, and Stomiidae, the genera are placed in a single, expanded Stomiidae. All of the traditionally recognized genera are found to be monophyletic, with the exception of *Stomias*, which is expanded to include *Macrostomias*. The character text includes detailed descriptions of stomiid morphology. Several alternative phylogenetic hypotheses are discussed. In the context of one or more of these hypotheses, patterns of character transformation are discussed, including the evolution of the pectoral girdle and its accessory light organs, placement of the vertical fins toward the posterior of the body, elaboration of the anterior and posterior portions of the pelvic girdle, increase and subsequent decrease of the number of radial elements of the pelvic girdles, and specializations of the head skeleton and anterior axial skeleton. The data matrix that was used to generate the phylogenetic hypotheses, and a brief discussion of fossils which have been assigned to the Stomiidae, are included in appendices.

Key words: *Stomiiformes, Astronesthidae, Chauliodontidae, Idiacanthidae, Malacosteidae, Melanostomiidae, Stomiidae, phylogenetics, character analysis.*

FRONTISPIECE: *Malacosteus* (top), *Eustomias* (bottom). From Zugmayer, 1911.

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INTRODUCTION

This paper is the third in a series designed to outline the phylogenetic relationships in the Stomiiformes, a large group of primarily mesopelagic fishes found in all of the world's oceans. The previous works include Weitzman's (1974) revision of the Sternoptychidae and classification of stomiiform subgroups at the "family" level and above, and Fink and Weitzman's (1982) study of *Diplophos* and diagnosis of the order. Herein, I consider the relationships of the twenty-six genera of stomiiform fishes known as dragonfishes, viperfishes, snaggletooths, and loosejaws. Traditionally these fishes have been placed in six families, Astronesthidae, Chauliodontidae, Idiacanthidae, Malacosteidae, Melanostomiidae, and Stomiidae, and most recently they were considered to comprise the superfamily Stomioidea (Weitzman, 1974). These generally elongate, darkly-pigmented fishes are characterized by numerous specializations, including presence of a mental barbel associated with the hyoid apparatus, lack of gill rakers in adults, and insertion on the PO (postorbital) photophore of a portion of the adductor mandibulae muscle. By inference from their morphology and numbers, it appears that these organisms are an important component of the oceanic vertebrate fauna.

Several recent workers (Greenwood, et al., 1966; Morrow, 1964a; Weitzman, 1974) have distributed the genera as follows:

ASTRONESTHIDAE

Astronesthes Richardson, 1844 (including *Cryptostomias* Gibbs and Weitzman, 1965; Gibbs, pers. comm.)
Borostomias Regan, 1908 (including *Diplolychnus* Regan and Trewavas, 1929; cf. Weitzman, 1967b)
Heterophotus Regan and Trewavas, 1929
Neonesthes Regan and Trewavas, 1929
Rhadinesthes Regan and Trewavas, 1929

CHAULIODONTIDAE

Chauliodus Bloch and Schneider, 1801

STOMIIDAE

Stomias Cuvier, 1817 (including *Macrostomias* Brauer, 1902; synonymized herein, based on Fink and Fink, in press).

MELANOSTOMIIDAE

Bathophilus Giglioli, in Giglioli and Issel, 1884
Chirostomias Regan and Trewavas, 1930

Echiostoma Lowe, 1843
Eustomias Vaillant, 1888
Flagellostomias Parr, 1927
Grammatostomias Goode and Bean, 1895
Leptostomias Gilbert, 1905
Melanostomias Brauer, 1902
Odontostomias Norman, 1930
Opostomias Günther, 1887
Pachystomias Günther, 1887
Photonectes Günther, 1887 (including *Photonectoides* Koefoed, 1956; Gibbs, pers. comm.)
Tactostoma Bolin, 1939
Thysanactis Regan and Trewavas, 1930

IDIACANTHIDAE

Idiacanthus Peters, 1877

MALACOSTEIDAE

Aristostomias Zugmayer, 1913
Malacosteus Ayres, 1848
Photostomias Collett, 1889 (including *Ultimostomias* Beebe, 1933; Goodyear, 1980)

The generic synonyms listed above are changes made since the review of Gibbs (1964a) and Morrow and Gibbs (1964). *Bathysphaera* Beebe (1932) is not discussed; no specimens have been captured, and there is the strong possibility that the description is based on misobservations (see Hubbs, 1935; Morrow and Gibbs, 1964).

It is my conclusion that the family names as used above are neither informative about relationships nor useful as indicators of gradal morphology and should be replaced. Use of most of these names would result in patently non-monophyletic taxa. For example, Idiacanthidae for *Idiacanthus* and Malacosteidae for *Aristostomias*, *Malacosteus*, and *Photostomias*, renders the large Melanostomiidae paraphyletic. Retention of the names at the family level would require a host of nomenclatural changes, including elevation of many genera to family rank; this does not seem a useful alternative, considering the need for a relatively stable nomenclature. To preserve as much of the traditional (generic) ranking order as possible, all of the above recognized genera are placed in the Stomiidae. A perusal of Regan and Trewavas's (1929, 1930) work will show that I am simply expanding their concept of the Stomiidae. One genus, *Macrostomias*, has been eliminated since to maintain it would render *Stomias* paraphyletic (Fink and Fink, in press). All other stomiid genera have been found to be monophyletic.

In order to leave this work as open to criticism as possible, I have tried to be as explicit about the characters and character polarities as I can. Additionally, the data matrix upon which the computer-aided analyses were based is in Appendix 1. This will assist other workers in understanding my interpretations of the data, but they are encouraged to examine the fishes and reinterpret and recode the characters as they see fit. I have no illusions that this work is anything but a beginning in unravelling stomiid interrelationships. Much work remains to be done at the intrageneric level, especially within *Eustomias* and *Photonectes*, and I hope that the hypotheses presented herein will be an aid to an understanding of relationships within those, and other, genera.

HISTORY OF CLASSIFICATION OF THE STOMIIDAE

There have been few analyses of relationships of stomiiforms using explicitly phylogenetic methods. In spite of this, it is useful to review past concepts of relationships in the group, however formulated, both to put the present study in historical perspective and to facilitate comparisons between my conclusions and those of earlier authors. I will concentrate here on works that dealt with stomiids as recognized herein but will include comments on groupings of other stomiiforms (and other teleosts) as necessary for clarity. In much of the text that follows I use taxonomic names as they were used by the authors under discussion. A history of classification of sternoptychids is available in Weitzman (1974).

Early classifications of stomiids were rather idiosyncratic, as was much of fish classification during the 19th and early 20th centuries. As new taxa were described, they were sometimes placed "near" other, already recognized, stomiiforms and sometimes not, illustrating the problems these morphologically diverse fishes presented for the systematic methods of the day. For example, Gill (1872) placed the three (then recognized) stomiiform families sequentially in his family list, but later (1893) placed the Ipnopidae between the Stomiatidae and Malacosteidae, also listing the Alepisauridae and Paralepidae between Idiacanthidae and Sternoptychidae.

Brauer (1906) was the first to place the stomiiform families into an arrangement close to that recognized in the most recent revision (Weitzman, 1974). Brauer placed the stomiiform genera in a continuous list, uninterrupted by genera now placed in non-stomiiform families. Brauer's classification is presumably based in part on work he published in 1908 on the histology of photophores of deep-sea fishes; the diagnoses in the 1906 paper include some photophore data, but not the more complete descriptions found in the later publication. Brauer seemed to grasp the importance of photophore structure in stomiiform classification, but he did not analyze it explicitly as a systematic character. It remained for Regan and Trewavas (1929) to utilize photophore structure in diagnosing phylogenetic groups.

Regan (1923) published the first classification of stomiiforms based primarily on skeletal characters. He defined the suborder based on its possession of photophores and divided it into two major groups, one consisting of the Gonostomatidae (in which he included some genera placed by Weitzman [1974] in the Photichthyidae) and Sternoptychidae, the other comprising the Astronesthidae, Chauliodontidae, Stomiatidae (including *Idiacanthus*) and Malacosteidae (*Malacosteus*, *Photostomias*, and *Aristostomias*). Regan considered the Gonostomatidae and Astronesthidae to be the primitive families of their respective subgroups. Many of the characters Regan used in his key to the families that I now place in the Stomiidae were not observed accurately or are primitive at that level, but the Chauliodontidae, Stomiatidae, and Malacosteidae were each recognized by at least one apparently apomorphic character.

Shortly after Regan's work, Parr (1927, 1930) proposed a classification of the stomiiforms which differed radically in concept from previous classifications. In his 1927 paper, Parr suggested that the Astronesthidae, Melanostomiatidae (Stomiatidae of Regan and Trewavas without *Stomias* and *Macrostomias*), and Idiacanthidae be considered as suborder Gymnophotodermi, of the Isospondyli, based primarily on their lack of scales and "shortness of the tail" (=shortness of the caudal peduncle). In 1930, Parr continued his reclassification, partly in response to the work of Regan and Trewavas (1930 see below). Stomiatidae (*Stomias* and *Macrostomias*) and, provisionally, the Chauliodontidae were placed in suborder Lepidophotodermi, and Gonostomatidae and Sternoptychidae were placed in the suborder Heterophotodermi. The Lepidophotodermi was defined by Parr's repetition of a statement of Regan and Trewavas (1930) about *Stomias*, i.e., that scales are present and the premaxillae are free from the maxillae; the Heterophotodermi was not redefined. Parr agreed with Regan and Trewavas (1930) in placing *Idiacanthus* in the Melanostomiatidae.

Parr's earlier work is the first that attempted to examine relationships among the genera in the families he investigated. He noted the difficulties encountered historically in defining genera due to discovery of new species, which often overlapped older "generic" limits, and the rarity of specimens, which did not permit detailed anatomical studies. Parr considered *Astronesthes* (including *Borostomias*) to be the most primitive genus in the suborder Gymnophotodermi, but his discussion of relationships among the melanostomiatid genera is confused and his evaluation of genera as primitive or advanced often seems contradictory.

In 1929 and 1930, Regan and Trewavas published their research based on the great DANA collections. The 1929 paper is a revision of the Astronesthidae (to which they added the new genera *Heterophotus*, *Neonesthes*, and *Rhadinesthes*) and the Chauliodontidae. The authors did not accept the classification of Parr (1927), which was not discussed, and in fact made no major alterations in Regan's (1923) classification. Perhaps the most noteworthy aspects of the Regan and Trewavas publication are the expanded definition of the suborder (of Regan [1923]) and utilization of photophore histology in

defining groups. The histological study of Brauer (1908) is not specifically mentioned, except in reference to the "Döppelorgan," but presumably Regan realized the significance of Brauer's work and incorporated it into the classification. As previously noted, Brauer did not fully appreciate photophore structure as a systematic character, nor evidently, did Regan when he wrote his classification of 1923.

Based on photophore structure, Regan and Trewavas (1929) recognized two groupings within the stomioids, one consisting of the Gonostomatidae and Sternoptychidae and the other including the Astronesthidae, Chauliodontidae, and Stomiatidae. However, in the descriptions of the new genera mentioned above, Regan and Trewavas made no comparisons with other genera, and no interfamilial relationships were proposed or discussed.

In their 1930 paper on the families Stomiatidae and Malacosteidae, Regan and Trewavas again defined the various stomioid groups, for the most part repeating what they had written in 1929. The Stomiatidae was recognized as including "those stomiatoids in which the dorsal and anal fins end at a short distance from the caudal, and a membrane connects the lower jaw with the hyoid arch" (this included *Idiacanthus*). The Malacosteidae was considered an "offshoot" of the Stomiatidae, differing primarily in lacking a membrane between the lower jaw and hyoid arch. The 1930 paper was the most important publication on stomiiforms up to that time; the authors were the first to have large series of several species available for investigation of individual variation and for skeletal comparisons. Although clearing and staining techniques were not used, and the dissections sometimes proved inadequate for accurate illustrations, Regan and Trewavas presented generic groupings within their Stomiatidae which are close to those proposed herein. Relationships were included in an introductory section on structure and classification, where genera were listed in an order more or less reflecting relationships (no formal generic classification or phylogeny was given). Regan and Trewavas utilized primitive as well as specialized characters in proposing relationships, a method which led them to consider some genera, such as *Chirostomias* and *Trigonolampa*, to be related based solely on shared primitive characters.

Beebe and Crane (1939) were the first workers after Regan and Trewavas (1930) to discuss relationships within the stomioids. Their classification was essentially that of Parr (1927) at the family level and above, but that of Regan and Trewavas (1930) at the generic level. Beebe and Crane reached a number of conclusions. First, they accepted division of the stomioids into three groups (Parr, 1927), but ranked them at the superfamilial rather than subordinal level, so as to leave unaltered the relative rank of the entire group in the order Isospondyli. Second, they accepted Parr's Melanostomiatidae (excluding *Malacosteus*, *Aristostomias*, and *Photostomias* which they recognized as the Malacosteidae, following Regan and Trewavas [1930]). Based on Beebe (1934), they accepted Idiacanthidae (including only *Idiacanthus*) as separate from the Melanostomiatidae. Stomiatidae of Beebe and Crane consisted only of *Stomias* and *Macrostomias*. The authors generally agreed with

Regan and Trewavas (1930) in their generic groupings, but went further than the latter authors in proposing a phylogeny, summarized in their Figure 12. From a reading of the text and an examination of the "phylogenetic tree," it can be seen that the phylogeny proposed by Beebe and Crane is a mixture of genealogical and grade concepts. They saw groups of genera or families arising out of other groups of genera; for example, they regarded the members of the Astronesthidae as together possessing all the characters necessary to give rise to the Melanostomiatidae. At the conclusion of their discussion of generic relationships, Beebe and Crane make the first attempt to correlate the functional anatomy and relationships of melanostomiatids.

The next major coverage of stomiiforms was that of Morrow (1964a–d), Morrow and Gibbs (1964) and Gibbs (1964a,b). Those publications were intended primarily for identification purposes and little discussion of relationships was presented. The various families and genera were accepted for historical reasons; the only comments about acceptance of any higher category were those of Gibbs (1964b) in explaining why *Idiacanthus* was kept in a family separate from the Melanostomiatidae.

Bassot (1966) provided stimulating new information on stomiiform photophore histology. He found a basic photophore structure to be shared by all members of the order, but modified into three types, which he labeled alpha, beta, and gamma. Type alpha photophores are found in *Maurolicus*, *Argyropelecus*, and *Sternoptyx* (all now in the Sternoptychidae, *sensu* Weitzman, 1974). Beta photophores are found in *Gonostoma*, *Cyclothone*, *Bonapartia*, and *Diplophos* (all in the Gonostomatidae of Weitzman, 1974). Gamma photophores are characteristic of *Vinciguerria*, *Ichthyococcus* (both now in Weitzman's [1974] Photichthyidae), the Chauliodontidae, and the Stomiatidae (all of these taxa now in the Photichthya of Weitzman).

Greenwood, *et al.* (1966) dismantled the order Isospondyli and placed its members in a number of other groups to reflect proposed evolutionary lineages rather than grade classification. The Stomiatoidei was placed as a suborder in the Salmoniformes, and the families accepted were Gonostomatidae, Sternoptychidae, Astronesthidae, Melanostomiatidae, Malacosteidae, Chauliodontidae, Stomiatidae, and Idiacanthidae. No higher taxonomic groups within the suborder were proposed, and the arrangement of families was made without comment.

Weitzman (1967a) was concerned primarily with relationships and the origin of the stomiiforms rather than with family level classification. In addition, he included valuable anatomical descriptions and illustrations. Weitzman (1967b) presented the first detailed discussion of the relationships among the genera in the Astronesthidae and of these to other stomioids. Using osteological data almost exclusively, Weitzman found difficulty in considering the Astronesthidae as a group of "closely related" genera but made no attempt at dismantling the family pending more detailed analyses of other genera. Weitzman (1967b) found that *Astronesthes* and *Borostomias* appear to be closely related, that *Heterophotus* and *Rhadinesthes*

may be closely related, and that *Neonesthes* appears close to no other genus. In his discussion of possible relatives of the astronesthid genera among other stomioids, Weitzman proposed that all were related to *Polymetme* and shared a common ancestor with that genus. Weitzman also considered the Melanostomiatidae to be descendants of an astronesthid ancestor more primitive than any living species and proposed that both the Malacosteidae and Idiacanthidae arose from genera within the Melanostomiatidae. He considered the Stomiatidae and Chauliodontidae to be related and to have arisen from a very primitive astronesthid-like ancestor.

Bassot's (1970) work, although without a discussion of relationships within the stomioids, did provide further evidence regarding relationships within the suborder. The paper is an elaboration of his earlier work (Bassot, 1966); its significance is discussed by Weitzman (1974).

Weitzman (1974) is the largest recent work on relationships within the stomiids. Although he was concerned primarily with the Sternoptychidae, he also proposed a new classification of the suborder at the familial level. His most important and radical departure from previous classifications was the fission of the Gonostomatidae into two groups, each forming a primitive sister group (at the family level) in separate infraorders. This separation was done to explicitly recognize hypothesized evolutionary lineages within the larger group; thus primitive members of their lineages were placed with the more derived members of the lineage, rather than being left in a grade-level classification in a single, paraphyletic family. (Evidence found during the current study and in the preparation of Fink and Weitzman (1982) has cast doubt on the naturalness of both families and Weitzman is now working on the interrelationships of the genera.) Relevant to the issues discussed in this paper is the grouping together, as superfamily Stomiatoidea, those families recognized herein as Stomiidae. Weitzman stated that "the relationships of these groups need considerable clarification and probably alteration," noting that "parts of the Astronesthidae, the Melanostomiatidae, and the Chauliodontidae might eventually be included in an expanded Stomiatidae," the course opted for herein. He also discussed previous groupings of the included families and genera.

Fink and Weitzman (1982) considered the monophyly of the stomiiforms and their relationships with other teleosts. They also provided a description of a morphologically primitive member of the group (*Diplophos*), in part for comparison with the taxa discussed herein. Fink and Weitzman found that the Stomiiformes is monophyletic and diagnosed it with eight synapomorphic characters. They agreed with Rosen (1973) that the group is the sister group of the Eurypterygii and should be removed from the Protacanthopterygii (= Salmoniformes) and placed as a separate order within the Neoteleostei.

Fink (1984) published a brief summary of his work to that date on the stomiids. There are few differences between his conclusions and those presented herein. Ahlstrom, Richards, and Weitzman (1984) reviewed the problems of relationships among the more primitive stomiiform genera,

with special emphasis on larval traits. Their conclusions are consistent with Weitzman's dismantling of the Gonostomatidae. Kawaguchi and Moser (1984) examined larval stomiids and presented a large amount of data that may contribute to an unraveling of stomiid relationships. Although the data from their study are not included herein, it is apparent that the degree of homoplasy found in adult stomiids should be expected in the larvae as well.

A number of fossil specimens have been referred to the Stomiidae. In most cases, the placement of those specimens in the group is not supportable, and in no case does a fossil taxon alter concepts of the modern genera. For further information, see Appendix 2.

METHODS

Many species of stomiids are poorly known, often only from type material, and large series of most species are not available. For this reason it has not been possible to determine the range of variability within species and genera in the skeleton of these fishes. Add to this the fact that many of the available specimens are juveniles, and it becomes clear that some of the morphological details described and the hypotheses proposed in the current study may be especially subject to change and reinterpretation. An attempt has been made to select for study those species in each genus which, based on outgroup comparison, appear to be the most phylogenetically and morphologically primitive, but this has not always been possible. Current knowledge of relationships within most genera prevents secure hypotheses of what species may be most primitive. An attempt has been made to secure representatives of those groups where subgenera or subgroups have been recognized historically, except when the species in a given subgroup appear to be highly specialized morphologically, compared to members of other subgroups. There has been no attempt to study or clarify relationships below the "generic" level, but some comments on these lower levels are included when information was found that might guide other researchers. Material examined is listed in Appendix 3.

My discussions of anatomy are in some places at variance with reports of earlier workers. In most cases, these can be attributed to availability of specimens in better condition and of cleared and stained material, which greatly facilitates osteological observation. I have not attempted to go through the literature and specify what I consider errors, mostly because it would be tedious for both me and the reader and would be of considerable length. For primitive stomiids, much of this work has been done by Weitzman (1967b).

Selection of characters for this study began by an examination of previously published studies, with an eye to determining what morphological structures had been used in the past, what their variation was, and what phylogenetic (or other "relationship") hypotheses had been inferred from them. I then examined the fishes in detail, both to confirm the previous observations of morphology and to search for other features. I soon realized that there is a fairly large degree of incongruence among many of the features, whether chosen by myself or other workers. After this realization, structures were chosen as characters regardless of how their distribution met with preconceived notions of relationship, no matter how far off the mark they seemed. For example, the rugose frontal bones of *Echiostoma*, *Melanostomias*, and *Trigonolampa* were coded as a character, even though my intuition told me that these taxa did not constitute a monophyletic group (this was eventually borne out in the parsimony analysis). Because of this character sampling technique, the data presented herein are somewhat more catholic than those often found in systematic presentations, and they certainly are "noiser", with relatively low consistency indices. An advantage of this selection procedure, however, is that it includes more of the morphology than would otherwise be the case, and it does so with less personal bias than may be present in some other studies.

This study began as an exercise in "Hennig argumentation" involving various three taxon-

statements. As the data base became large and rather unwieldy, I turned to numerical methods, all of which are based on use of parsimony in hypothesis choice. During the course of the work, several efficient computer programs have become available, and the final analyses were done using PAUP (Phylogenetic Analysis Using Parsimony), version 2.3 on the Michigan Terminal System (MTS) Amdahl computer. Consensus trees were generated by CONTREE, also running on MTS. Both of these programs were written and made available by David Swofford. Additive binary coding was used for the numerical analyses. Characters not present (either primarily or secondarily) were coded as "missing" and thus had no influence on placement of those taxa on the cladogram. Character states are assigned during the optimization procedure to taxa originally coded as missing, after the tree-building procedure. The matrix is available in Appendix 1.

For each character described in the Characters section, the derived state (with the range of its consistency indices, C.I.; Kluge and Farris, 1969) and the taxa that possess it are listed first, followed by a paragraph describing the outgroup condition. Exceptions and details of anatomy are also listed. The search for outgroup conditions included broad surveys of basal euteleosts as described and listed by Fink and Weitzman (1982). In the final analysis, characters were examined in members of the Photichthya (*sensu* Weitzman, 1974). Due to uncertainties about the monophyly and interrelationships of this large assemblage, its members are referred to below as "photichthyans". Stomiid photichthyans clearly constitute a monophyletic group and the other genera most probably do not, so any characters consistently present in the latter and modified in the former should be confidently assessed as derived in the Stomiidae. In many cases, when dealing with relatively phylogenetically-derived genera, the outgroup search was limited to other stomiids or some subgroup of stomiids, as indicated in the character descriptions.

When it appears probable, based on other characters, that a trait has developed within a genus, that character is coded as primitive rather than as diagnostic of the genus; in the descriptive text, these characters are indicated by the phrase "in some species. . ." For *Stomias*, evidence from Fink and Fink (in press) has been used to determine the primitive states of characters for the genus. For characters which were missing and about which polarity evidence was unavailable, no *a priori* decisions were made about whether the absence is primary (not present in ancestors) or secondary (present in ancestors and lost in the descendant). To have made such decisions would have presumed a tree topology, a practice inconsistent with phylogenetic reasoning. Examples of such characters are features of the secondary pectoral girdle of *Photostomias*; members of that genus lack that part of the girdle, so when outgroups possess both primitive and derived states, it is not possible to assign a state unambiguously to the ingroup taxon. With such characters, one approach would be to assume the primitive state, no evolutionary change. Another approach is to be "agnostic" about such characters and eliminate them from the tree-building process. Because of my own "agnostic" leanings, in the discussion of character evolution in the text I relied on the data matrix with "missing" characters so coded. The choice of any particular equal length tree over another may cause one to accept certain character state resolutions for characters originally coded as missing, and in this sense, to choose one tree over another is to give up some degree of agnosticism regarding character evolution. Since I am presenting all of the equal length cladograms in this study, the issue is not relevant here, but it should be kept in mind when discussing character change in phylogenetic analyses.

The PAUP program has several optimization routines which allow one to make assumptions about the nature of character change. I used only the standard Farris optimization and the MINF optimization, which attempts to minimize the number of groups that are diagnosed on the basis of arbitrary resolutions. Swofford (1983) should be consulted for further information regarding these optimization procedures. Because Farris optimization is the method most often used in current numerical phylogenetic analyses, I have presented the data using that optimization in the Discussion section and in the Results section documenting support for the most parsimonious cladograms. I chose this approach as a conservative one. Work in progress by Swofford and Wayne Maddison will discuss the alternative optimization procedures now available.

Other than character choice, no character weighting was employed, primarily because I know of no reasonable way to do such weighting. Most methods proposed so far make assumptions about evolutionary process which I am unwilling to include *a priori*. One attractive weighting scheme, which weighs characters based on their within-group variation (in this case it would probably have been within-genus variation), was not used simply because we have such skimpy knowledge about morphological variation in stomiids at any taxonomic level.

Material from several institutions was used, including: Museum of Comparative Zoology, Harvard University (MCZ), National Museum of Natural History, Smithsonian Institution (USNM), Los Angeles County Museum (LACM), and Scripps Institution of Oceanography (SIO), and specimens on loan to the USNM from the DANA collections. Specimens were cleared and stained according to an enzyme procedure modified from Taylor (1967) and stored in glycerine or ethanol. In the figures, by convention, fine stipple represents bone, large stipple, cartilage. Most drawings were outlined using a Zeiss IVB zoom microscope with camera lucida, and details were subsequently filled in using a Leitz RS widefield stereo microscope. Occasionally, a Zeiss compound microscope was used for elucidation of very small detail.

Unless otherwise stated, the term "cross-section" is used to signify a section through a bone, or other object, perpendicular to the long axis of that object rather than to the long axis of the fish body.

RESULTS

The summary cladogram and character distributions are presented at this point to give the reader a context in which to examine the following sections, which include presentation of the data and discussions of stomiid subgroups and character transformations. The cladogram in Fig. 1 is a strict consensus tree (Rohlf, 1982) of the six fully resolved, equally parsimonious cladograms generated from the data. Selected subunits of the phylogeny are presented in Figs. 2 through 6, and the supporting data, as numbered in the Characters section, are listed in the figure captions. Alternate cladograms are considered in the Discussion section.

CHARACTERS

Neurocranium

1. In *Malacosteus* (Fig. 7), the anterodorsal border of the neurocranium, from the anterior opening of the frontal sensory canal to the anteroventral margin of the supraethmoid, is highly convex from lateral view; the entire anterodorsal surface of the ethmoid is approximately vertical; and the lateral processes of the ethmoid cartilage are very small. (CI = 1.0)

In other stomiids, the anterodorsal border of the neurocranium is, at most, moderately convex; the anterodorsal surface of the ethmoid region slopes ventrally more gradually; and the lateral processes of the ethmoid cartilage project further laterally.

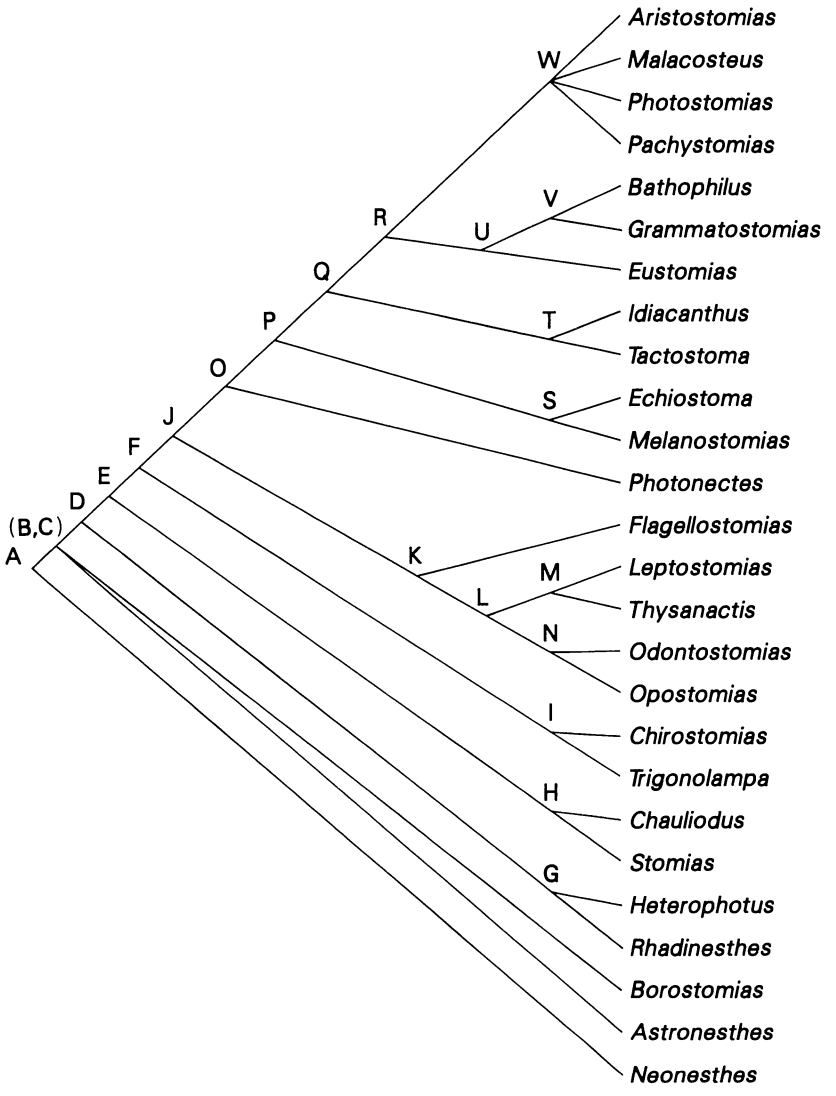

FIG. 1. Summary of interrelationships among stomiid genera. The resolved cladograms of this topology have a length of 496 and consistency index of .494, without the seventy-eight generic apomorphies. With generic apomorphies included, the length is 574, the consistency index .563. Figs. 2 through 6 present portions of the alternative resolved cladograms and their supporting characters.

2. In *Photostomias* (Fig. 8), the anterior half of the neurocranium is greatly foreshortened, with the distance from the anterior margin of the prootic to the anterior margin of the neurocranium less than half the length of the neurocranium; there is a single ossification present in the position of the pterosphenoid and lateral ethmoid bones; and the supraethmoid is ossified

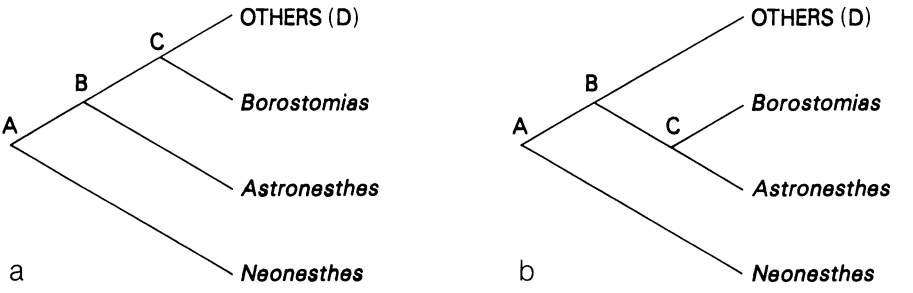

FIG. 2. Figure caption conventions are as follows. If there is no notation accompanying a character number, the character is unique and unreversed. If there is a "c" with the number, the character is found somewhere else in the tree (i.e., it is a "convergence"). An "r" next to the number indicates that the character exhibits a reversal at some lower level (less general grouping) of the tree; an "R" means the character is in its reversed state for that taxon. If an "(r)" follows the "R", it means that the character will reverse again at some lower level in the tree. If a "(1)" follows the "R", it means that the character has reversed again in that taxon to a condition similar to the initial derived state. Clade A: 33, 53, 71r, 84, 103, 168, 187, 193r (b and d), 211r, 223r, 228, 269, 290, 293r, 317r, 320r; Clade B: 15r (a only), 111r, 128r, 156r, 157r, 158r, 165r, 175r, 179, 180r (b only), 268, 285; Clade C(a): 180r; Clade C(b): 15, 193cR; *Astronesthes*: 34c, 39c, 40c, 88, 104c, 180R (b only), 199, 211R, 223cR, 284c; *Borostomias*: 50, 145c, 151; Neonesthes: 73, 109c, 154, 193c (a only), 222c.

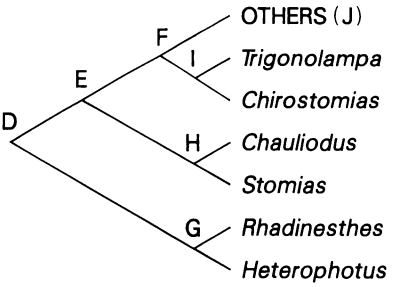

FIG. 3. For character conventions, see FIG. 2 caption. Characters supporting Clade D: 15R (FIG. 2a only), 87, 90, 126r, 149r, 193cr (FIG. 2a only), 220r, 225r; Clade E: 39c, 137r, 148r, 175R, 194, 203r, 210r, 215, 216r, 223cR(r); Clade F: 5c, 65r, 67r, 80r, 94r, 105, 106r, 108r, 115, 143, 149R(r), 225R, 267; Clade G: 57, 76c, 140c, 235, 284c; Clade H: 16, 40c, 51, 109c, 111cR, 128R, 167, 178, 185c, 195c, 202, 222c, 226c, 317R, 318, 319; Clade I: 42c, 63, 120; *Chauliodus*: 17c, 27c, 34c, 66, 78c, 104c, 125c, 135, 140c, 180R, 198c, 204c, 210cR, 216R, 217, 220R, 223R(1), 224, 229c, 232, 248c, 293cR; *Chirostomias*: 81c, 83, 126cR, 134, 220cR, 238, 249c, 251, 265c; *Heterophotus*: 5c, 64c, 150, 153, 173c, 193cR (FIG. 2b only), 193R (FIG. 2a only), 213, 220cR, 222c, 233, 265c, 313; *Rhadinesthes:* 126cR, 171, 266, 292; *Stomias:* 38, 42c, 61c, 69c, 71R, 72, 101, 102, 137cR, 148R, 181c, 182c, 190, 197, 203cR, 256c, 282, 296c, 304c, 306; *Trigonolampa:* 25c, 43c, 136, 188, 230c, 250c, 252c, 315.

on the interior surface of the ethmoid cartilage. The interior and dorsal ossifications of the supraethmoid are continuous around the medial margin of the olfactory foramen. (CI = 1.0)

In other stomiids, the distance from the anterior margin of the prootic

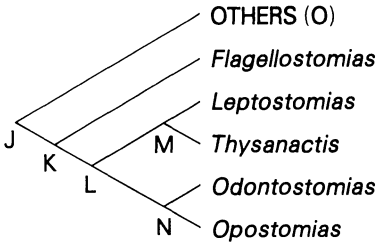

FIG. 4. For character conventions, see FIG. 2 caption. Characters supporting Clade J: 64c, 141, 159r, 181c, 200, 214, 240, 259, 270, 271, 296c; Clade K: 10, 11c, 44, 56, 59, 65R, 106R, 108cR, 195c, 204c, 205c, 272r, 274, 275r, 278r; Clade L: 4, 41, 55, 78c, 94cR, 124c (FIG. 6a and d), 124cr (Figs. 6b,c), 140c, 142, 156cR, 157R, 186, 191, 198c, 201c, 248c, 264, 280c; Clade M: 6, 68c, 117, 196c, 263, 265c, 273; Clade N: 239, 272R, 275R, 284c; *Flagellostomias*: 107c, 219c, 293cR, 294c; *Leptostomias*: 107c, 139, 176c; *Odontostomias:* 137cR, 278R; *Opostomias:* 36, 109c, 111cR, 156R(1), 227c; *Thysanactis:* 54c, 316.

bone to the anterior margin of the neurocranium is more than half the length of the neurocranium; the lateral ethmoid is either a separate ossification from the pterosphenoid or is absent altogether; and there is no supraethmoid ossification on the interior surface of the ethmoid cartilage.

3. In *Aristostomias* (Fig. 9), *Malacosteus* (Fig. 7b), and *Pachystomias* (Fig. 10b), the distance from the posteriormost point of the neurocranium to the anteriormost point of the prootic is less than the depth of the neurocranium at the midlength of the prootic. (CI = .5–1.0)

In other stomiids, that distance is equal to, or greater than, the depth of the neurocranium at the midlength of the prootic.

4. In *Leptostomias*, *Odontostomias*, *Opostomias*, and *Thysanactis*, there is an elongate lump on the dorsal surface of the cartilage of the posterodorsal portion of the neurocranium along the midline. (CI = 1.0)

In other stomiids, the cartilage in that region of the neurocranium is smoothly sloping.

5. In *Heterophotus* and members of Clade F, the rostrodermethmoid is absent, leaving only the supraethmoid ossification (Figs. 7–17). (CI = .5)

In other stomiids and "photichthyans," the rostrodermethmoid is present; it appears to be fused to the supraethmoid in the former.

6. In *Leptostomias* and *Thysanactis*, a groove is present in the anterior half of the supraethmoid in the midline. (CI = 1.0)

In other stomiids, the anterior half of the supraethmoid may be either convex or concave near the midline, but no groove is present (the curvature of the neurocranium is in the region of the frontal rather than of the supraethmoid).

7. In *Aristostomias* (Fig. 9b) and *Eustomias* (Fig. 12b), the supraethmoid ossification extends as a rounded or flattened tube around the lateral process of the ethmoid, covering the ventral as well as the dorsal surface of the cartilage process. (CI = .5)

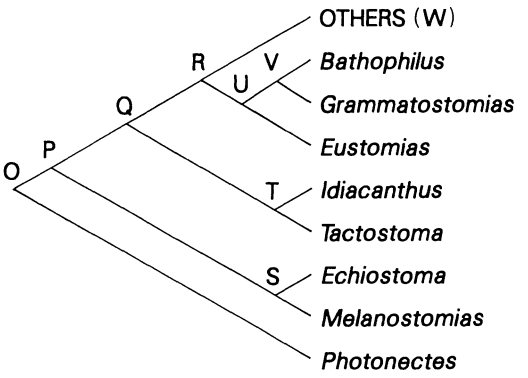

FIG. 5. For character conventions, see FIG. 2 caption. Characters supporting Clade O: 43c, 61c, 69cr, 70, 79r, 93, 112r, 113r, 122r, 123, 127r, 138, 144, 182c, 245r, 250cr, 257, 284c, 286r, 288, 289r, 291, 297r (FIG. 6a, b, and c only), 299; Clade P: 28r, 81cr, 94cR(r), 132r, 140c, 163r, 212r; Clade Q: 12r, 17cr, 54c, 195c, 196cr, 229cr, 231, 256cr, 261; Clade R: 32c, 40c, 45, 62r, 74, 75r, 85r (FIG. 6a, b, and c only), 91r, 94R(1), 113R, 122R, 158R, 161, 162r (FIG. 6d only), 165R(r) (FIG. 6d only), 169c, 172r, 173cr, 183r, 185c, 206r, 300cr (FIG. 6d only); Clade S: 9, 14, 24, 25c, 118c, 129, 176c, 205c, 227c, 230c, 245cR, 280c, 281; Clade T: 49, 68c, 76c, 77, 82c, 166c, 170, 189, 242c, 245c (FIG. 6c only), 246c, 247c, 279c; Clade U: 85c (FIG. 6b and d only), 95c, 96, 107c, 152, 155r, 198cr, 205c, 253c, 256cR, 276, 297R(r) (FIG. 6a, b, and c only); Clade V: 8, 62R, 69cR, 92c, 97, 118c, 162c (FIG. 6a, b, and c only), 164, 165 (FIG. 6d only), 166c, 236, 245cR, 249c, 254c, 300c (FIG. 6a, b, and c only), 301c; *Bathophilus*: 37, 119, 155R, 262, 283, 293cR, 295c, 298, 303c, 308; *Echiostoma*: 26, 58, 69cR, 132cR, 286cR, 297cR (FIG. 6a, b, and c only), 305c; *Eustomias*: 7c, 13c, 27c, 28cR, 52, 60, 75R, 91R, 126cR, 133c, 162cR (FIG. 6d only), 165cR (FIG. 6a, b, and c only), 192, 204c, 208c, 219c, 221, 234, 243, 245c (FIG. 6c only), 250R, 287c, 289cR, 300cR (FIG. 6d only); *Grammatostomias*: 89, 145c, 177, 198R, 203cR, 255, 297R(1) (FIG. 6a, b, and c only), 297c (FIG. 6d only); *Idiacanthus*: 17R, 114, 130, 133c, 203cR, 218, 222c, 226c, 227c, 229R, 286cR, 297cR (FIG. 6a, b, and c only), 304c, 312c, 322, 323; *Melanostomias:* 11c, 27c, 28cR, 79cR, 133c, 204c, 252c, 287c, 289cR, 297c (FIG. 6d only), 300c; *Photonectes:* 27c, 29c, 32c, 46, 76c, 95c, 100, 110c, 125c, 169c, 185c, 198c, 203cR, 244, 245c (FIG. 6c only), 246c, 247c, 252c, 253c, 254c, 258c, 297c (FIG. 6d only); *Tactostoma:* 12cR, 35, 80cR, 81cR, 127cR, 132cR, 212R, 280c, 287c, 289cR, 297c (FIG. 6d only), 305c.

In other stomiids, the supraethmoid ossification does not extend onto the ventral surface of the lateral process of the ethmoid.

8. In *Bathophilus* (Fig. 13) and *Grammatostomias*, the anterior part of the ethmoid, in the region of the supraethmoid and vomer, particularly the anteromedian ethmoid process, is produced ventrally. The latter process also has a narrow concavity from dorsal view. (CI = 1.0)

In other stomiids, the anterior part of the ethmoid is not produced ventrally, and the anteromedian process is either convex or broadly concave.

9. In *Echiostoma* (Fig. 14b) and *Melanostomias* (Fig. 15b), there is a small, conical bone in a pocket on the ventrolateral surface of the ethmoid cartilage. (CI = 1.0)

In other stomiids, this bone is not present.

It is also absent, apparently secondarily, in some *Echiostoma*.

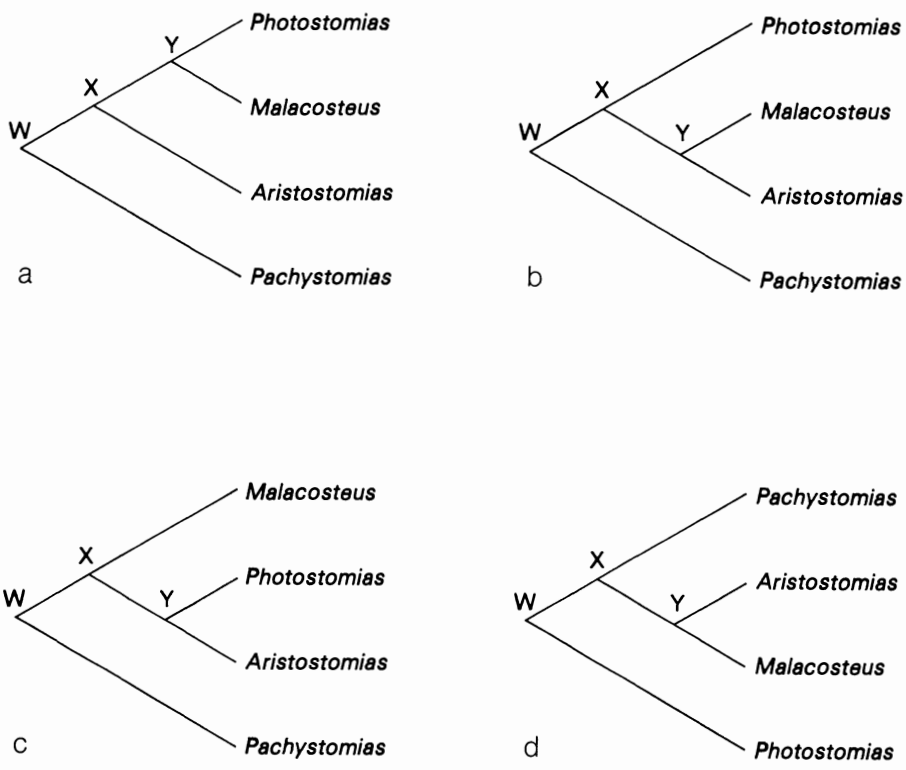

FIG. 6. For character conventions, see FIG. 2 caption. Characters supporting Clade W: 3r (not in d), 18, 20r (a only), 22, 23r (not in d), 29c, 30, 31r, 34c, 47, 79cR(r), 80cR, 81cR, 98, 108cR(r), 110cr, 121r (b and d), 125cr (d only), 127cR, 146r, 147r (c only), 163R(r) (a only), 203cR, 207r (not in d), 222c, 225R(1), 226c, 237r (d only), 241, 260, 277, 304cr (d only), 309r (not in d), 310, 312r (not in d), 321r (d only); Clade X(a): 92cr, 112R(r), 125c, 162c, 165cR, 183R(r), 237, 246cr, 258cr, 293cR(r), 300c, 304c, 320R, 321; Clade X(b): 112R(r), 124cr, 125c, 126cR(r), 162c, 165cR, 173R(r), 174r, 237, 246cr, 293cR(r), 300c, 304c, 320R, 321; Clade X(c): 92cr, 124cr, 125c, 126cR(r), 162c, 165cR, 173R(r), 174r, 183R(r), 237, 258cr, 300c, 304c, 320R, 321; Clade X(d): 3, 20r, 23, 147r, 163R(r), 207, 245cR(r), 297c, 309, 312, 313; Clade Y(a): 20R, 124c, 126cR, 163R(1), 173R, 174, 297cR; Clade Y(b): 85c, 92c, 121R, 183R, 258c; Clade Y(c): 112R, 147R, 245c, 246c, 247c, 293cR; Clade Y(d): 85c, 92c, 121R, 183R, 258c, 320R; *Aristostomias* (a and d): 7c, 19, 21, 112cR (d only), 146R, 147R (d only), 196R, 245R(1) (d only), 247c, 249c, 256cR, 293cR (d only), 294c, 317cR (d only); (b and c): 7c, 19, 20c, 21, 124R, 126R(1), 146R, 163cR, 173R(1), 174R, 196R, 247c (b only), 249c, 256cR, 294c; *Malacosteus:* 1, 13c, 20R (d only), 31R, 48, 67R, 79R(1), 82c, 86, 108R(1), 110R, 112R(1) (a and b), 118c, 124c (d only), 126cR (d only), 131, 133c, 147c (a and b), 160, 163R(1) (d only), 173cR (d only), 174c (d only), 205c, 208c, 245cR (a and b), 246R (a and b), 293R(1) (a and b); *Pachystomias* (a): 85cR, 121c, 147c, 159R, 245cR, 311; (b): 20c, 147c, 159R, 163cR, 245cR, 311; (c): 20c, 85cR, 121c, 159R, 163cR, 311; (d): 125R, 159R, 162cR, 165cR(1), 237R, 300cR, 304R, 311, 321R; *Photostomias:* 2, 3R (not in d), 12cR, 23R (not in d), 27c, 28cR, 85cR (a and c), 92R (a and c), 99, 112cR (d only), 116, 121c (a and c), 124c (d only), 126cR (d only), 132cR, 149R(1), 172R, 173cR (d only), 183R(1) (a and c), 184, 201c, 206R, 207R (not in d), 209, 242c, 246c (d only), 258R (a and c), 279c, 287c, 293cR (d only), 295c, 297R (b and c), 301c, 302, 303c, 307, 309R (not in d), 312R (not in d).

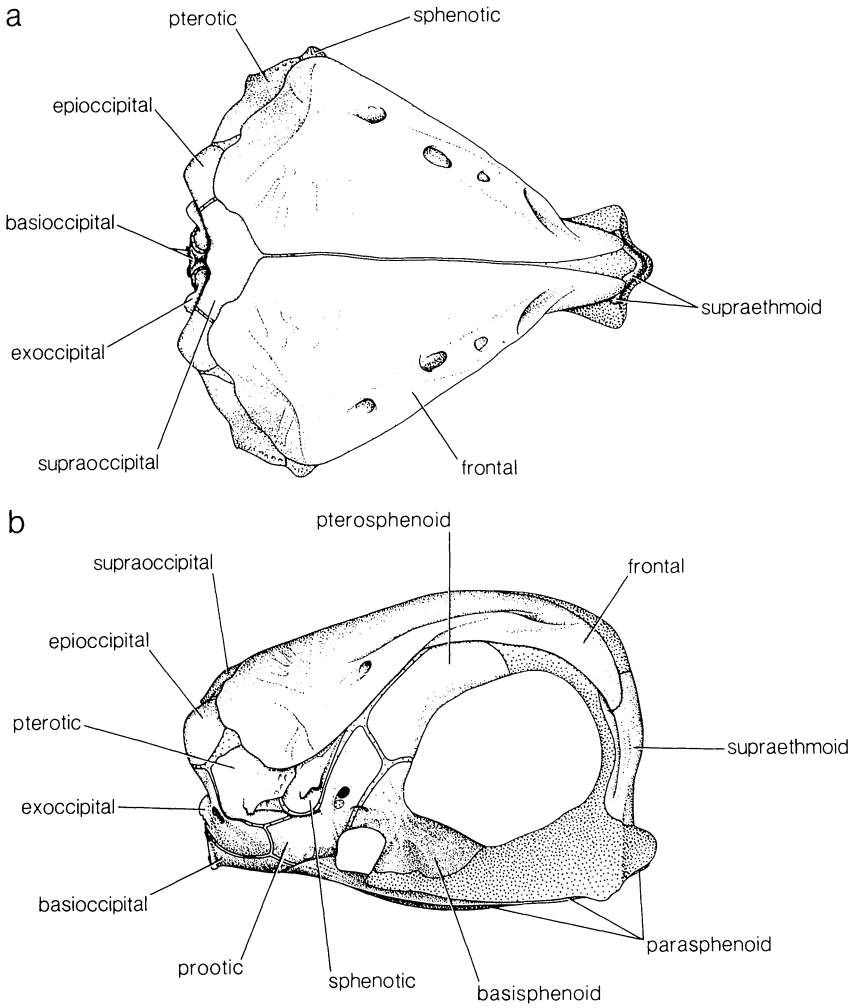

FIG. 7. Neurocranium of *Malacosteus* sp. (MCZ 53286). a, dorsal view; b, lateral view.

10. In *Flagellostomias* (Fig. 11), *Leptostomias*, *Odontostomias*, *Opostomias*, and *Thysanactis*, the ventrolateral process of the lateral ethmoid is anteriorly elongate, so that from lateral view, the ventral border is about one-fifth the length of the ventral border of the neurocranium. (CI = 1.0)

In other stomiids, the ventrolateral process projects more directly laterally, and the length of the ventral portion of the lateral ethmoid is less than one-fifth the length of the ventral border of the neurocranium.

11. In *Flagellostomias* (Fig. 11a), *Leptostomias*, *Melanostomias* (Fig. 15a), *Odontostomias*, *Opostomias*, and *Thysanactis*, the distal cartilage tips of the lateral ethmoid and the supraethmoid are fused together, leaving a rounded opening medial to the lateral margin of the ethmoid cartilage. (CI = .5)

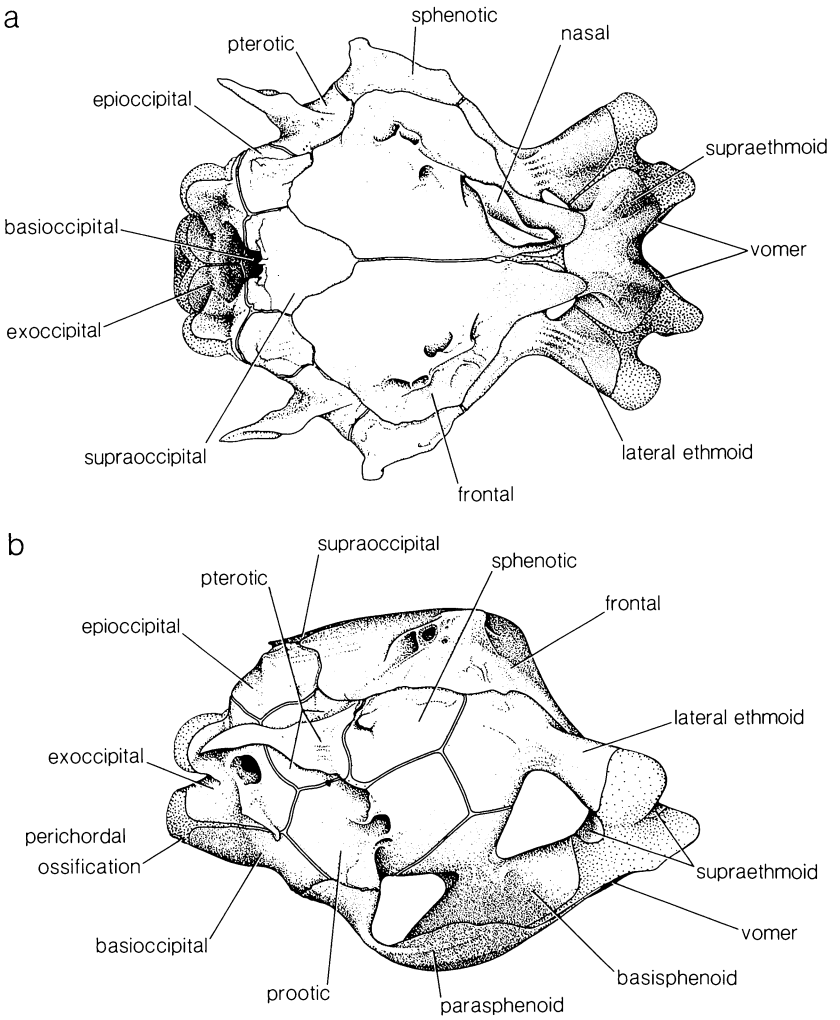

FIG. 8. Neurocranium of *Photostomias guernei* (USNM 272952). a, dorsal view; b, lateral view.

In other stomiids, the distal cartilage tips remain unfused.

12. In *Aristostomias* (Fig. 9), *Bathophilus* (Fig. 13), *Eustomias* (Fig. 12), *Grammatostomias*, *Idiacanthus*, *Malacosteus (Fig. 7), and Pachystomias* (Fig. 10), the lateral ethmoid is reduced in size or absent. (CI = .33)

In other stomiids, a larger lateral ethmoid ossification is present.

13. In *Eustomias* (Fig. 12) and *Malacosteus* (Fig. 7), the lateral ethmoid is absent. (CI = .5)

In other stomiids, there is a lateral ethmoid ossification.

14. In *Echiostoma* (Fig. 14b) and *Melanostomias* (Fig. 15b), there is an elongate groove in the lateral ethmoid and pterosphenoid bones associated with the exit of the supraorbital nerve trunk from the orbital region. (CI = 1.0)

In other stomiids, there is no groove.

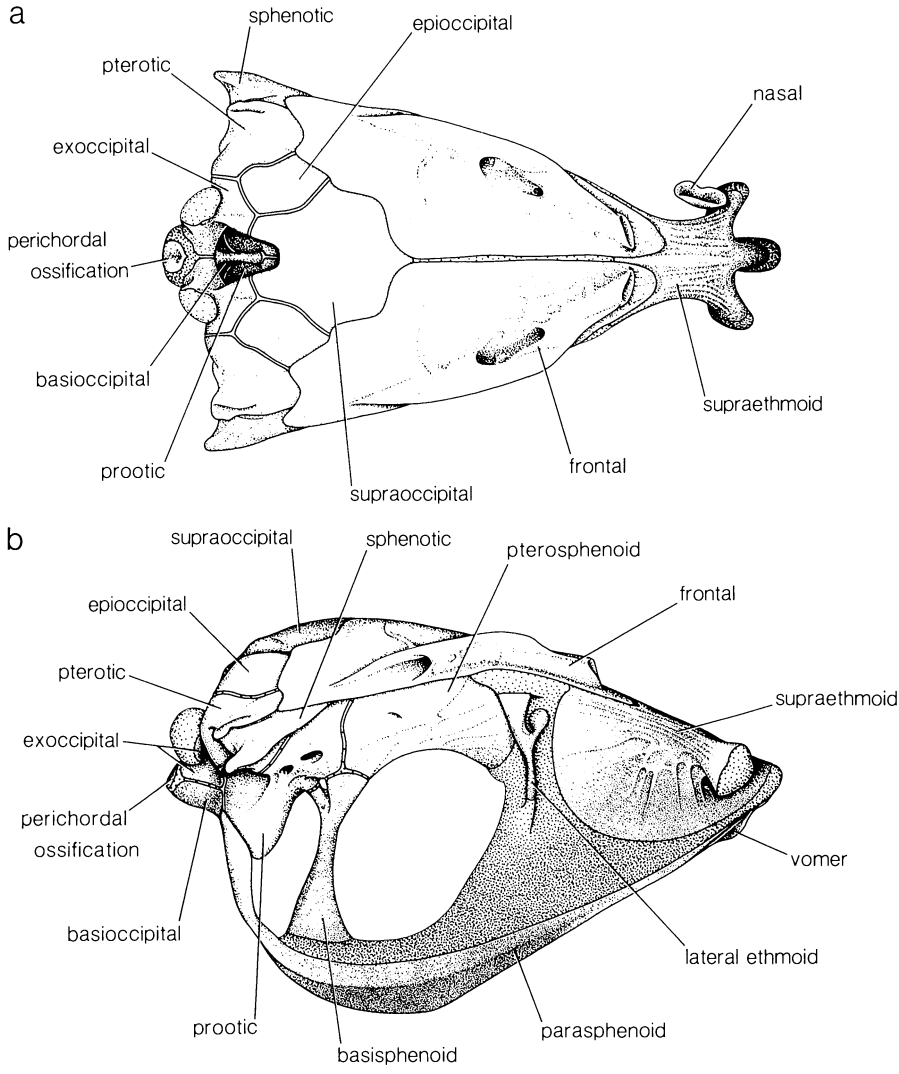

FIG. 9. Neurocranium of *Aristostomias xenostoma* (USNM uncat. DANA st. 48 2/7 1G). a, dorsal view; b, lateral view.

15. In *Astronesthes* and *Borostomias* a parasphenethmoid bone is present (see Weitzman, 1967b, Fig. 2). (CI = .5–1.0)

In other "photichthyans", no such bone is present.

16. In *Chauliodus* and *Stomias* (Fig. 17), the lateral wall of the nasal bone is much larger than the medial wall and forms a cup-like wall to the nasal capsule. (CI = 1.0)

In other "photichthyans," the lateral and medial walls of the nasal bone are about equal in size, forming a tubular structure.

17. In *Aristostomias*, *Bathophilus*, *Chauliodus*, *Eustomias*, *Grammatostomias*, *Malacosteus*, *Pachystomias*, *Photostomias*, and *Tactostoma*, there are no

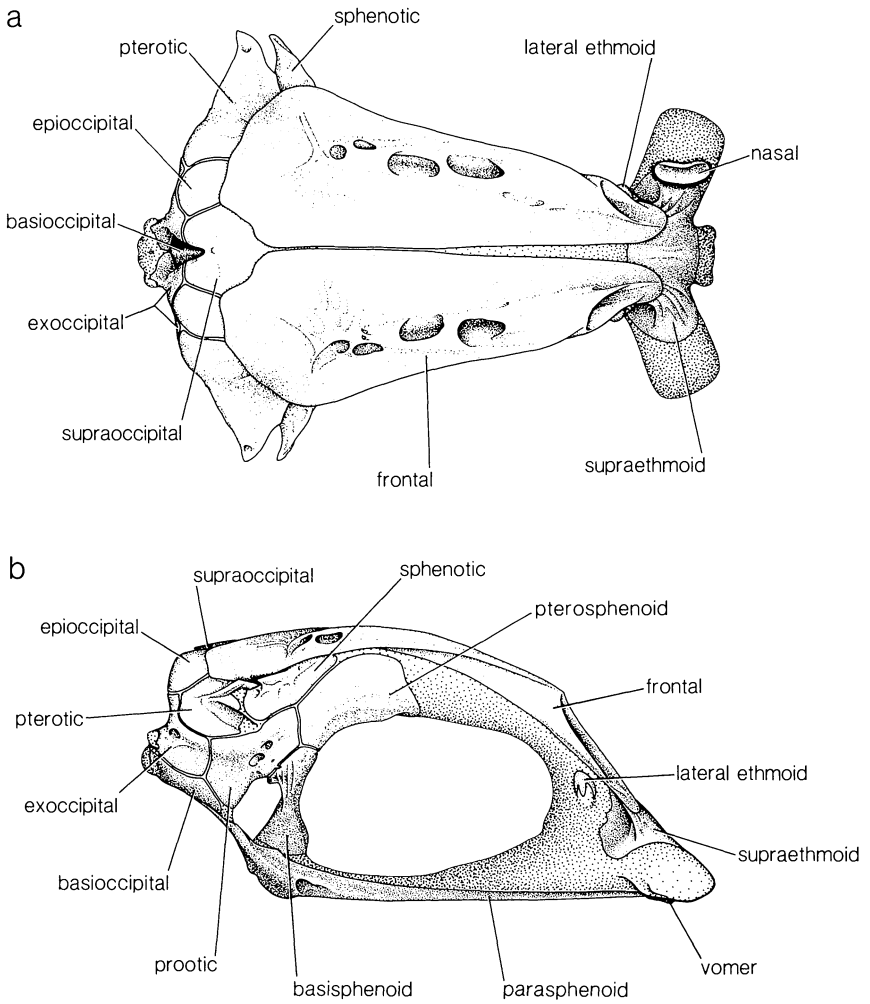

FIG. 10. Neurocranium of *Pachystomias microdon* (USNM uncat. DANA st. 459/71). a, dorsal view; b, lateral view.

vomerine teeth (Figs. 7b–10b, 12b, 13b). (CI = .33)

In other stomiids, there are vomerine teeth.

18. In *Aristostomias*, *Malacosteus*, *Pachystomias*, and *Photostomias*, the parasphenoid terminates posteriorly well anterior to the posteroventral margin of the basioccipital (Figs. 7b–10b). (CI = 1.0)

In other stomiids, the parasphenoid posteriorly terminates only slightly anterior to the posteroventral margin of the basioccipital.

19. In *Aristostomias* (Fig. 9b), the ventral portion of the neurocranium (the parasphenoid and associated cartilage and the ventral part of the basisphenoid) extends well ventral to its position in other stomiids. (CI = 1.0)

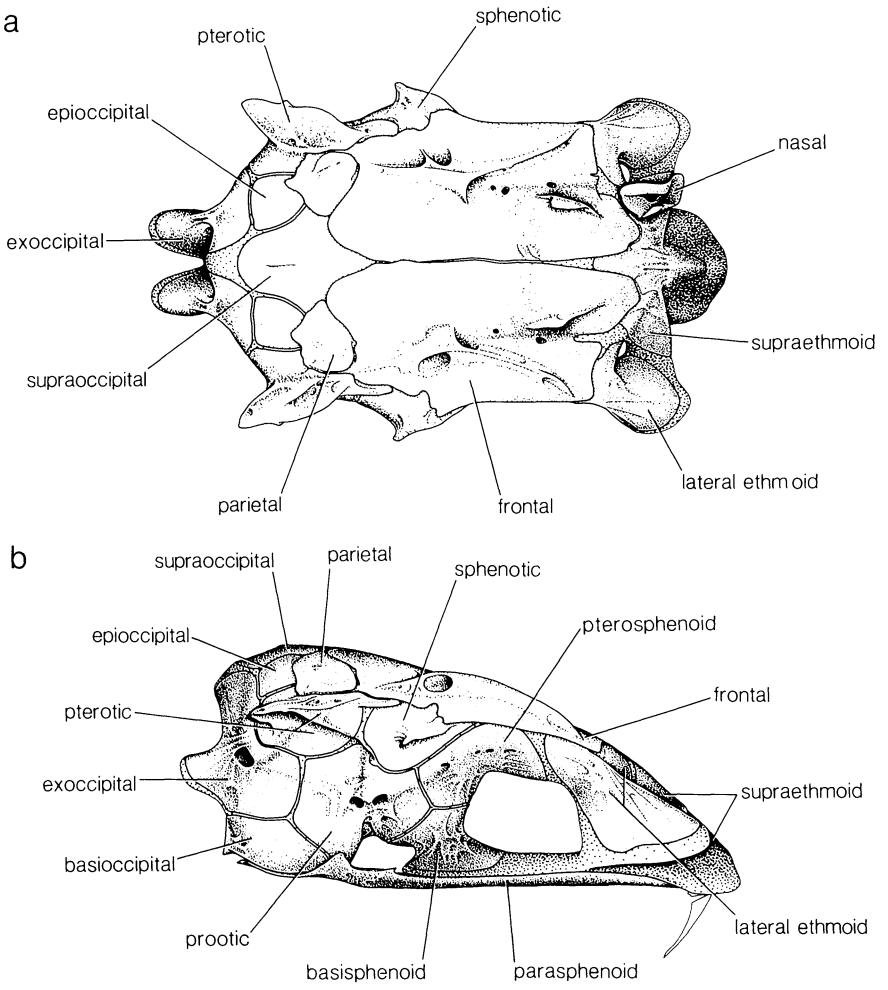

FIG. 11. Neurocranium of *Flagellostomias boureei* (USNM 206681). a, dorsal view; b, lateral view.

20. In *Aristostomias* (Fig. 9b) and *Pachystomias* (Fig. 10b), the greatest width of the basisphenoid, from lateral view, is half or less its height, and the bone is positioned in about the posterior third of the skull. (CI = .5)

In other stomiids, the greatest width of the basisphenoid is more than half its height, and the bone is positioned in about the midlength of the skull.

21. In *Aristostomias* (Fig. 9), the sphenotic spine extends posteriorly approximately as far as the pterotic process and the posterior border of the prootic. (CI = 1.0)

In other stomiids, the sphenotic spine extends no further posteriorly than a vertical line drawn slightly posterior to the midlength of the prootic.

22. In *Aristostomias*, *Malacosteus*, *Pachystomias*, and *Photostomias*, the sphenotic spine extends posterior to the midlength of the prootic and the

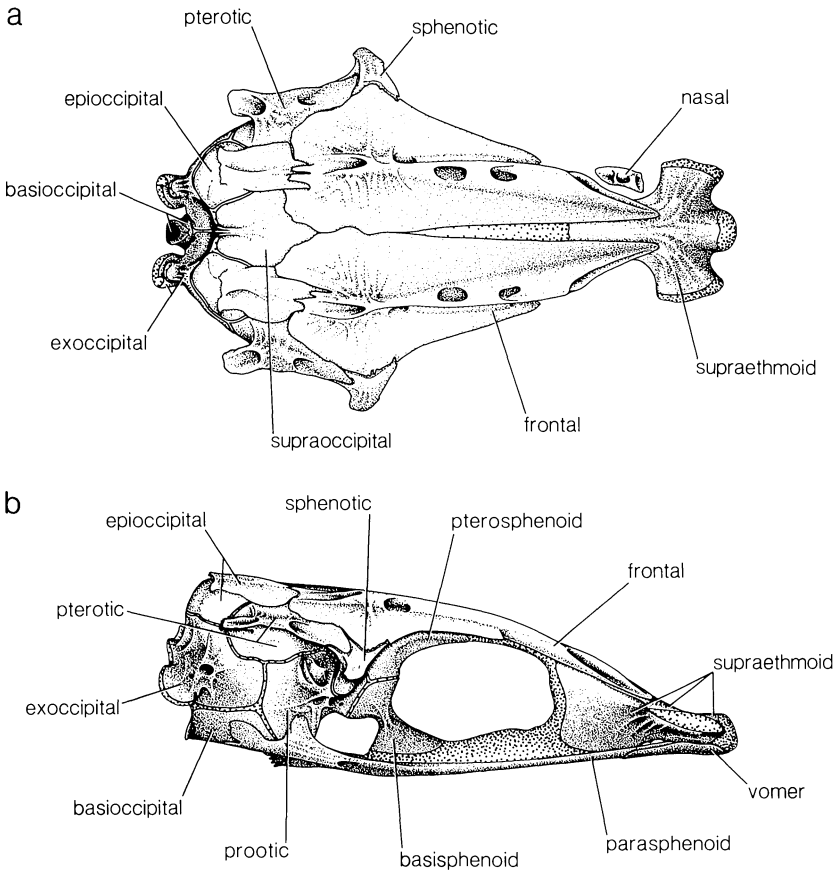

FIG. 12. Neurocranium of *Eustomias* cf. *macrurus* (USNM 272913). a, dorsal view; b, lateral view.

anterior margin of the facet for the hyomandibula (Figs. 7–10). (CI = 1.0)

In other stomiids, the spine terminates at, or anterior to, the midlength of the prootic bone, and anterior to the facet for the hyomandibula.

23. In *Aristostomias* (Fig. 9), *Malacosteus* (Fig. 7), and *Pachystomias* (Fig. 10), the pterotic is produced laterally and does not bear a sensory canal. (CI = .5–1.0)

In other stomiids, the pterotic is produced posterolaterally and bears a sensory canal.

24. In *Echiostoma* (Fig. 14b) and *Melanostomias* (Fig. 15b), the posterior process of the pterotic is robust and projects posterodorsally. (CI = 1.0)

In other stomiids, the process is more slender and projects either directly posteriorly or posteroventrally.

25. In *Echiostoma* (Fig. 14), *Melanostomias* (Fig. 15), and *Trigonolampa*, rugosities are present on the dorsal ridges of the frontal sensory canals. (CI = .5)

In other stomiids, no rugosities are present.

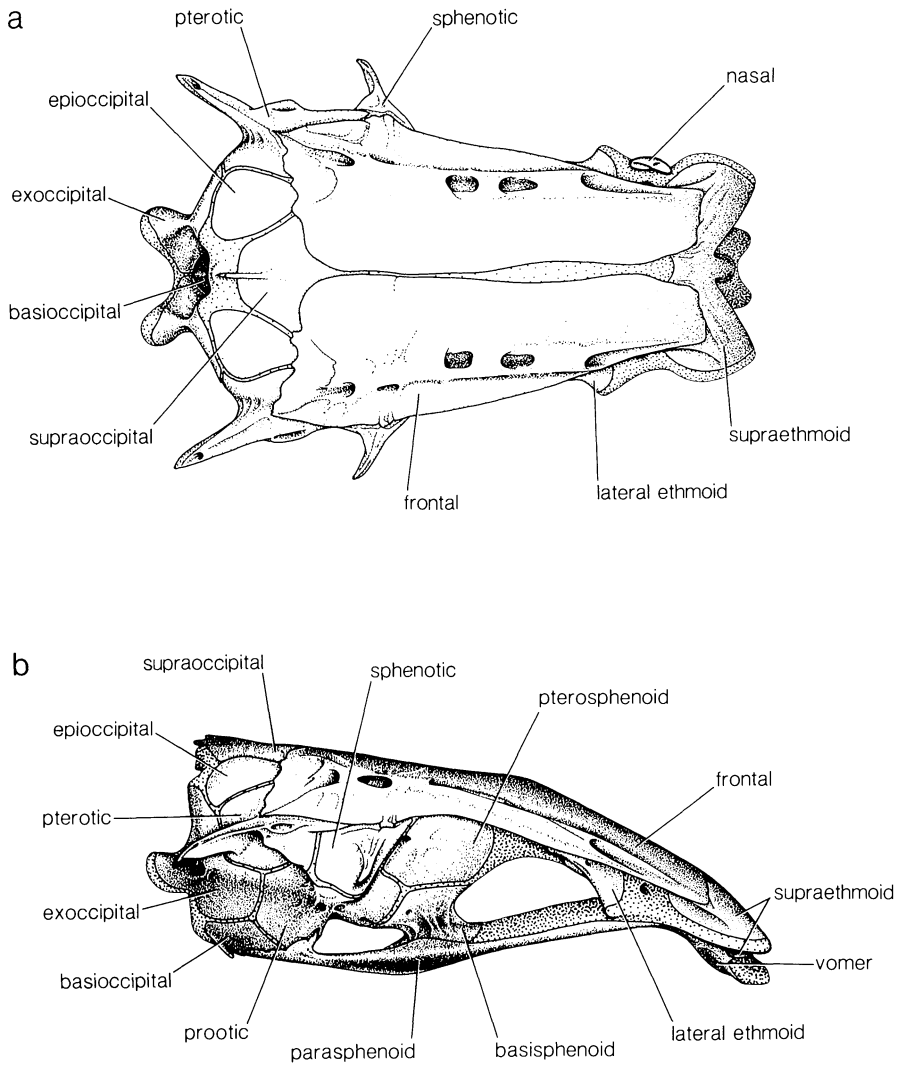

FIG. 13. Neurocranium of *Bathophilus pawneei* (USNM 159052). a, dorsal view; b, lateral view.

26. In *Echiostoma* (Figs. 14b, 18), the rugosities on the frontal sensory canals are large and pointed, and there are similar rugosities present on the ridges of the antorbital (see also Character 58). (CI = 1.0)

In other stomiids, the rugosities are either much less marked or not present.

27. In *Chauliodus*, *Eustomias*, *Melanostomias*, *Photonectes*, and *Photostomias*, the parietal is fused with the epioccipital. (CI = .20)

In other stomiids with a parietal, it is autogenous (in a specimen of *Trigonolampa*, one side is fused and the other is free). See also Character 28.

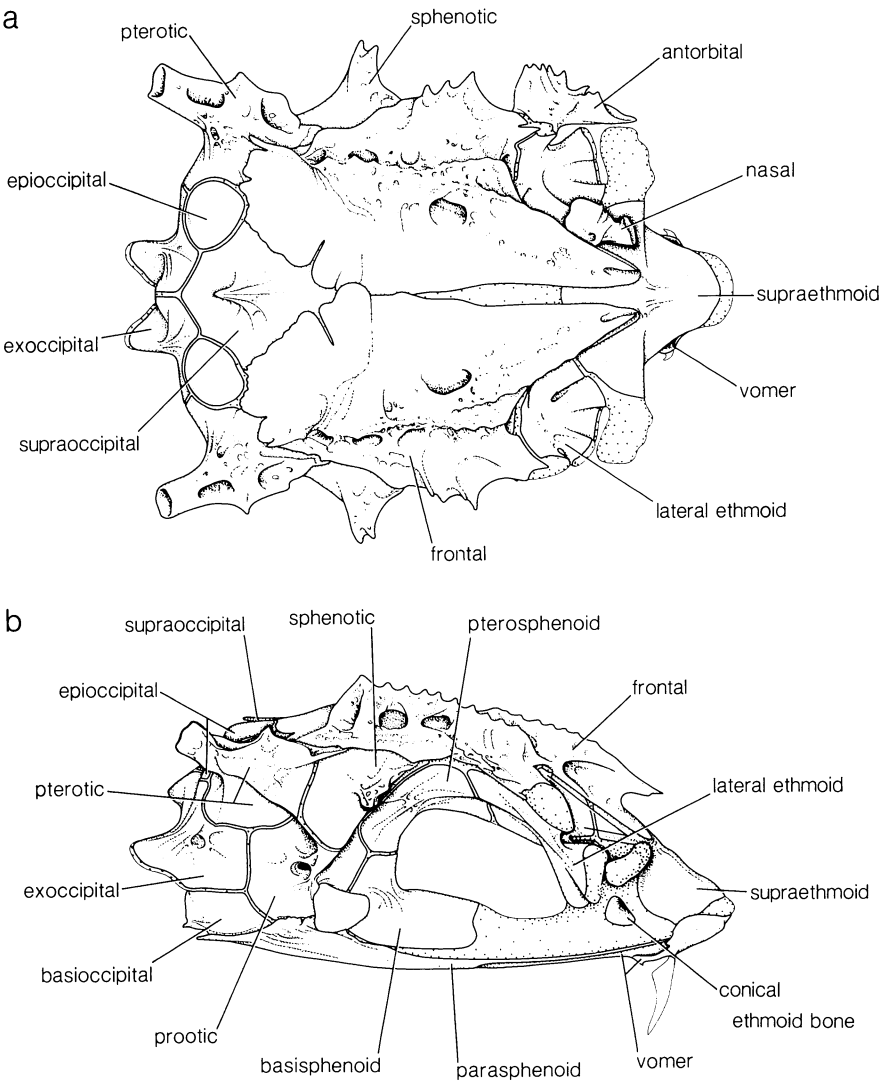

FIG. 14. Neurocranium of *Echiostoma barbatum* (USNM 199839). a, dorsal view; b, lateral view.

Presence of the parietal in these taxa is suggested by the shape of the single epioccipital element. Primitively in stomiids, the epioccipital is a simple perichondral element, but in these taxa this element bears an anterior extension or elaboration superficial to the perichondral portion which topographically resembles the parietal. For example, compare *Flagellostomias* (Fig. 11), in which the parietal is autogenous, lying dorsal to the epioccipital and ventral to the frontal, with *Melanostomias* (Fig. 15), in which the parietal portion of the epioccipital appears clearly recognizable in the same relative

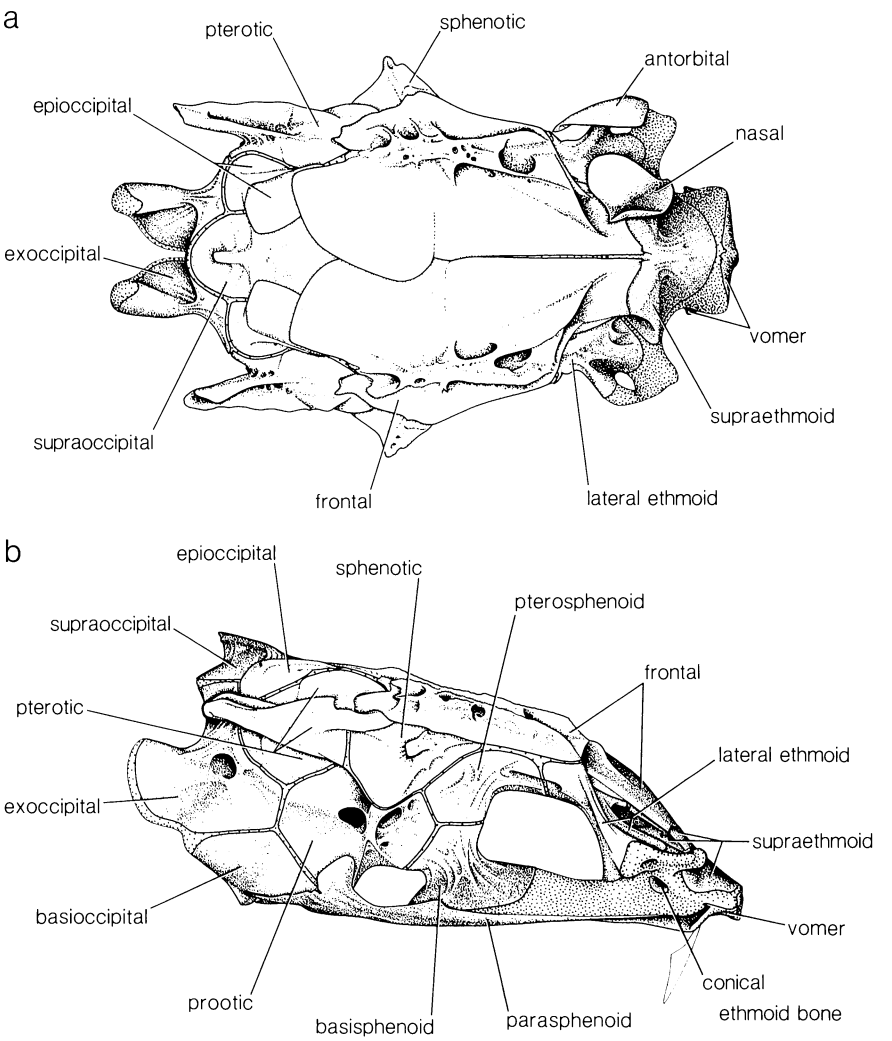

FIG. 15. Neurocranium of *Melanostomias tentaculatus* (USNM 199848). a, dorsal view; b, lateral view.

position dorsal to the epioccipital and ventral to the frontal. In *Photonectes* (Fig. 16) the parietal portion is more reduced than in *Melanostomias*, and has lost contact with the frontal. Information about the ontogeny of this fusion pattern would be the best test of this hypothesis of parietal/epioccipital fusion.

28. In *Aristostomias*, some *Astronesthes* species, *Bathophilus*, *Echiostoma*, *Grammatostomias*, *Idiacanthus*, *Malacosteus*, *Pachystomias*, some *Stomias* species, and *Tactostoma*, the parietal is absent. (CI = .25)

In other stomiids, the parietal is present, either as an autogenous element or fused with the epioccipital (see Character 27).

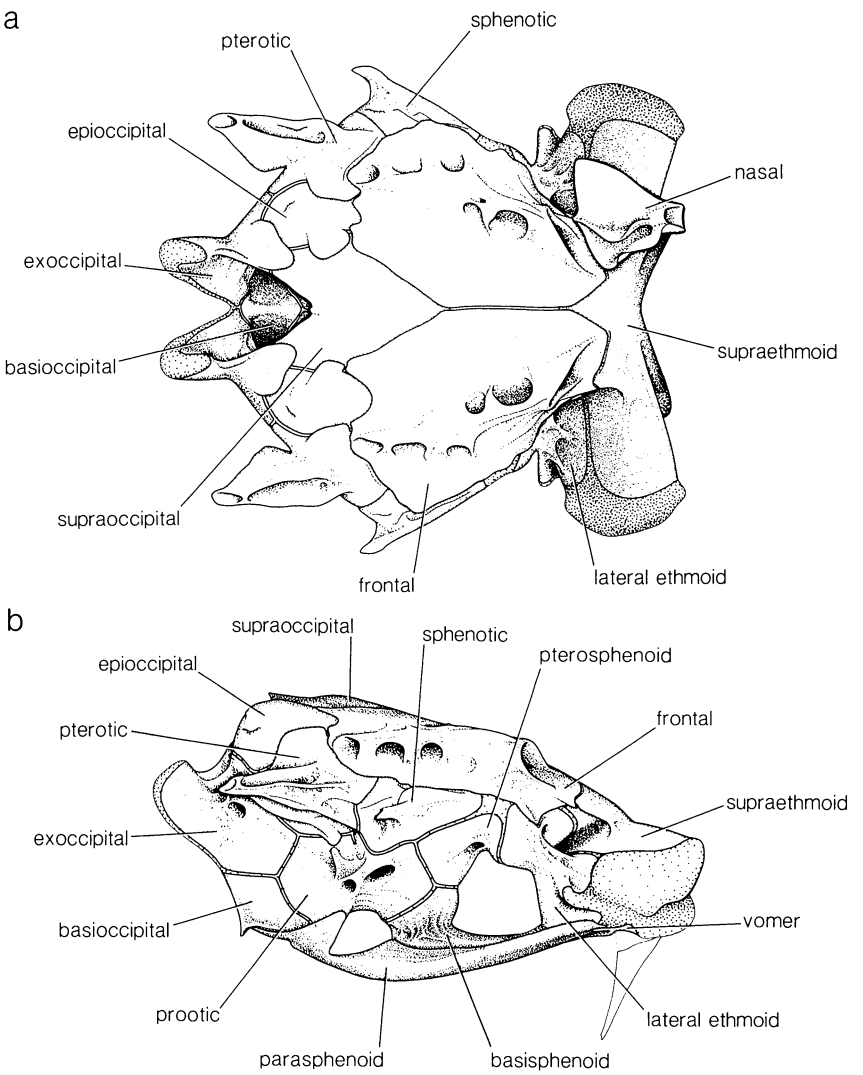

FIG. 16. Neurocranium of *Photonectes margarita* (USNM 272908). a, dorsal view; b, lateral view.

29. In *Aristostomias*, *Malacosteus*, *Pachystomias*, *Photonectes*, and *Photostomias*, the external and internal ossifications of the supraoccipital are continuous around the dorsal margin of the foramen magnum (Figs. 7–10, 16). (CI = .5)

In other stomiids, the external and internal ossifications do not meet.

30. In *Aristostomias*, *Malacosteus*, *Pachystomias*, and *Photostomias*, the cartilage of the posterior process of the exoccipital projects anterodorsal to the posterodorsal bony border of the process (Figs. 7–10). (CI = 1.0)

In other stomiids, the cartilage projects only posteriorly from the bony margin of the process.

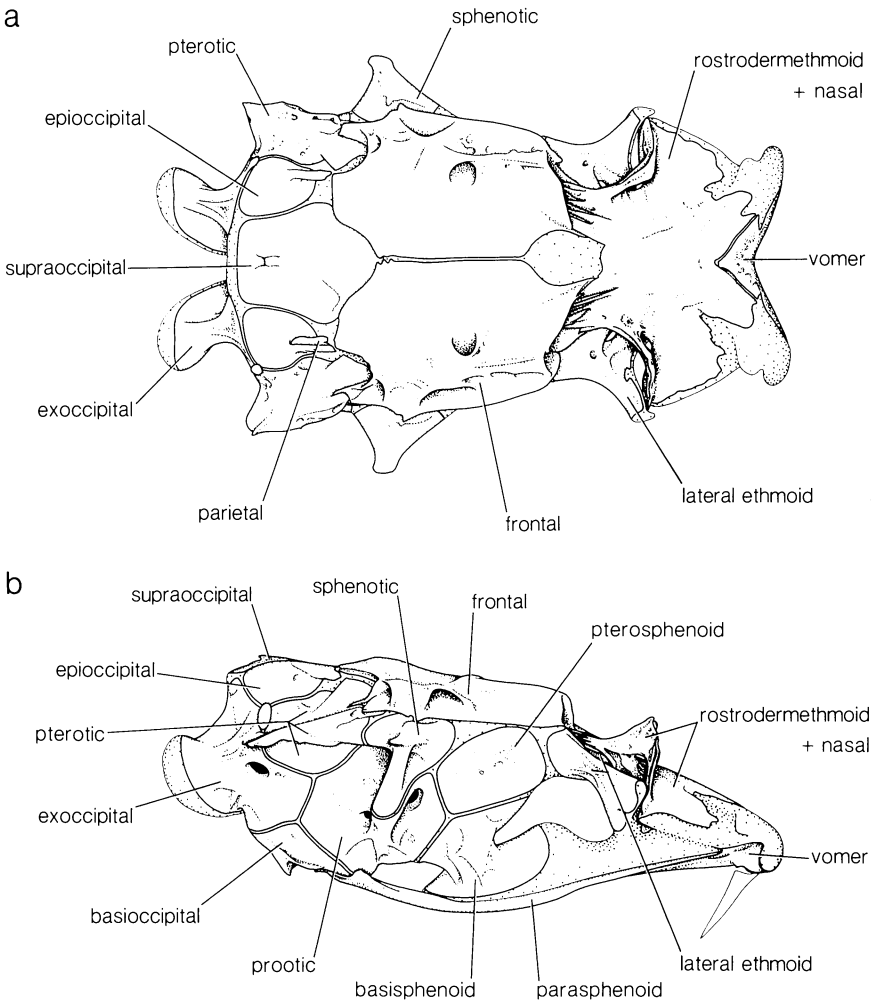

FIG. 17. Neurocranium of *Stomias lampropeltis* (USNM 199857). a, dorsal view; b, lateral view.

31. In *Aristostomias* (Fig. 9), *Pachystomias* (Fig. 10), and *Photostomias* (Fig. 8), the basioccipital condyle is largely convex instead of largely concave. (CI = .5)

In other stomiids, the basioccipital condyle is largely concave rather than convex.

32. In *Aristostomias*, *Bathophilus*, *Eustomias*, *Grammatostomias*, *Malacosteus*, *Pachystomias*, *Photonectes*, and *Photostomias*, the dorsal border of the foramen magnum is concave from dorsal aspect and part of the interior of the cranium is visible (Figs. 7a–10a, 12a, 13a, 16a). (CI = .5)

In other stomiids, the border is straight or convex and the interior of the cranium is not visible.

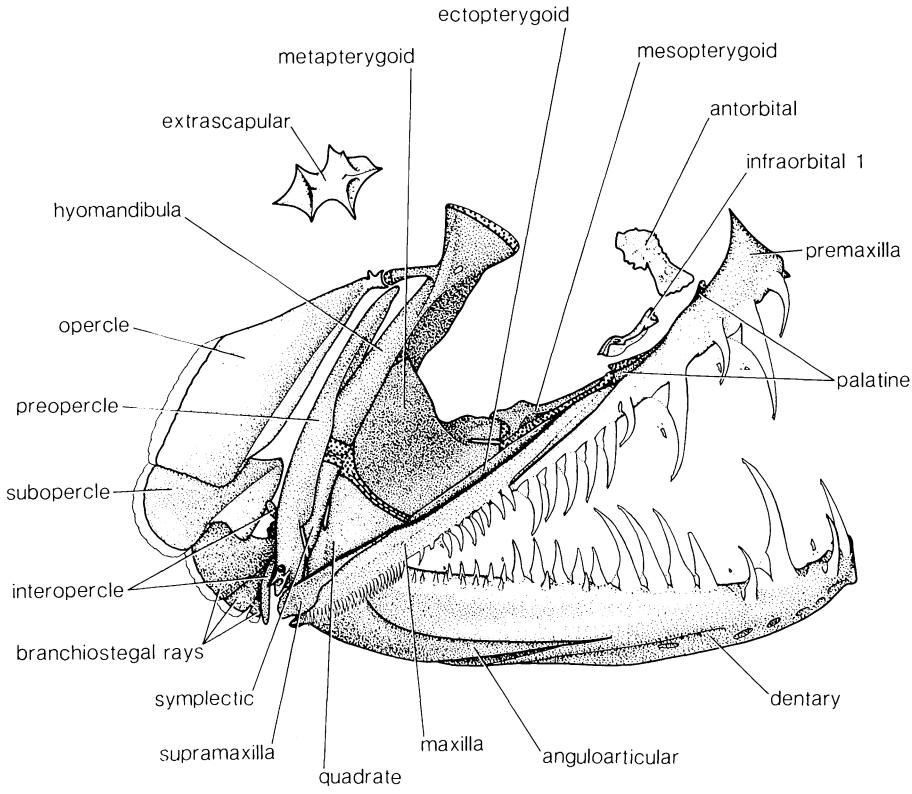

FIG. 18. Jaws and suspensorium of *Echiostoma barbatum* (USNM 199839). Right side, lateral view. Light stipple indicates unossified membrane.

SUSPENSORIUM AND JAWS

33. In stomiids, all infraorbitals except the first are absent. (CI = 1.0)

In other stomiiforms, between two and six infraorbitals are present.

34. In *Aristostomias*, *Astronesthes*, *Chauliodus*, *Malacosteus* (Fig. 26), *Pachystomias* (Fig. 27), and *Photostomias* (Fig. 25), the jaw teeth of adults are fixed and not depressible (Type 1 attachment; Fink, 1981). (CI = .33)

In other "photichthyans," at least some Type 3 (hinged, anterior axis of rotation) or Type 4 (hinged, posterior axis of rotation) teeth are on the jaws in adults. See Fink (1981) for a discussion of actinopterygian tooth attachment morphology and its systematic implications.

35. In *Tactostoma* (Fig. 19), both adults and juveniles have type 4 tooth attachment (hinged, with posterior axis of rotation; see Fink, 1981). Retention of this mode of attachment in adults is considered a paedomorphic feature. (CI = 1.0)

In other stomiids, Type 4 teeth are found only in early post-larval ontogenetic stages.

36. In *Opostomias*, there is a large foramen passing vertically through the premaxilla, just lateral to the symphysis. A large mandibular tooth extends

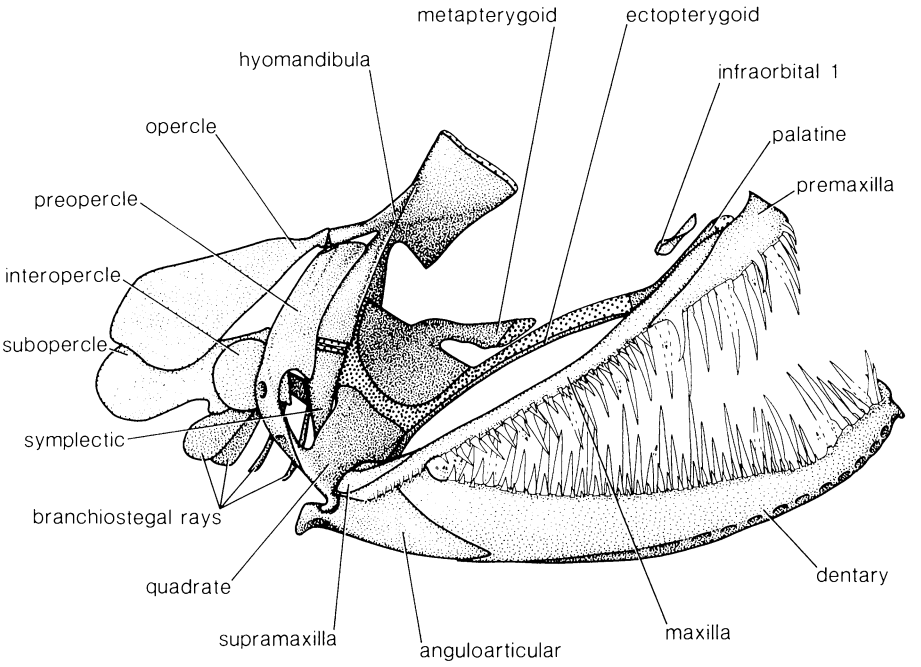

FIG. 19. Jaws and suspensorium of *Tactostoma macropus* (USNM 187654). Right side, lateral view.

up into the foramen when the mouth is closed. (CI = 1.0)

In other stomiids, no such foramen is present and the mandibular teeth, if sufficiently enlarged, extend anterior to the premaxilla.

37. In *Bathophilus* (Fig. 20), the premaxilla has a process which articulates along the anterodorsal margin of the maxilla. (CI = 1.0)

In other stomiids, the premaxilla articulates only along the anteroventral surface of the maxilla.

38. In *Stomias* (Fig. 21), the maxillae closely approach each other at the midline, anterior to the ethmoid region. This is part of the morphological complex of the protrusible upper jaw in which the maxillae act as links between the premaxillae and the ethmoid ossification. (CI = 1.0)

In other stomiids, the maxillae never closely approach the midline. *Eustomias* species have protrusible upper jaws, but the mechanism of protrusion is quite unlike that in *Stomias*. See Character 52.

39. In all stomiid genera except *Borostomias*, *Heterophotus*, *Neonesthes*, and *Rhadinesthes*, there are regularly and closely set teeth posteriorly on the ventral border of the maxilla which are about equal in length, or which become sequentially enlarged posteriorly (e.g., Figs. 18–30). In many of these taxa (see Character 40) there may also be larger teeth more anteriorly on the maxilla. (CI = .5)

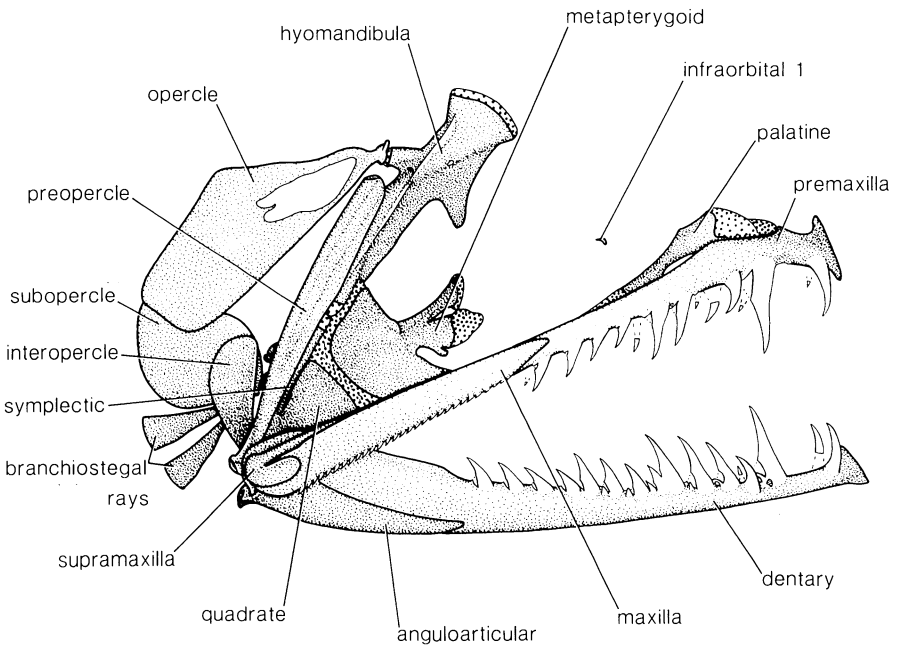

FIG. 20. Jaws and suspensorium of *Bathophilus pawneei* (USNM 159052). Right side, lateral view.

In the four stomiids noted and in most stomiiforms, the posterior maxillary teeth are irregularly and/or more distantly set, and include teeth of various sizes (e.g. some large teeth along with some much smaller teeth). Those stomiiforms with maxillary teeth approaching a condition as described here for the many above genera include some sternoptychids (see figures in Weitzman, 1974) and *Woodsia* (in which the highly specialized closely-set teeth are also present on the dentary).

40. In *Aristostomias*, *Astronesthes*, *Bathophilus*, *Chauliodus*, *Eustomias*, *Grammatostomias*, *Malacosteus*, *Pachystomias*, *Photostomias*, and *Stomias*, only small, closely- and regularly-set teeth are present on the maxilla (Figs. 20, 21, 23–27). (CI = .33)

In other stomiids, larger, less closely spaced, and less regularly-set teeth are also present.

41. In *Leptostomias* (Fig. 28), *Odontostomias*, *Opostomias*, and *Thysanactis*, the jaws are relatively short and deep, with the depth of the lower jaw at the coronoid process at least one-fourth the length of the lower jaw. (CI = 1.0)

In other stomiids, the jaws are more elongate and slender.

42. In *Chirostomias* (Fig. 29), *Stomias* (Fig. 21), and *Trigonolampa* (Fig. 22) the supramaxilla is extremely reduced, usually to a small sliver of bone. (CI = .5)

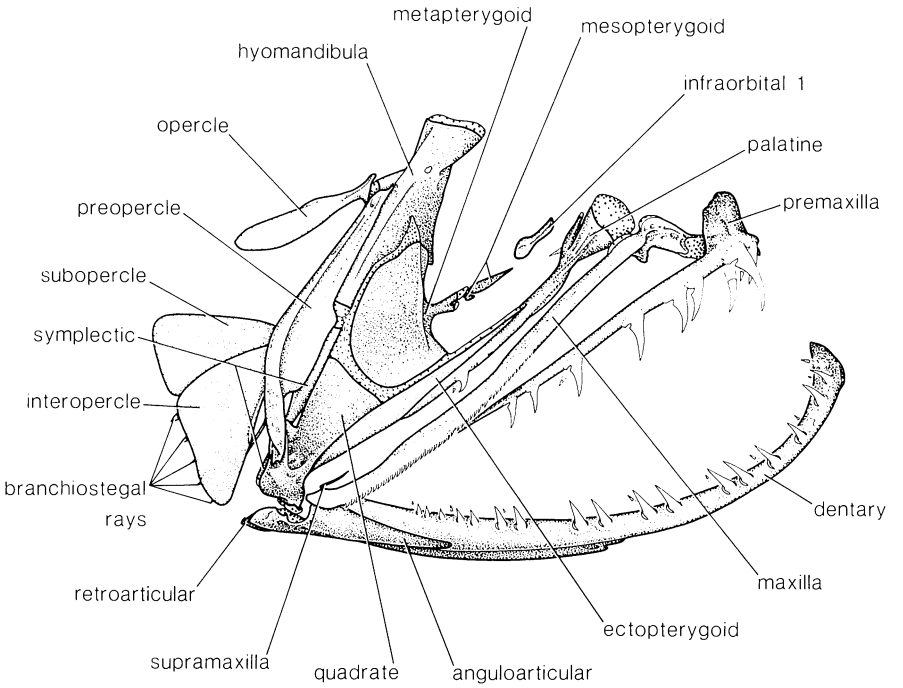

FIG. 21. Jaws and suspensorium of *Stomias lampropeltis* (USNM 199857). Right side, lateral view. Premaxilla in protruded position.

In other stomiids, the supramaxilla is variously sized, depending on the genus, but never as small as in the above three genera.

In presumed primitive *Astronesthes* species such as *A. splendidus* and *A. boulengeri* (Weitzman, 1967b, Fig. 25), the supramaxilla is reduced as an elongate slender ossification (although it is still larger than in the three genera above); in presumed phylogenetically derived species, such as *A. niger* (Weitzman, 1967b, Fig. 8) the supramaxilla is absent altogether.

43. In *Aristostomias, Bathophilus, Echiostoma, Eustomias, Grammatostomias, Idiacanthus, Malacosteus, Melanostomias, Pachystomias, Photonectes, Photostomias, Tactostoma,* and *Trigonolampa,* there is no retroarticular. (CI = .5)

In other "photichthyans," the retroarticular is present in at least some members of each genus.

44. In *Flagellostomias, Leptostomias* (Fig. 28), *Odontostomias, Opostomias,* and *Thysanactis,* the second large tooth from the symphysis of the dentary projects into the mouth at about a 60 degree angle. (CI = 1.0)

In other stomiids, none of the teeth on the anterolateral portion of the dentary project inward at that great an angle.

45. In *Aristostomias, Bathophilus, Eustomias, Grammatostomias, Malacosteus, Pachystomias,* and *Photostomias,* there is a ligament which attaches near the dorsoanterior border of each dentary, at the symphysis, and extends as a loop posteriorly in the anterior portion of the floor of the mouth. (CI = 1.0)

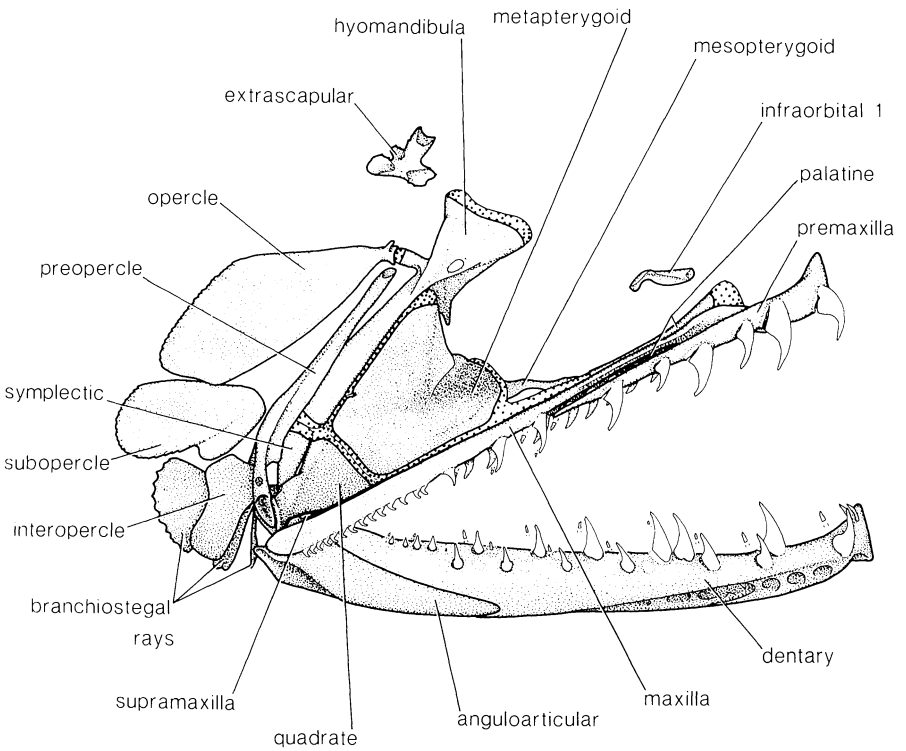

FIG. 22. Jaws and suspensorium of *Trigonolampa miriceps* (MCZ 35775). Right side, lateral view.

In other stomiids, no such ligament is present.

46. In *Photonectes* (Fig. 30), the process of the anguloarticular posterior to the articulation with the quadrate is elongate, almost equal to the length of the anterodorsal border of the quadrate. (CI = 1.0)

In other stomiids, the process is roughly half or less that length.

47. In *Aristostomias*, *Malacosteus*, *Pachystomias* (Fig. 27), and *Photostomias* (Fig. 25), the cartilage of the palatine arch is interrupted between the posterior margin of the palatine and the rest of the suspensorium, and the palatine itself terminates posteriorly in a bony point. (CI = 1.0)

In other stomiids, the cartilage of the palatine arch is uninterrupted.

48. In *Malacosteus* (Fig. 26), the palatine is represented by a cartilage body lying dorsomedial to the maxilla. (CI = 1.0)

In other stomiids, the palatine is ossified.

49. In *Idiacanthus* and *Tactostoma* (Fig. 19), the ventral border of the palatine arch is dorsally arched from lateral view. (CI = 1.0)

In other stomiids, the border is approximately straight or slightly arched ventrally from lateral view.

50. In *Borostomias*, the palatine bone extends posteriorly beyond the anterior border of the quadrate bone (see Weitzman, 1967b, Figs. 26, 27). (CI = 1.0)

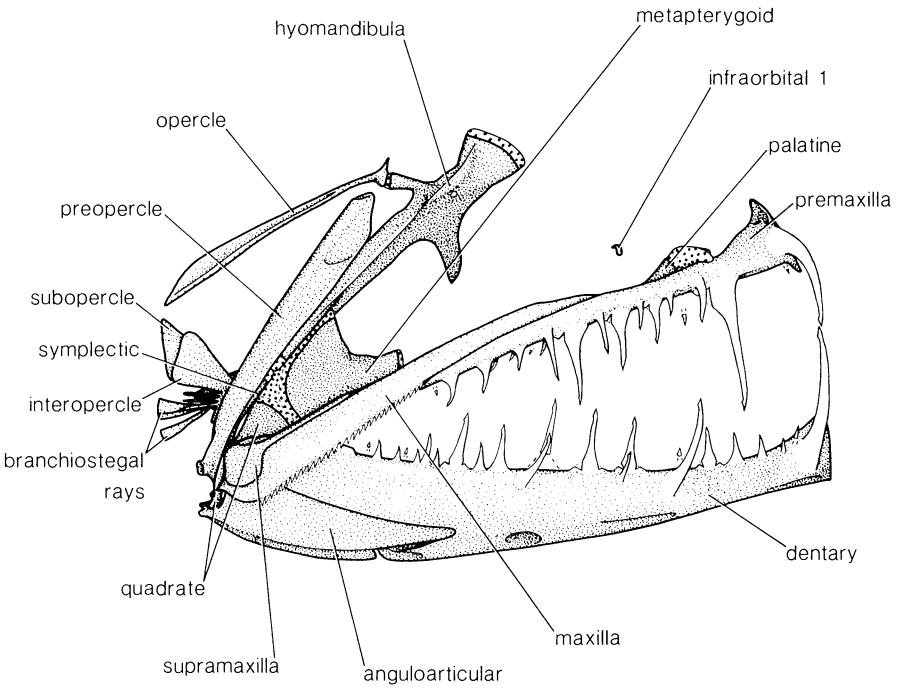

FIG. 23. Jaws and suspensorium of *Grammatostomias dentatus* (USNM 272903). Right side, lateral view.

In other "photichthyans", the palatine never extends as far posteriorly.

51. In *Chauliodus* and *Stomias* (Fig. 21), the palatine teeth are distributed in two areas: one or two teeth lie near the articulation of the palatine to neurocranium and one or more teeth lie well posterior. When more than one tooth is present posteriorly, the teeth are closely spaced. (CI = 1.0)

In other "photichthyans", the palatine teeth, when present, are either limited to the anterior area or are more or less evenly distributed along the bone; there is no distinct posterior grouping of teeth.

52. In *Eustomias* (Fig. 24), the ectopterygoid and palatine are largely separate from the quadrate, metapterygoid, and other bones of the jaw suspensory apparatus, the only attachment being by a thick ligament between the posterior tip of the ectopterygoid and the ventral, articular process of the quadrate. The ectopterygoid and palatine instead form a unit which is bound along the anterior three-fourths of its length to the posterior face of the maxilla. In addition, the anterior head of the palatine is large, with both the bony and cartilage portions projecting well dorsal to the margin of the maxilla. (CI = 1.0)

In other stomiids, the ectopterygoid is bound to the plate formed of the quadrate and metapterygoid rather than to the maxilla; the palatine articulates with the maxilla only.

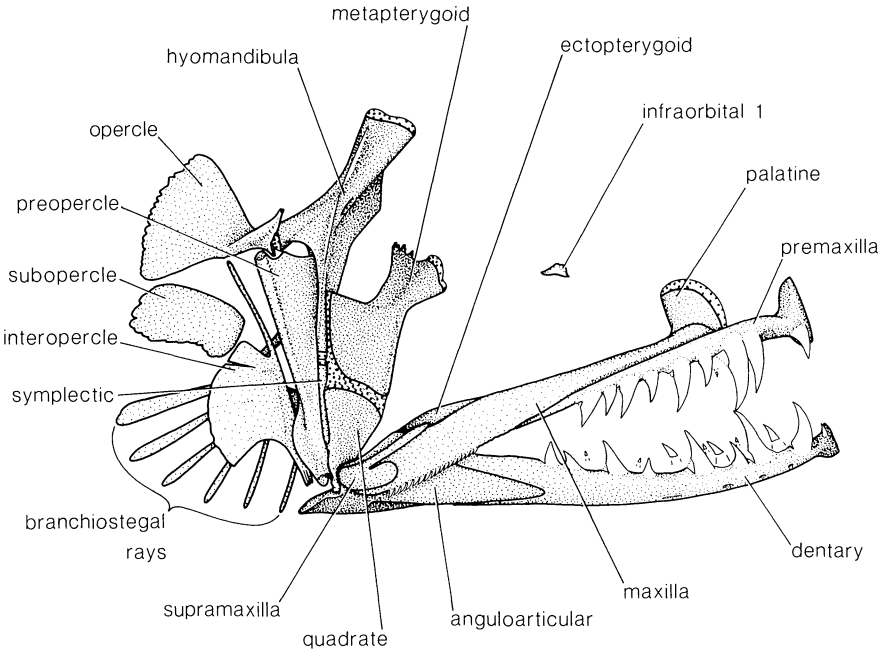

FIG. 24. Jaws and suspensorium of *Eustomias* cf. *macrurus* (USNM 272913). Right side, lateral view.

53. In stomiids, the mesopterygoid is reduced in size, so that the dorsomedial margin does not approach the parasphenoid. (CI = 1.0)

In other "photichthyans", the mesopterygoid is the most extensive bone of the suspensorium and closely approaches the parasphenoid.

54. In *Aristostomias*, *Bathophilus*, *Eustomias*, *Grammatostomias*, *Idiacanthus*, *Malacosteus*, *Pachystomias*, *Photostomias*, *Tactostoma*, and *Thysanactis*, the mesopterygoid is absent. (CI = .5)

In other stomiiforms, it is present.

55. In *Leptostomias*, *Odontostomias*, *Opostomias*, and *Thysanactis*, the orientation of the hyomandibula is nearly perpendicular to the long axis of the fish. (CI = 1.0)

In other stomiids, the hyomandibula lies at a more oblique angle to the long axis of the fish.

56. In *Flagellostomias*, *Leptostomias* (Fig. 28), *Odontostomias*, *Opostomias*, and *Thysanactis*, the opercular process of the hyomandibula is elongate and projects well posterior to the body of the hyomandibula, as does the dorsal ramus of the preopercle, leaving a large triangular space dorsally between the two bones. (CI = 1.0)

In other stomiids, the opercular process of the hyomandibula is generally not elongate; if elongate, it lies closer to the main axis of the hyomandibula.

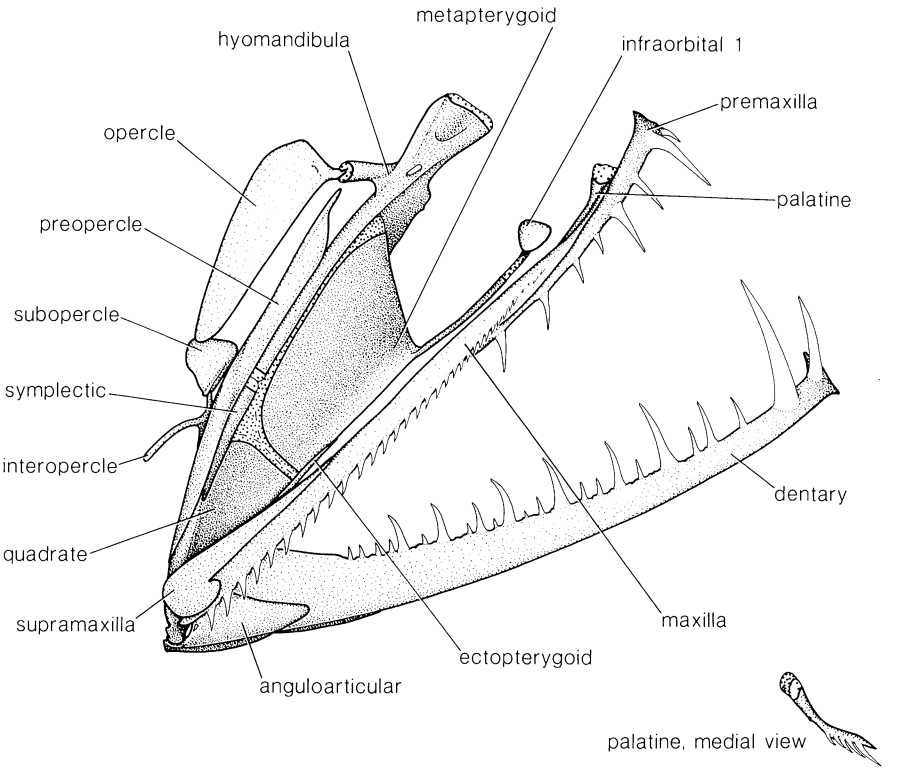

FIG. 25. Jaws and suspensorium of *Photostomias guernei* (USNM 272952). Right side, lateral view. Branchiostegal rays not shown.

The dorsal arm of the preopercle also lies closer to the main body of the hyomandibula, so that only a small space or no space is present between the two bones dorsally.

57. In *Heterophotus* and *Rhadinesthes,* the preopercle is very narrow at the symplectic-hyomandibular joint, so that the joint between the interhyal and the suspensorium is visible from lateral view (see Figs. 28 and 29 in Weitzman, 1967b). (CI = 1.0)

In other "photichthyans", the preopercle overlies the lateral surface of the interhyal-suspensorial joint.

58. In *Echiostoma* (Fig. 18), the preopercle has spinous lateral extensions ventrally, and the supramaxilla and antorbital are spinous or rugose. (CI = 1.0)

In other stomiids, there are no such extensions on these bones.

59. In *Flagellostomias, Leptostomias* (Fig. 28), *Odontostomias, Opostomias,* and *Thysanactis,* the interopercle has a characteristic shape, with a distinct triangular anterior process and an elongate slender posterodorsal process, the front border of which is aligned with the front border of the ventral portion of the bone. (CI = 1.0)

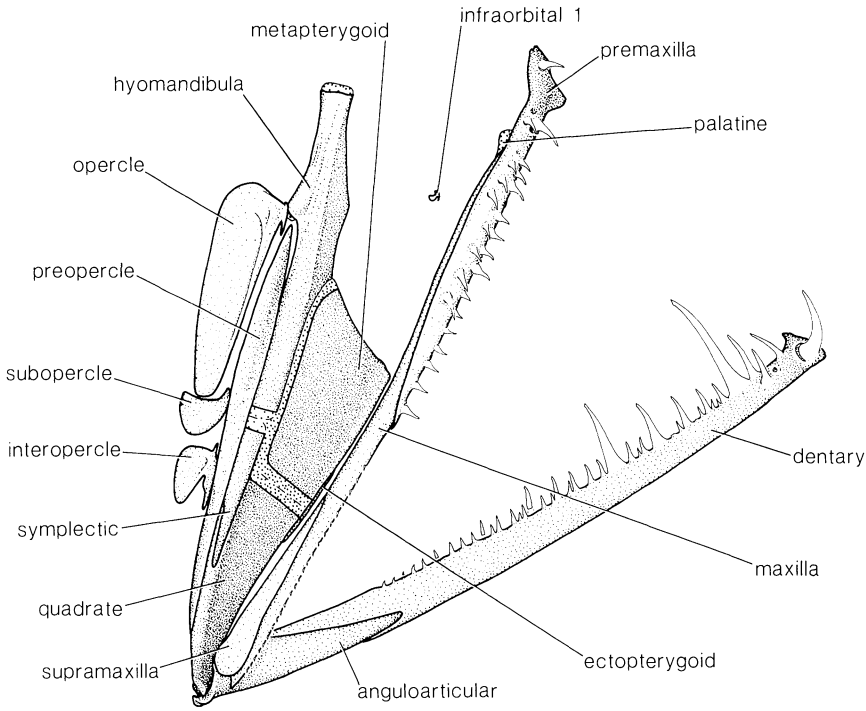

FIG. 26. Jaws and suspensorium of *Malacosteus* sp. (MCZ 53286). Right side, lateral view. Branchiostegal rays not shown. Left side, lateral view, reversed.

In other stomiids, no distinct triangular anterior process is present and any dorsal process, if present, is aligned more nearly horizontally.

60. In *Eustomias* (Fig. 24), the interopercle has an elongate dorsal ramus, along which runs the interopercle-opercle ligament; in many species there is also a ventral ramus associated with the interoperculo-mandibular ligament. (CI = 1.0)

In other stomiids, the dorsal border of the interopercle may be somewhat dorsally extended, but not nearly to the degree found in *Eustomias*.

61. In *Bathophilus*, *Echiostoma*, *Grammatostomias*, *Idiacanthus*, *Melanostomias*, *Photonectes*, *Stomias*, and *Tactostoma*, the ligament between the posteroventral process of the mandible and the posterior ceratohyal attaches well anterior to the point at which the posterior ceratohyal articulates with the interhyal. This feature was coded as missing in *Aristostomias*, *Eustomias*, *Malacosteus*, *Pachystomias*, and *Photostomias* (see Character 62). (CI = .5)

In other "photichthyans", the ligament attaches near the joint with the interhyal.

62. In *Aristostomias*, *Eustomias*, *Malacosteus*, *Pachystomias*, and *Photostomias*, there is no ligament between the mandible and the ceratohyal. (CI = .5)

See Character 61 for the primitive condition.

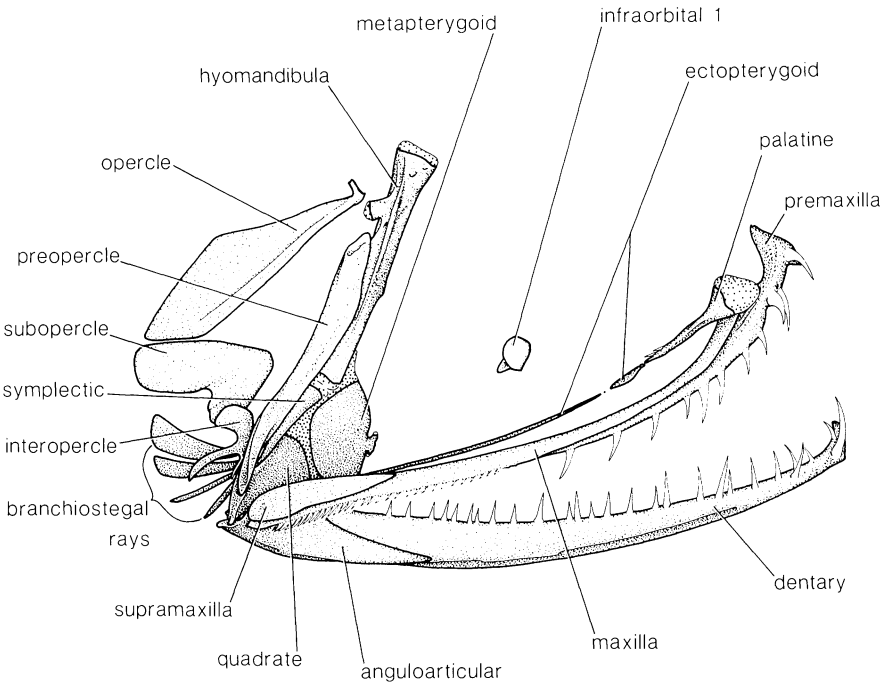

FIG. 27. Jaws and suspensorium of *Pachystomias microdon* (USNM uncat. DANA st. 4591). Right side, lateral view.

63. In *Chirostomias* and *Trigonolampa,* the ligament between the posterior ceratohyal and posteroventral process of the mandible attaches anterior to the posteroventral point of the mandible, near the articulation with the quadrate. In addition, the ligament between the posteroventral process of the mandible and the interopercle is absent. (CI = 1.0)

In other stomiids, the ligament from the posterior ceratohyal attaches to the posteroventral point of the lower jaw process, and a ligament from the interopercle also attaches to that point.

64. In *Heterophotus* and members of Clade J, the ligament between the interopercle and the interhyal is absent. (CI = .5)

In other "photichthyans", such a ligament is present.

65. In *Aristostomias, Bathophilus, Chirostomias, Echiostoma, Eustomias, Grammatostomias, Idiacanthus, Malacosteus, Melanostomias, Pachystomias, Photonectes, Photostomias, Tactostoma,* and *Trigonolampa,* there is no ligament between the interopercle and the posterior ceratohyal. (CI = .5)

In other stomiids (except *Chauliodus*; see Character 66), there is a ligament between the interopercle and the posterior ceratohyal near or along its posteroventral border.

66. In *Chauliodus,* there is a ligament between the subopercle and the posterior borders of both the interhyal and the posterior ceratohyal along

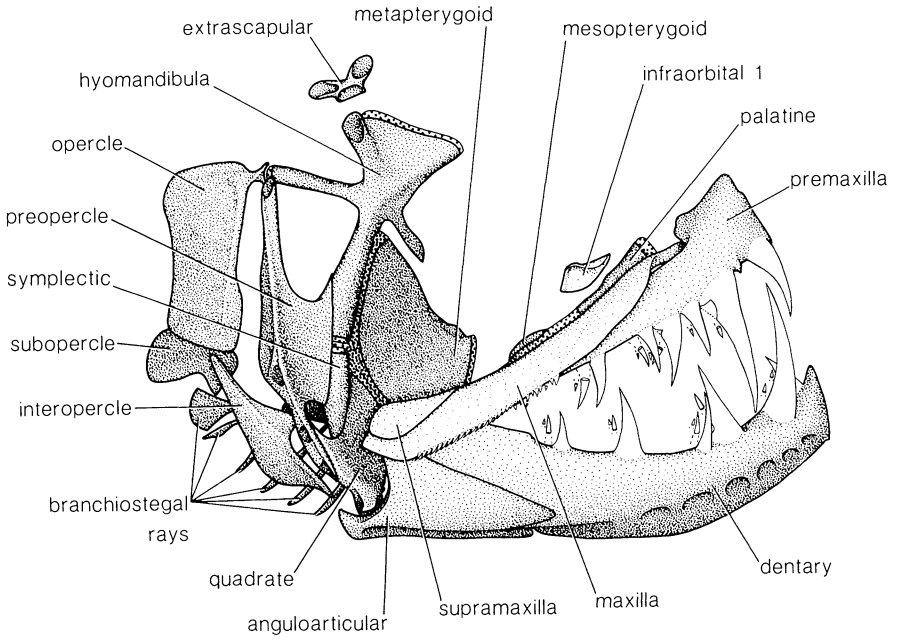

FIG. 28. Jaws and suspensorium of *Leptostomias gladiator* (USNM 199845). Right side, lateral view.

the joint between the two bones (the joint is nearly immobile). (CI = 1.0)

In other primitive stomiids and in some other stomiiforms, a similar ligament extends between the interopercle and the posteroventral border of the posterior ceratohyal.

67. In all members of Clade F except *Malacosteus,* there is a ligament between the ventral border of the suspensorium near its articulation with the lower jaw (i.e., the quadrate and/or the ectopterygoid) and the posterior region of the upper jaw (usually to the maxilla, but in *Echiostoma* to the posterior termination of the premaxilla). (CI = .5)

In other stomiids, no such ligament is present.

68. In *Idiacanthus*, *Leptostomias*, *Tactostoma,* and *Thysanactis,* the ligament between the ventral border of the suspensorium and the maxilla attaches to a flange of bone which projects anteroventrally from the quadrate. (CI = .5)

In other stomiids with such a ligament, there is no marked projection, either on the quadrate or the ectopterygoid, for attachment of the ligament.

The flange of bone is distinctly larger in *Tactostoma* and *Idiacanthus* than in *Leptostomias* or *Thysanactis.*

69. In *Aristostomias*, *Eustomias*, *Idiacanthus*, *Malacosteus, Melanostomias, Pachystomias, Photonectes, Photostomias, Stomias,* and *Tactostoma,* there is a ligament between the interopercle and the anterior border of the opercle. (CI = .25)

In other stomiids no such ligament is present.

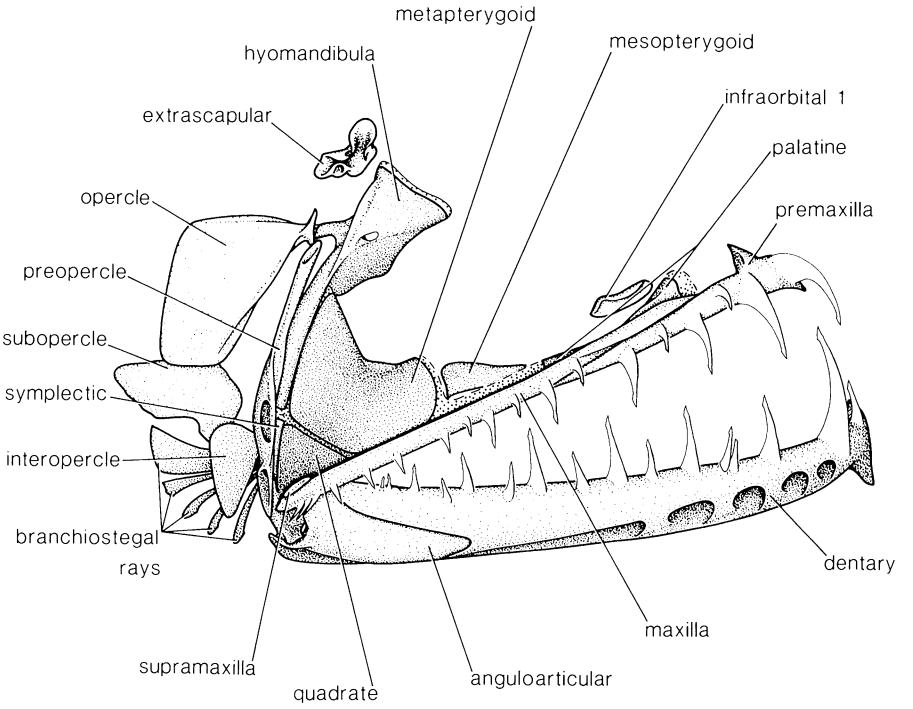

FIG. 29. Jaws and suspensorium of *Chirostomias pliopterus* (USNM 272905). Left side, lateral view, reversed. Cartilage partially dissolved; approximate extent indicated by dashed lines.

BRANCHIAL BASKET AND HYOID

70. In *Aristostomias*, *Bathophilus*, *Echiostoma*, *Eustomias*, *Grammatostomias*, *Idiacanthus*, *Malacosteus*, *Melanostomias*, *Pachystomias*, *Photonectes*, *Photostomias*, and *Tactostoma*, the interhyal articulates along or anterior to the front margin of the cartilage between the hyomandibula and symplectic and is bound to the metapterygoid by a ligament from the anterior margin of the interhyal. (CI = 1.0)

In other stomiids, the interhyal articulates along the posterior margin of that cartilage and is bound by a ligament to it and sometimes also to the hyomandibula (*Neonesthes*) or the posteroventral corner of the metapterygoid (*Astronesthes*).

71. In all stomiids but *Stomias*, the ventral end of the interhyal is bony, rather than cartilaginous as in other stomiiforms (Figs. 31, 32). (CI = .5)

The condition in *Stomias* (Fig. 31a) is hypothesized to be secondary and associated with an elongation of the posterior, cartilage-tipped process of the posterior ceratohyal (see Character 72).

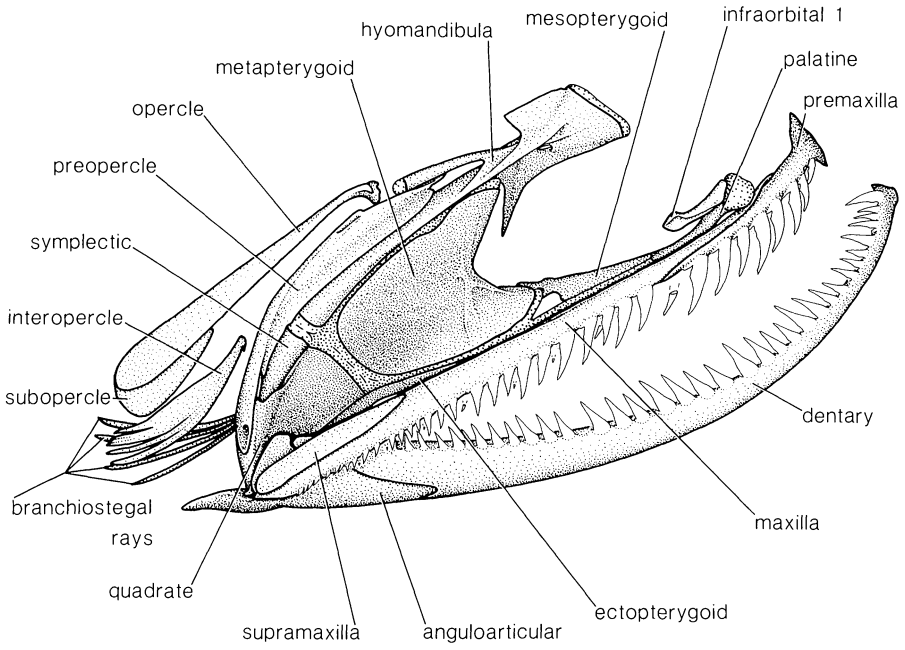

FIG. 30. Jaws and suspensorium of *Photonectes margarita* (MCZ 53260). Right side, lateral view. Opercle slightly displaced.

72. In *Stomias*, the interhyal is posteroventrally elongate and has a large ventral cartilaginous tip (actually a continuation of the cartilage core of the bone). (CI = 1.0)

In other stomiids, the interhyal is fully ossified ventrally.

73. In *Neonesthes* (Fig. 31d), the medial surface of the hyoid bar bears a row of toothplates which extends along nearly its entire length. (CI = 1.0)

In other "photichthyans", the hyoid bar lacks toothplates.

74. In *Aristostomias*, *Bathophilus*, *Eustomias* (Fig. 32c), *Grammatostomias* (Fig. 31e), *Malacosteus*, *Pachystomias* (Fig. 32d), and *Photostomias* (Fig. 32e), the basihyal is at least as long as the length of the anterior border of the hypohyal element (which includes the cartilage and both dorsal and ventral ossifications). (CI = 1.0)

In other "photichthyans", the basihyal is shorter.

75. In *Aristostomias*, *Bathophilus*, *Grammatostomias*, *Malacosteus*, *Pachystomias* and *Photostomias*, the posterior face of the basihyal is slightly concave. This feature is not visible in the figures. (CI = .5)

In other "photichthyans", it is slightly convex.

76. In *Heterophotus*, *Idiacanthus*, *Photonectes* (Fig. 32b), *Rhadinesthes*, and *Tactostoma*, the greatest length of the basihyal is no longer than about half the length of the anterior margin of the hypohyal element. (CI = .33)

In other stomiids, the basihyal is longer.

77. In *Idiacanthus* and *Tactostoma,* the basihyal is reduced to a thin, cylindrical element no broader distally than proximally and there is no ligament between its distal tip and the hypohyal element. (CI = 1.0)

In other stomiids, the basihyal is a larger element, broader distally than proximally, and the ligament is present.

78. In *Chauliodus, Leptostomias, Odontostomias* (Fig. 31c), *Opostomias,* and *Thysanactis,* there is a process proximally on the posterior face of the basihyal for attachment of a ligament to each dorsal hypohyal. (CI = .5)

In other stomiids, the process is absent, although the ligaments usually are present.

79. In *Bathophilus, Echiostoma, Eustomias, Grammatostomias, Idiacanthus, Malacosteus, Photonectes,* and *Tactostoma,* the urohyal is no longer than approximately the length of basibranchial 2. This is hypothesized to be a synapomorphy for a group comprised of the above genera plus *Aristostomias, Pachystomias,* and *Photostomias.* The presence of a urohyal about one-half (*Photostomias*) or one and one-third (the other two) the length of basibranchial 2 is interpreted as a reversal. (CI = .25)

In other "photichthyans", the urohyal is longer than the length of basibranchial 2.

80. In *Bathophilus, Chirostomias, Echiostoma, Eustomias, Flagellostomias, Grammatostomias, Idiacanthus, Leptostomias, Melanostomias, Odontostomias, Opostomias, Photonectes, Thysanactis,* and *Trigonolampa,* the width of the urohyal anteriorly is at least slightly greater than the width of the cartilage between basibranchials 2 and 3 at its widest point. (CI = .33)

In other "photichthyans", the width of the urohyal anteriorly is equal to or less than the width of the cartilage at its widest point.

81. In *Bathophilus, Chirostomias, Echiostoma, Eustomias, Grammatostomias, Idiacanthus,* and *Melanostomias,* the width of the urohyal anteriorly is roughly twice the width of the cartilage between basibranchials 2 and 3 at its widest point. (CI = .25)

In other stomiids, the width of the urohyal anteriorly is not as great.

(Because all components of the gill arches in these fishes change in proportion to each other, it is difficult to find a constant against which to measure the width of the urohyal. In *Idiacanthus,* the urohyal is actually broader than twice the width of the basibranchial 2-3 region because the latter region is unusually narrow. In *Bathophilus,* the latter region is unusually broad relative to the length of the basibranchial series, so that by this measure the urohyal is not quite twice the width.)

82. In *Idiacanthus, Malacosteus,* and *Tactostoma,* the posterior process of the urohyal is nearly absent. (CI = .5)

In other stomiids, the posterior process is distinctly longer.

83. In *Chirostomias,* the urohyal anteriorly has a pair of ventral processes longer than the anterior margin of the basihyal element. (CI = 1.0)

In other stomiids, any ventral processes are not as elongate.

84. In stomiids, the depth of the urohyal posteriorly is less than the depth of the basibranchial series. (CI = 1.0)

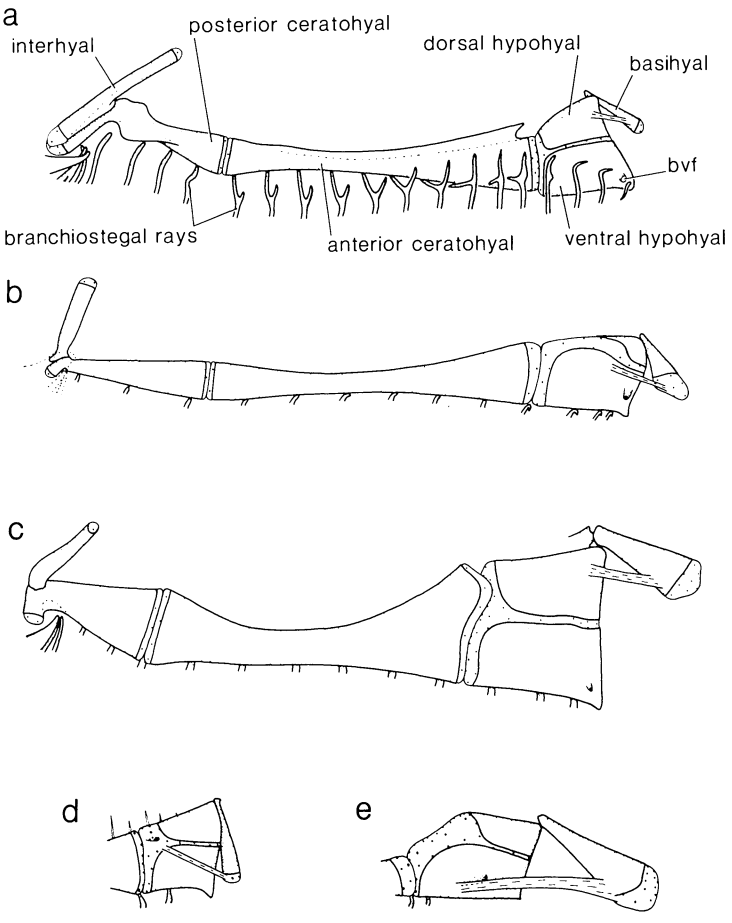

FIG. 31. Hyoid arch, including interhyal and basihyal. Right side, lateral view; bvf = blood vessel foramen. a, *Stomias brevibarbatus* (MCZ 58850); b, *Trigonolampa miriceps* (USNM 206683); c, *Odontostomias micropogon* (USNM 199849); d, *Neonesthes capensis* (USNM 272906); e, *Grammatostomias dentatus* (272903).

In other "photichthyans", the depth of the urohyal posteriorly is greater than the depth of the basibranchial series.

85. In *Aristostomias*, *Bathophilus*, *Eustomias*, *Grammatostomias*, and *Malacosteus*, the ligaments between the urohyal and the hypohyals are elongate, at least roughly half the length of the basibranchial 2 ossification. (CI = .33–.5)

In other stomiids, these ligaments are short.

86. In *Malacosteus*, the ligaments between the urohyal and the hypohyals are very elongate, about the length of basibranchial 2. (CI = 1.0)

In other stomiids, these ligaments are shorter.

87. In members of Clade D, the blood vessel which passes through the hypohyal element penetrates the lateral face of the element in the ventral hypohyal (Figs. 31a–31c, 31e). (CI = 1.0)

In other "photichthyans", this blood vessel penetrates the lateral face in the cartilage near the dorsal border of the hypohyal element (Fig. 31d).

88. In *Astronesthes*, the blood vessel which passes through the hypohyal element exits the dorsal hypohyal on the lateral face of the bone, then reenters the lateral face in the ventral hypohyal. (CI = 1.0)

In other "photichthyans", and in *Astronesthes niger* (a phylogenetically derived species in the genus), this lateral exit and the second entrance are not present.

89. In *Grammatostomias* (Fig. 31e), the foramen for passage of the blood vessel through the hypohyal element is located at about the midlength of the element (near the ventral border). (CI = 1.0)

In other stomiids with a foramen near the ventral border of the hypohyal element, the foramen is near the anteroventral corner of the element.

90. In members of Clade D, the ligament between the basihyal and the hypohyal attaches on the anterior half of the hypohyal element. (CI = 1.0)

In other "photichthyans", such as *Photichthys* and *Woodsia*, as well as *Diplophos*, the ligament attaches on the posterior half of the hypohyal element. In many primitive stomiiforms, the basihyal is reduced and closely bound to the front of the hypohyal element.

91. In *Aristostomias*, *Bathophilus*, *Grammatostomias* (Fig. 31e), *Malacosteus*, *Pachystomias* (Fig. 32d), and *Photostomias* (Fig. 32e), the ligament between the basihyal and the hypohyal element attaches to the latter ventral to its midheight. (CI = .5)

In other stomiids, the ligament attaches more dorsally.

92. In *Aristostomias*, *Bathophilus*, *Grammatostomias* (Fig. 31e), and *Malacosteus*, the ligament from the anterior of the basihyal attaches adjacent to the ventral border of the ventral hypohyal. (CI = .33–.5)

In other "photichthyans", the ligament (when present) attaches more dorsally, either near the dorsal margin of the ventral hypohyal or on the dorsal hypohyal.

93. In *Aristostomias*, *Bathophilus*, *Echiostoma*, *Eustomias*, *Grammatostomias*, *Idiacanthus*, *Malacosteus*, *Melanostomias*, *Pachystomias*, *Photonectes*, *Photostomias*, and *Tactostoma*, the front margin of the hypohyal element is oriented at roughly a 60 degree angle to the dorsal margin of basibranchial 1. In most cases, this results in the anterior margin of the urohyal being at about the level of a vertical drawn from the anterior margin of basibranchial 2, although the anterior margin of the urohyal is further anterior in those genera with an elongate basibranchial 1 (*Aristostomias*, *Pachystomias*, *Photonectes*, and *Photostomias*; see Character 110). (CI = 1.0)

In other stomiids, the front margin of the hypohyal element is at roughly a 90 degree angle to the dorsal margin of the first basibranchial, and the anterior margin of the urohyal is ventral to the first basibranchial.

94. In *Aristostomias*, *Bathophilus*, *Chirostomias*, *Eustomias* (Fig. 32c),

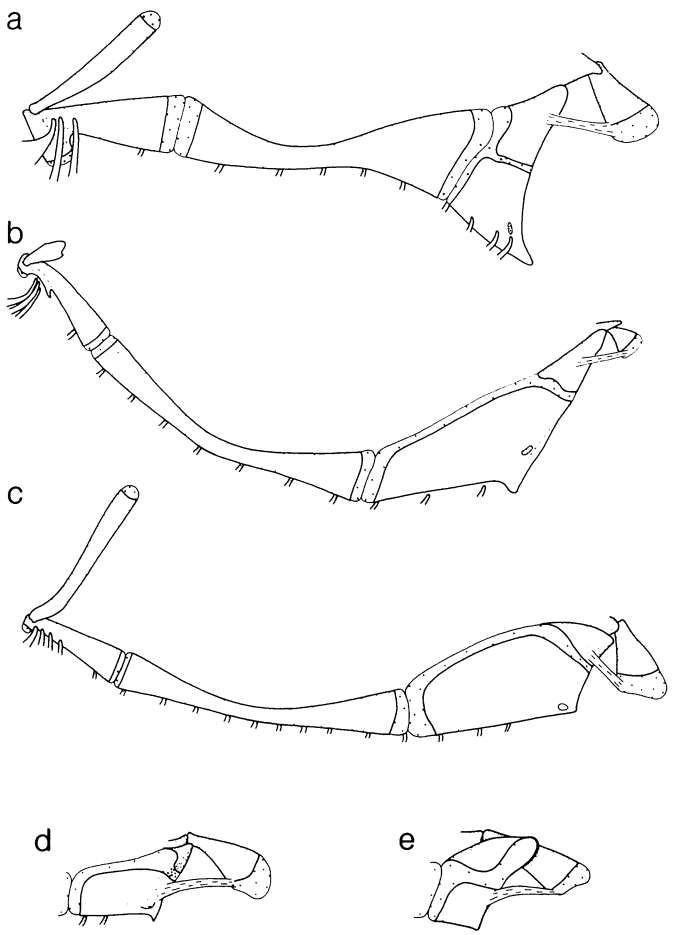

FIG. 32. Hyoid arch, including interhyal and basihyal. Right side, lateral view. a, *Melanostomias tentaculatus* (USNM 199848); b, *Photonectes leucospilus* (USNM 272911); c, *Eustomias* cf. *macrurus* (USNM 272913); d, *Pachystomias microdon* (USNM uncat. DANA st. 4591-6); e, *Photostomias guernei* (USNM 272952).

Flagellostomias, *Grammatostomias* (Fig. 31e), *Malacosteus*, *Pachystomias* (Fig. 32d), *Photonectes* (Fig. 32b), and *Trigonolampa* (Fig. 31b), the dorsal hypohyal is a small triangular ossification from lateral view, much smaller than the ventral hypohyal, and its dorsal border extends no more than approximately halfway across the dorsal border of the hypohyal element. Because of the peculiar morphology of the hypohyal element in *Photostomias* (see Character 99), it is difficult to tell whether the condition is present in that genus; if the anterior face of the dorsal hypohyal is equivalent to the lateral face in other stomiids, then the feature is present in *Photostomias* also. Because of this ambiguity, this character is coded as missing in *Photostomias*. (CI = .25)

In most other "photichthyans", the dorsal hypohyal is approximately rectangular from lateral view, is only slightly smaller than the ventral hypohyal, and extends across most of the dorsal border of the hypohyal element.

95. In *Bathophilus*, *Eustomias* (Fig. 32e), *Grammatostomias*, and *Photonectes* (Fig. 32b), the length of the hypohyal element is approximately one-half or more the length of the anterior ceratohyal. (CI = .5)

In other stomiids, the hypohyal element is shorter relative to the anterior ceratohyal.

96. In *Bathophilus*, *Eustomias*, and *Grammatostomias*, the hypohyal element is about twice as long anteroposteriorly as it is dorsoventrally, and its longest dorsoventral distance is posterior to the anterior border of the element. This character is not accurately depicted in Figs. 31 and 32 due to foreshortening. (CI = 1.0)

In other stomiids, the hypohyal is shorter, and its longest point dorsoventrally is along its anterior border.

97. In *Bathophilus* and *Grammatostomias* (Fig. 31e), the hypohyal element is deepest (dorsoventrally) posterior to the midlength of the element. (CI = 1.0)

In other stomiids, it is deepest anterior to the midlength.

98. In *Aristostomias*, *Malacosteus*, *Pachystomias* (Fig. 32d), and *Photostomias* (Fig. 32e), the anterodorsal region of the hypohyal element projects anterolaterally. (CI = 1.0)

In other stomiids, the hypohyal element is more nearly flat.

99. In *Photostomias* (Fig. 32e), the dorsal border of the hypohyal element is curved so far anteriorly that it projects anterior to the anteromedial border of the element, and from lateral view the dorsal surface of the dorsal hypohyal has a lateral depression. (CI = 1.0)

In other stomiids, the hypohyal element is only moderately curved or nearly flat.

100. In *Photonectes* (Fig. 32b), the anterodorsal section of the hypohyal element is elongate and the corner forms a highly acute angle. (CI = 1.0)

In other stomiids, no such elongation is present and the corner forms only a slightly to moderately acute angle.

101. In *Stomias* (Fig. 31a), the posterior ceratohyal has a dorsally directed bony process which serves as the attachment site for the ceratohyal-retroarticular ligament. (CI = 1.0)

In other stomiids, there is no dorsal process on the posterior ceratohyal. The ceratohyal-retroarticular ligament extends from the posterior ceratohyal near its articulation with the interhyal.

102. In *Stomias* (Fig. 31a), the cartilage-tipped posterior ramus of the posterior ceratohyal is elongate and in many species is equal in length to the main body of the bone. This ramus articulates posteriorly with the interhyal. (CI = 1.0)

In other "photichthyans", this ramus (sometimes directed ventrally) is short, and the interhyal articulates near the dorsoposterior apex of the posterior ceratohyal.

103. In stomiids, gill rakers are absent in adults. See Gibbs and Weitzman (1965) for a brief discussion of gill-raker ontogeny in certain stomiids. (CI = 1.0)

In other "photichthyans", gill rakers are present.

104. In *Astronesthes* and *Chauliodus*, the basibranchials are very narrow relative to their length; the cartilage between basibranchials 2 and 3 at its widest point is less than one-fourth the length of basibranchial 2 (the length being measured between the articulations of hypobranchials 1 and 2). (CI = .5)

In other stomiids and in *Woodsia* among "photichthyans", the basibranchials are not as narrow. This feature in *Astronesthes* and *Chauliodus* is a reversal relative to other "photichthyans", which have very narrow basibranchials.

105. In members of Clade F, there is no more than one pair of toothplates associated with any basibranchial ossification. (CI = 1.0)

In other "photichthyans", there are either more than one pair of toothplates associated with some basibranchials, or no toothplates at all (see Character 109).

106. In *Chirostomias*, *Trigonolampa*, and members of Clade O, the toothplates associated with the basibranchials are large relative to those associated with the hypobranchials, ceratobranchials, and epibranchials. (CI = .5)

In other stomiids, the toothplates are about equal in size.

107. In *Bathophilus*, *Eustomias*, *Flagellostomias*, *Grammatostomias*, *Leptostomias*, and some *Melanostomias*, there is only one tooth per toothplate on the bilateral pairs of basibranchial toothplates. (CI = .33)

In other stomiids with bilateral pairs of toothplates, there are usually more teeth per toothplate (*Idiacanthus* and some *Echiostoma* may have only one tooth per toothplate on basibranchial 2, and some *Malacosteus* specimens have only one tooth per toothplate on one side of basibranchial 1).

108. In *Bathophilus*, *Chirostomias*, *Echiostoma*, *Eustomias*, *Grammatostomias*, *Idiacanthus*, *Malacosteus*, *Melanostomias*, *Photonectes*, *Tactostoma*, and *Trigonolampa*, the teeth associated with the basibranchials are large. (CI = .25)

In other stomiids, the teeth are moderate in size, small, or absent.

109. In *Chauliodus*, *Neonesthes*, *Opostomias*, and *Stomias*, there are no teeth or toothplates associated with any basibranchials. (CI = .33)

In other stomiids, toothplates are associated with at least two, and primitively three, of the basibranchials.

110. In *Aristostomias*, *Pachystomias*, *Photonectes*, and *Photostomias*, basibranchial 1 is slender and elongate, more slender anteriorly, and the ossification surrounds the ventral cartilage margin of the copula except for a small cartilage process at the anteroventral border of the element. (CI = .33)

In almost all other stomiids, basibranchial 1 is about as deep as it is long, and the cartilage of the copula extends ventral to the margin of the ossifica-

tion (in *Flagellostomias*, there is an intermediate condition in which the basibranchial is slightly longer than it is deep and the ventral cartilage is interrupted by bone at approximately its midlength).

111. In members of Clade (B,C), with the exceptions noted below, there are one or more toothplates associated with basibranchial 1. The absence of such toothplates in *Opostomias* and in the group *Chauliodus* plus *Stomias* (Character 109) is considered due to reversals. (CI = .33)

In *Neonesthes* and in most "photichthyans" (all but *Photichthys*), such toothplates are absent.

112. In *Bathophilus*, *Echiostoma*, *Eustomias*, *Grammatostomias*, *Idiacanthus*, *Malacosteus*, *Melanostomias*, *Pachystomias*, *Photonectes*, and *Tactostoma*, the toothplate (*Idiacanthus*) or toothplates (the other taxa) associated with basibranchial 1 are positioned at or adjacent to the anterodorsal margin of the basibranchial. (CI = .33–.5)

In other stomiids, the toothplates are positioned more posteriorly on the basibranchial.

113. In *Echiostoma*, *Idiacanthus*, *Melanostomias*, some *Photonectes* species, and *Tactostoma*, the bilateral toothplates associated with the first basibranchial project anterior to the basibranchial-basihyal articulation. In *Idiacanthus*, the projection is slight; in the others, it is well developed. This character is coded as missing in *Photonectes* because I am unable to estimate whether species with the trait are phylogenetically primitive. (CI = .5)

In other stomiids, the tooth plates do not project anterior to the articulation.

114. In *Idiacanthus*, the pair of toothplates associated with basibranchial 1 are fused in the midline. (CI = 1.0)

In other stomiids with such toothplates, no fusion is present.

115. In members of Clade F, the toothplates associated with basibranchials 1 and 2 are limited to two per basibranchial, arranged in a closely associated bilateral pair. This is hypothesized to be a synapomorphy for a group comprised of the above genera plus *Opostomias*, which has lost all basibranchial toothplates (and is coded as missing). (CI = 1.0)

In other stomiids with basibranchial toothplates, there may be either one or two toothplates laterally on each basibranchial, the number may vary between one side and the other, and the plates are not arranged in closely bilateral pairs.

116. In *Photostomias*, there is a bilateral pair of toothplates situated with their midlengths between basibranchials 1 and 2 and another with their midlengths between basibranchials 3 and 4 (see also Character 120). (CI = 1.0)

In other stomiids with paired basibranchial toothplates, any equivalent toothplates are positioned on basibranchials 1 and 3.

117. In *Leptostomias* and *Thysanactis*, the lateral margins of the cartilage core in basibranchial 2 projects posterolaterally from the midlength of the basibranchial at roughly a 60 degree angle from the longitudinal axis of the basibranchials. (CI = 1.0)

In other stomiids, those margins project at an angle roughly 30 degrees or less.

118. In *Bathophilus*, *Echiostoma*, *Grammatostomias*, *Malacosteus*, and *Melanostomias*, the width of basibranchial 2 is about half its length. (CI = .33)

In other stomiids, basibranchial 2 is narrower.

119. In *Bathophilus*, the width of basibranchial 2 is greater than half its length. (CI = 1.0)

In other stomiids, the width is less.

120. In *Chirostomias* and *Trigonolampa*, the bilateral toothplates associated with basibranchials 2 and 3 are usually fused to the basibranchials (in one of two specimens of *Trigonolampa* examined, one toothplate on one side of basibranchial 3 was autogenous). (CI = 1.0)

In other stomiids and most other "photichthyans" with such toothplates, no such fusion is present (present in *Pollichthys* on basibranchial 2).

121. In *Pachystomias* and *Photostomias*, there is a pair of toothplates situated with their midlengths between basibranchials 2 and 3. (CI = .5)

In other stomiids with paired basibranchial toothplates, the equivalent pair is located on basibranchial 2.

122. In *Echiostoma*, *Idiacanthus*, *Melanostomias*, *Photonectes*, and *Tactostoma*, the dorsal surface of the third basibranchial lies at an angle to the dorsal surface of the first and second basibranchials. (CI = .5)

In other stomiids, the dorsal surfaces of basibranchials 1–3 are all in one plane.

123. In members of Clade O and some species of *Stomias*, basibranchial 3 is about four-fifths the length of basibranchial 2 or shorter. (CI = 1.0)

In other stomiids and most other "photichthyans", basibranchial 3 is about equal in length to or longer than basibranchial 2.

124. In *Leptostomias*, *Malacosteus*, *Odontostomias*, *Opostomias*, *Photostomias*, and *Thysanactis*, the lateral margins of the cartilage core in basibranchial 3 projects posterolaterally from the midlength of the basibranchial at roughly a 60 degree angle from the longitudinal axis of the basibranchials. (CI = .33–.5)

In other stomiids, those margins project at an angle roughly 30 degrees or less.

125. In *Aristostomias*, *Chauliodus*, *Malacosteus*, *Photonectes*, and *Photostomias*, basibranchial 3 is about two-thirds the length of basibranchial 2. (CI = .25–.33)

In other stomiids, basibranchial 3 is longer relative to basibranchial 2.

126. In *Aristostomias*, *Bathophilus*, *Chauliodus*, *Echiostoma*, *Flagellostomias*, *Grammatostomias*, *Heterophotus*, *Idiacanthus*, *Leptostomias*, *Melanostomias*, *Odontostomias*, *Opostomias*, *Pachystomias*, *Photonectes*, *Stomias*, *Tactostoma*, *Thysanactis*, and *Trigonolampa*, there are no toothplates associated with basibranchial 3. In *Odontostomias*, there was a toothplate present on one side in one of four specimens examined. (CI = .20–.167)

In other "photichthyans", there are toothplates associated with basibranchial 3 which are anterior continuations of the ceratobranchial se-

ries (associated either with basibranchial 3 or hypobranchial 3 in most "photichthyans").

127. In *Bathophilus, Echiostoma, Eustomias, Grammatostomias, Idiacanthus, Melanostomias,* and *Photonectes,* the fourth basibranchial is only as long as it is wide. (CI = .33)

In other stomiids, it is more elongate.

128. In members of Clade (B,C), with the exception of *Chauliodus* and *Stomias,* the fourth basibranchial is no more than twice as long as it is wide. (CI = .5)

In the above-mentioned two genera, *Neonesthes,* and "photichthyans", it is more elongate.

129. In *Echiostoma* and *Melanostomias,* the fourth basibranchial is approximately square from dorsal aspect. (CI = 1.0)

In other stomiids, it is oblong and narrows posteriorly, or it is "U"-shaped (see Character 130).

130. In *Idiacanthus,* the fourth basibranchial is very small and is "U"-shaped in dorsal view, with the arms of the "U" wrapping around the posterior tip of the third basibranchial. The fourth ceratobranchial articulates laterally with the joint between the fourth basibranchial and the third hypobranchial, and the third ceratobranchial articulates laterally on the third hypobranchial, just anterior to the posterior cartilage tip of the latter element. (CI = 1.0)

In other stomiids, the fourth basibranchial is approximately square or oblong in dorsal view, the fourth ceratobranchial articulates on the lateral surface of the fourth basibranchial, and the third ceratobranchial articulates with the posterior cartilage of the third hypobranchial.

131. In *Malacosteus,* there is a median toothplate associated with basibranchial 4. (CI = 1.0)

In other stomiids no toothplates are associated with basibranchial 4.

132. In *Aristostomias, Bathophilus, Eustomias, Grammatostomias, Idiacanthus, Malacosteus, Melanostomias,* and *Pachystomias,* the ligament between the first hypobranchial and the hypohyal element attaches near the posterior termination of the hypobranchial and at the midlength or near the posterior border of the hypohyal element. (CI = .25)

In most other stomiids, the ligament attaches near the middle or anteriorly on the hypobranchial, and anteriorly on the hypohyal element. In *Photonectes,* there are two ligaments attaching to the hypobranchial, one near its midlength and one posteriorly. The anterior ligament is broad and attaches to the hypohyal element somewhat posterior to its midlength; the posterior ligament becomes diffuse in connective tissue and does not attach to the hypohyal element. In *Stomias,* the ligament attaches posterior to the midlength of the hypobranchial, but near the midlength of the hypohyal element.

133. In *Eustomias, Idiacanthus, Malacosteus,* and *Melanostomias,* the first and second hypobranchials have a rounded anterior tip. (CI = .25)

In other stomiids, the anterior tips are dorsoventrally elongate, with ei-

ther a single, elongate tip or a bifurcated tip.

134. In *Chirostomias*, the anterior tips of the first and second hypobranchials are bifurcated, articulating dorsally and ventrally with the basibranchial cartilage. (CI = 1.0)

In most other stomiids, the anterior tips of the first and second hypobranchial are single. In *Bathophilus* and *Flagellostomias*, there is a bifurcation present only on the second hypobranchial; in *Tactostoma,* a bifurcation is present only on the first hypobranchial.

135. In *Chauliodus*, hypobranchial 2 is less than half the length of hypobranchial 1. (CI = 1.0)

In other stomiids, hypobranchial 2 is longer in proportion to hypobranchial 1.

136. In *Trigonolampa,* the third hypobranchials are fused to the third basibranchial. (CI = 1.0)

In other stomiids, no such fusion is present.

137. In *Chauliodus* and members of Clade F (but see below), there are no toothplates associated with hypobranchial 3. This feature is hypothesized to have arisen independently in *Chauliodus* (associated with other toothplate reduction) and in the members of Clade F. In *Odontostomias,* a toothplate was present on one side of two specimens examined, and on each side in two other specimens; this condition in the genus is considered a reversal. (CI = .33)

In other "photichthyans", tooth plates (and/or gill-raker homologues) are associated with hypobranchial 3.

138. In members of Clade O, the proximal ends of ceratobranchials 1 and 2 are enlarged in a roughly vertrolateral direction, providing an increased area of attachment for the obliqui ventrales muscles. In most cases, this results in the anterior termination of the ceratobranchials being distinctly larger than the posterior termination of the hypobranchials (in *Idiacanthus*, hypobranchial 1 is enlarged at its posterior end so that it extends further ventrally than the ceratobranchial). (CI = 1.0)

In other stomiids, no enlarged attachment site is present.

139. In *Leptostomias*, the toothplates along the posterior edge of ceratobranchial 4 are reduced to tiny discs of bone and lack teeth. (CI = 1.0)

In *Odontostomias, Opostomias,* and *Thysanactis,* the toothplates are larger and almost invariably bear one tooth each.

140. In *Aristostomias*, *Bathophilus*, *Chauliodus*, *Echiostoma*, *Eustomias*, *Grammatostomias*, *Heterophotus*, *Idiacanthus*, *Leptostomias*, *Malacosteus*, *Melanostomias, Odontostomias, Opostomias, Pachystomias, Photonectes, Photostomias, Rhadinesthes, Tactostoma,* and *Thysanactis,* there are no teeth attached to ceratobranchial 5. (CI = .25)

In other "photichthyans" (except *Ichthyococcus*), there are teeth attached to ceratobranchial 5.

141. In *Flagellostomias*, there is only a single tooth attached to the fifth ceratobranchial. (CI = 1.0)

In other stomiids, there are either no teeth or more than one. This char-

acter is coded as missing in all taxa listed as having the derived state of Character 140.

142. In *Leptostomias* and *Thysanactis,* only one toothplate is associated with the anterior border of the fifth ceratobranchial. (CI = 1.0)

In other stomiids with such toothplates, more than one is present. This character is coded as missing in those stomiids without such toothplates (see Character 140).

143. In members of Clade F, the main, cartilage-filled body of the third pharyngobranchial has a distinctly concave medial border, viewed from dorsal aspect. (CI = 1.0)

In other stomiids, the medial border of the third pharyngobranchial is only slightly concave, if at all.

144. In members of Clade O, the cartilage portion of the third pharyngobranchial is more curved in a horizontal plane than it is in other stomiids. (CI = 1.0)

145. In *Borostomias, Grammatostomias,* and some *Photonectes* species, the short process on the third pharyngobranchial for articulation with the second epibranchial is absent. (CI = .5)

In other stomiids, there is a short process on the third pharyngobranchial for articulation with the second epibranchial.

146. In *Malacosteus, Pachystomias,* and *Photostomias,* the third pharyngobranchial is very short relative to its width and has the medial border deeply concave. (CI = .5)

In other stomiids, the third pharyngobranchial is more elongate relative to its width and is either less curved or straight.

147. In *Malacosteus* and *Pachystomias,* the toothplate portion of the third pharyngobranchial overlaps the toothplate of the fourth pharyngobranchial. (CI = .5)

In other stomiids, the toothplates do not overlap or the toothplate of the fourth pharyngobranchial overlaps the ossification of the third pharyngobranchial.

148. In *Chauliodus* and members of Clade F, the fourth pharyngobranchial is fused to the third pharyngobranchial. (CI = .5)

In other stomiids, the third and fourth pharyngobranchials are separate.

149. In *Chauliodus, Heterophotus, Photostomias, Rhadinesthes,* and *Stomias,* the toothplate of the fourth pharyngobranchial tapers posteriorly to a point. (CI = .33)

In other "photichthyans", the toothplate posterior border is broadly rounded.

150. In *Heterophotus,* there is a small, separate cartilage articulating between the anterior tip of the second epibranchial and the short, anterolateral process of the third pharyngobranchial. (CI = 1.0)

In other stomiids, no such cartilage is present; the epibranchial articulates directly with the short anterolateral process of the third pharyngobranchial.

151. In *Borostomias,* the second epibranchial does not articulate with the

third pharyngobranchial. (CI = 1.0)

In other stomiids, the second epibranchial articulates with the third pharyngobranchial.

152. In *Bathophilus*, *Eustomias*, and *Grammatostomias*, the third epibranchial articulates with the third pharyngobranchial at a point anterior to the posterior border of the pharyngobranchial ossification. (CI = 1.0)

In other stomiids, the third epibranchial articulates with the third pharyngobranchial adjacent to the posterior border of the pharyngobranchial ossification.

153. In *Heterophotus*, the third epibranchial articulates dorsal to the third pharyngobranchial, anterior to the joint between the third and fourth pharyngobranchial. (CI = 1.0)

In almost all other stomiids, the third epibranchial articulates lateral to the joint between the third and fourth pharyngobranchials (see Character 154).

154. In *Neonesthes,* the third epibranchial articulates dorsal to the middle of the joint between the third and fourth pharyngobranchials. (CI = 1.0)

In almost all other stomiids, the third epibranchial articulates lateral to the joint between the third and fourth pharyngobranchials (see Character 153).

155. In *Eustomias* and *Grammatostomias*, the fourth epibranchial has a relatively small, round anterior tip which articulates with the medial portion of the posterior border of the fourth pharyngobranchial. (CI = .5)

In other stomiids, the fourth epibranchial has a wide articulation along most or all of the posterior border of the fourth pharyngobranchial.

156. In members of Clade (B,C), with the exception of *Leptostomias*, *Odontostomias,* and *Thysanactis,* there are no toothplates associated with epibranchial 4. This is hypothesized to be synapomorphic for members of Clade (B,C), with two reversals: 1) a reappearance of toothplates in a group comprised of *Leptostomias*, *Odontostomias, Opostomias,* and *Thysanactis* (associated with the reappearance of toothplates on the back edges of the gill arches), and 2) a subsequent loss of the toothplates again in *Opostomias.* (CI = .33)

In *Neonesthes* and most other "photichthyans", toothplates are present on the anterior margin of epibranchial 4 (gill rakers in *Ichthyococcus*).

157. In members of Clade (B,C), with the exception of *Leptostomias*, *Odontostomias, Opostomias,* and *Thysanactis,* there are no toothplates on the posterior edges of gill arches 1–3 and ceratobranchial 4 (see also Character 156). (CI = .5)

In most other "photichthyans", such toothplates are present (absent in *Ichthyococcus*).

158. In *Astronesthes*, *Borostomias*, *Chauliodus*, *Chirostomias*, *Echiostoma*, *Flagellostomias*, *Heterophotus*, *Idiacanthus*, *Leptostomias*, *Melanostomias* (Fig. 32a), *Odontostomias* (Fig. 31c), *Opostomias, Photonectes* (Fig. 32b), *Rhadinesthes, Stomias* (Fig. 31a), *Tactostoma, Thysanactis,* and *Trigonolampa* (Fig. 31b), the branchiostegal rays articulating along the ventral hypohyal extend to the

anterior border of the bone. (CI = .5)

In other "photichthyans", the branchiostegal rays articulate no further anteriorly than half the length of the ventral hypohyal.

159. In members of Clade J, with the exception of *Pachystomias,* there are fewer than six branchiostegal rays articulating with the ossification of the posterior ceratohyal (Figs. 31c, 31e, 32a, 32b, 32c). (CI = .5)

In other stomiids, and in "photichthyans" which I hypothesize to be closely related to stomiids (*Woodsia* and *Photichthys*), the number of such rays is six or more. Other stomiiforms have fewer than six, and the presence of fewer than six in the members of Clade J is considered a secondary reduction.

160. In *Malacosteus,* there are no branchiostegal rays along the anterior one-third of the anterior ceratohyal. (CI = 1.0)

In other stomiids, such rays are present.

161. In *Aristostomias, Bathophilus, Eustomias* (Fig. 32c), *Grammatostomias* (Fig. 31e), *Malacosteus, Pachystomias* (Fig. 32d), and *Photostomias* (Fig. 32e), there are no branchiostegal rays articulating on the ventral hypohyal near its anterior border. (CI = 1.0)

In other members of Clade (B,C), such branchiostegal rays are present.

162. In *Aristostomias, Bathophilus, Grammatostomias* (Fig. 31e), *Malacosteus,* and *Photostomias* (Fig. 32e), there are no branchiostegal rays articulating along most (*Grammatostomias*) or all (others) of the length of the hypohyal element. (CI = .33–.5)

In other stomiids, rays articulate along about half or more of the hypohyal element.

163. In *Bathophilus, Echiostoma,* some *Eustomias* species, *Grammatostomias, Idiacanthus, Malacosteus, Melanostomias* (Fig. 32a), *Photostomias* and *Tactostoma,* the number of branchiostegal rays articulating with the posterior ceratohyal ossification is fewer than five (three in *Bathophilus* and *Grammatostomias,* four in all others). (CI = .33)

In other stomiids, the number of such rays is five or more.

164. In *Bathophilus* and *Grammatostomias,* there are three branchiostegal rays articulating with the posterior ceratohyal ossification. (CI = 1.0)

In other stomiids, there are at least four such rays.

165. In *Astronesthes, Bathophilus, Borostomias, Chauliodus, Chirostomias, Echiostoma, Flagellostomias, Grammatostomias, Heterophotus, Idiacanthus, Leptostomias,* some species of *Melanostomias, Odontostomias* (Fig. 31c), *Opostomias, Pachystomias, Photonectes* (Fig. 32b), *Rhadinesthes, Stomias* (Fig. 31a), *Tactostoma, Thysanactis,* and *Trigonolampa* (Fig. 31b), the posterior branchiostegal rays overlap at their proximal tips. (CI = .25–.33)

In *Neonesthes* and in other "photichthyans", the proximal tips may be closely spaced but they do not overlap.

166. In *Bathophilus, Grammatostomias, Idiacanthus,* and *Tactostoma,* the posterior two branchiostegal rays are fused proximally. (CI = .5)

In other stomiids, no such fusion is present.

167. In *Chauliodus* and *Stomias* (Fig. 31a), the branchiostegal rays are

deeply bifurcated dorsally, with one or both of the two rami elongated.(CI = 1.0)

In other "photichthyans", the branchiostegals have a single dorsal termination, or very short bilateral rami (e.g., in *Aristostomias*).

Muscles and Ligaments of the Head

168. In stomiids, there are two main bodies of the geniohyoideus muscle, including a ventral (lateral primitively, e.g., in *Neonesthes*) portion which extends into the barbel (in those species with a barbel). In most stomiids, this ventral portion has two subsections anteriorly (but sometimes it has only one; see Character 172). (CI = 1.0)

In other stomiiforms and many other teleosts, the geniohyoideus is but a single broad muscle which inserts only on the lower jaw. See Winterbottom (1974) for a discussion of this muscle (as protractor hyoidei).

169. In *Aristostomias*, *Bathophilus*, *Eustomias*, *Grammatostomias*, *Malacosteus*, *Pachystomias*, *Photonectes*, and *Photostomias*, the dorsal portion of the geniohyoideus has a muscular insertion on the dentary. (CI = .5)

In most other stomiids, this muscle attaches to the dentary via a tendon. But see also Character 170.

170. In *Idiacanthus* and *Tactostoma* the dorsal portion of the geniohyoideus has both a tendinous and muscular insertion on the dentary. (CI = 1.0)

In most other stomiids, the insertion is tendinous. See also Character 169.

171. In *Rhadinesthes*, there is a muscle which extends between the barbel and the dentary. The muscle extends from the dentary near the symphysis into the barbel shaft; it may be a modification of the ventral portion of the geniohyoideus, with which it appears to merge in the proximal part of the barbel. (CI = 1.0)

In other stomiids, there is no muscle between the barbel and the dentary.

172. In *Aristostomias*, *Bathophilus*, *Eustomias*, and *Grammatostomias*, *Malacosteus*, and *Pachystomias*, the ventral portion of the geniohyoideus muscle has only one distal attachment site. (CI = .5)

In other stomiids, the muscle has two attachments in the barbel (or in the tissue overlying the hypohyals, if the barbel is absent). I am unable to confirm the single attachment site figured by Regan and Trewavas (1930, Fig. 23C) in my examination of *Photonectes* species, although I did not have the species they figured.

173. In *Aristostomias*, *Bathophilus*, *Eustomias*, *Grammatostomias*, *Heterophotus*, and *Pachystomias*, the ventral portion of the geniohyoideus has anterior and posterior muscular portions separated by a tendon. See Regan and Trewavas, 1930, Figs. 14, 28A; see Character 174. (CI = .25–.33)

In other stomiids, the ventral portion of the geniohyoideus has a single muscle body. In *Echiostoma* and *Melanostomias*, there is a partially tendinous area in the muscle, but that area is very small and has muscle tissue in it. I

was unable to confirm the apparently muscular anterior portion figured by Regan and Trewavas (1930, Fig. 23C) in *Photonectes* species I examined.

174. In *Malacosteus* and *Photostomias,* the ventral portion of the geniohyoideus distally overlies the dorsal portion of the geniohyoideus, wrapping over it dorsomedially and inserting in a connective tissue mass near the anterior of the hyoid. In both these genera, a barbel is absent. (CI = .5–1.)

In other stomiids, the ventral portion of the geniohyoideus lies ventral to the dorsal portion of the geniohyoideus.

175. In *Astronesthes, Borostomias, Heterophotus,* and *Rhadinesthes,* the dorsal portion of the geniohyoideus is subdivided into dorsal and ventral bodies. (CI = .5)

In other stomiids, the dorsal portion of the geniohyoideus is unsubdivided.

176. In *Echiostoma, Leptostomias, Melanostomias,* and some derived *Stomias* species (Fink and Fink, in press), the levator externus of the third epibranchial is absent. (CI = .5)

In other stomiids, this muscle is present.

177. In *Grammatostomias,* the levator internus to the posterior pharyngobranchial toothplate is absent. (CI = 1.0)

In other stomiids, the muscle is present.

178. In *Chauliodus* and *Stomias,* there is a ligament (or tendon, with some fibers of levator externus 4 attaching to it) from the dorsolateral tip of the fourth epibranchial to the cleithrum near its dorsal tip. (CI = 1.0)

In other stomiids, no such ligament is present.

179. In members of Clade (B,C), there are ventral rector gill arch muscles attaching to the fifth ceratobranchial and there is at least some development of a "rector communis" condition, in which fibers span the distance between two or more gill arches. (CI = 1.0)

In other stomiiforms, no rector muscle attaches to the fifth ceratobranchial and no fibers extend between non-adjacent gill arches.

180. In members of Clade (B,C), with the exception of *Astronesthes* and *Chauliodus,* the rector communis muscle extends anteriorly to attach at least as far forward as the anterior of the second hypobranchial. (CI = .33–.5)

In most other "photichthyans", there is no development of a rectus communis muscle. In *Astronesthes* and *Chauliodus,* the muscle extends anteriorly only to the third hypobranchial.

181. In members of Clade J and *Stomias,* the rector communis muscle extends anteriorly to attach at least as far forward as the second basibranchial. (CI = .5)

In other stomiids with such a muscle, the attachment site is not as far forward.

182. In members of Clade O and *Stomias,* the rector communis muscle extends anteriorly at least as far forward as the first basibranchial. (CI = .5)

In other stomiids with such a muscle, the attachment site is not as far forward.

183. In *Bathophilus, Eustomias, Grammatostomias, Pachystomias,* and

Photostomias, the rector communis muscle attaches anteriorly, at least in large part, to the ventral hypohyal (some attachment to basibranchial 1 may also be present; see Character 182). (CI = .33–.5)

In other stomiids with such a muscle, the attachment site does not include the hypohyal.

184. In *Photostomias,* the rector communis muscle attaches anteriorly solely to the ventral hypohyal. (CI = 1.0)

In other stomiids which have attachment of the muscle to the ventral hypohyal, some other attachment is also present.

185. In *Aristostomias, Bathophilus, Chauliodus, Eustomias, Grammatostomias, Malacosteus, Pachystomias, Photonectes, Photostomias,* and *Stomias,* the obliquus superioris muscle extends anteriorly to or beyond the level of the adductor arcus palatini. The muscle inserts on the parasphenoid or the vomer. In some genera, such as *Aristostomias* and *Photonectes,* some fibers may insert in a raphe with the adductor arcus palatini. (CI = .33)

In other stomiids, the obliquus superioris muscle reaches anteriorly only to the basioccipital bone, well posterior to the adductor arcus palatini.

186. In *Leptostomias, Odontostomias, Opostomias,* some apparently derived species of *Photonectes,* and *Thysanactis,* the adductor arcus palatini extends over the entire floor of the orbit. (CI = 1.0)

In other stomiids, the muscle lies primarily in the posterior half of the orbit floor.

187. In stomiids, a portion of the adductor mandibulae inserts on the PO photophore. This muscle rotates the organ so that the luminescent portion is rolled inwardly and the darkly pigmented surface is placed laterally, allowing the fish to "turn off" the photophore. In some derived species of *Astronesthes, Eustomias,* and *Stomias,* the photophore is small and the muscle may be absent. (CI = 1.0)

In other stomiiforms, no adductor musculature inserts on the PO or any other photophore.

188. In *Trigonolampa,* the portion of the adductor mandibulae inserting on the PO photophore forms the posterior muscular border of the orbit and has its origin on the sphenotic and pterotic bones. (CI = 1.0)

In other stomiids, the muscle lies posterior to the border of the eye and has its origin either as a fascia in the A_2A_3 musculature, or on the hyomandibula, or rarely, on the pterotic. See also Character 190.

189. In *Idiacanthus* and *Tactostoma,* the dorsal section of the medial division of the adductor mandibulae has its origin anterior or anteromedial to the insertion of the levator arcus palatini. (CI = 1.0)

In other stomiids, this section has its insertion lateral to the levator arcus palatini.

190. In *Stomias,* the A_2 portion of the adductor mandibulae has its origin on the sphenotic spine anteriorly, and is joined along its anterodorsal border by a raphe to the levator arcus palatini. (CI = 1.0)

In other stomiids, the A_2 has its origin posterior to the sphenotic spine and is not joined to the levator arcus palatini.

Postcranial Axial Skeleton

191. In *Leptostomias, Odontostomias, Opostomias,* and *Thysanactis,* the anterior few vertebral centra (3–6) are very narrow, with intercentral notochord spaces wider than the width of the centra. (CI = 1.0)

In most other stomiids, the anterior centra are broader than the intercentral spaces (many anterior centra are missing altogether in *Chauliodus* and *Eustomias*).

192. In *Eustomias* (Fig. 33), the notochord is greatly curved. This is part of a highly specialized morphology involving reduction of vertebral centra and hypertrophy of the neural arches. (CI = 1.0)

In other stomiids, the anterior vertebral region specializations do not include curvature of the notochord.

193. In stomiids, with the exception of *Astronesthes, Borostomias,* and *Heterophotus,* supraneurals are absent for the posterior half of the distance between the posterior margin of the neurocranium and the dorsal-fin origin. (CI = .33)

In the three above-mentioned genera and other "photichthyans", supraneurals are present for most or all of that distance.

194. In the members of Clade E (Fig. 34), most or all of the supraneurals are absent; the few remaining (if any) are at the anterior of the vertebral column. (CI = 1.0)

In other "photichthyans", supraneurals are present along almost half to all the distance between the posterior margin of the neurocranium and the dorsal-fin origin.

195. In *Aristostomias, Bathophilus, Chauliodus, Eustomias, Flagellostomias, Grammatostomias, Idiacanthus, Leptostomias, Malacosteus, Odontostomias, Opostomias, Pachystomias, Photostomias, Stomias, Tactostoma,* and *Thysanactis,* no more than one supraneural (that associated with the first neural arch) is present. (CI = .33)

In other "photichthyans", more than one supraneural is present.

196. In *Bathophilus, Eustomias, Grammatostomias, Idiacanthus, Leptostomias, Malacosteus, Pachystomias, Photostomias, Tactostoma,* and *Thysanactis,* all supraneurals are absent. (CI = .33)

In other stomiids, at least one supraneural is present.

197. In *Stomias* (Fig. 34), the anterior supraneural is proximally greatly expanded in an anteroposterior plane. (CI = 1.0)

In other "photichthyans", the anterior supraneural is not greatly expanded proximally (although it may be slightly larger in circumference) relative to more posterior supraneurals (Fink and Weitzman, 1982, Fig. 5).

198. In *Bathophilus, Chauliodus, Eustomias* (Fig. 33), *Leptostomias, Odontostomias, Opostomias, Photonectes,* and *Thysanactis,* the anterior accessory neural arch is present as a rounded cartilage. (CI = .20)

Such a cartilage is present on one side of a *Heterophotus ophistoma* specimen (USNM DANA st. 3751); on the other side, the neural arch of the anterior vertebra has a large anterior lobe, indicating that presence of such a

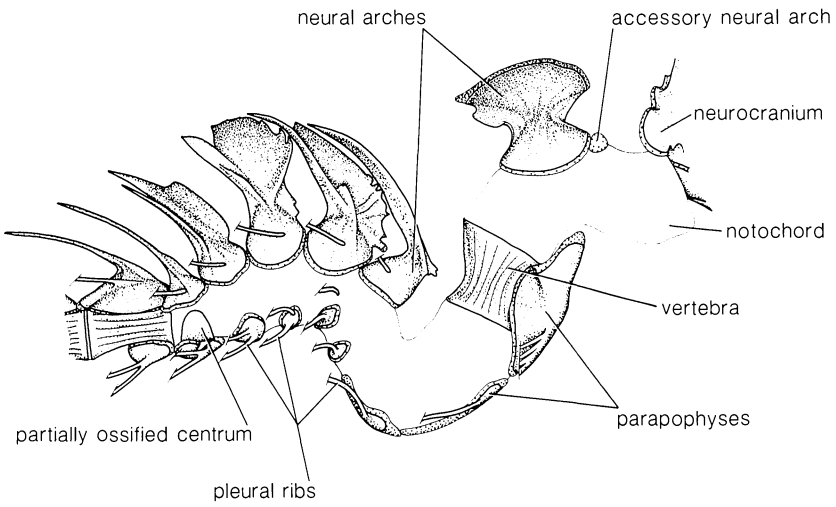

FIG. 33. Anterior vertebral region of *Eustomias* cf. *macrurus* (USNM 272913). Right side, lateral view.

lobe in other stomiids may be due to fusion of the anterior two neural arches. Such a lobe is present in *Borostomias*, *Heterophotus*, *Neonesthes*, *Stomias*, and other primitive "photichthyans".

199. In *Astronesthes*, the prezygapophyses of some of the anterior 10–20 neural arches are enlarged, closely approximate each other dorsally, and extend anteriorly over the neural tube as a bony hood (Fig. 13 in Weitzman, 1967b). (CI = 1.0)

In other "photichthyans", the prezygapophyses are not so enlarged, and no hood encloses the neural tube.

This character is more or less developed, depending upon the species of *Astronesthes* involved, and may be useful in elucidating relationships within the genus.

200. In members of Clade J, the spinous portion of most of the neural arches between the anterior arch and the dorsal-fin origin do not meet in the midline. (CI = 1.0)

In other stomiids, all neural arches meet in the midline.

201. In *Leptostomias*, *Odontostomias*, *Opostomias*, *Photostomias*, and *Thysanactis*, the spiny portion of the neural arches posterior to the first is progressively reduced in size until by the twentieth (or before), there is only a very short spiny process or none at all. This feature appears to have evolved independently in *Photostomias* on the one hand (see Character 209), and in the other four genera on the other. (CI = .5)

In other stomiids, the length of the neural spines decreases only slightly between the anterior vertebrae and the dorsal-fin origin.

202. In *Chauliodus* and *Stomias* (Fig. 34), the anterior portion of the neural arch of the first centrum is greatly enlarged compared to those of other centra. (CI = 1.0)

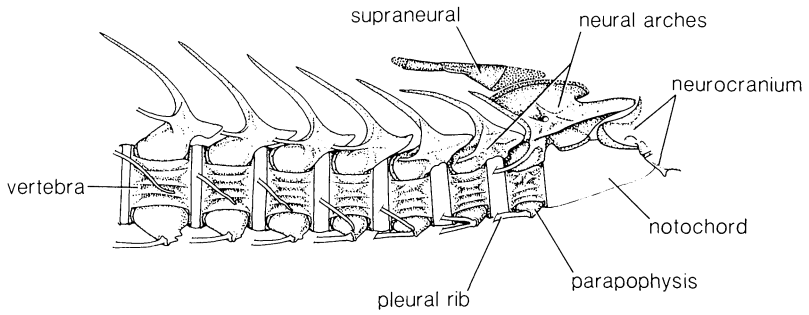

FIG. 34. Anterior vertebral region of *Stomias lampropeltis* (USNM 199857). Right side, lateral view.

In most other "photichthyans", the anterior neural arch is more or less identical to more posterior arches, although it may be slightly larger (see Fink and Weitzman, 1982, Fig. 5). In *Eustomias*, several of the anterior neural arches may be enlarged as a part of the complex modification of the anterior vertebral column in that genus (see Character 192). The condition in *Eustomias* is regarded as independently acquired.

203. In *Bathophilus*, *Chauliodus*, *Chirostomias*, *Echiostoma*, *Eustomias*, *Flagellostomias*, *Leptostomias*, *Melanostomias*, *Odontostomias*, *Opostomias*, *Tactostoma*, *Thysanactis*, and *Trigonolampa*, the anterior parapophysis has an anterior lobe. (CI = .167)

In other "photichthyans", no anterior lobe is present.

204. In *Chauliodus*, *Eustomias* (Fig. 33), *Flagellostomias*, *Leptostomias*, *Melanostomias*, *Odontostomias*, *Opostomias*, and *Thysanactis*, the anterior parapophysis has a large anterior lobe which projects well anterior to the border of the vertebra. (CI = .25)

In other stomiids, the anterior parapophysis has no anterior lobe or only a small anterior lobe.

205. In *Bathophilus*, *Echiostoma*, *Eustomias*, *Flagellostomias*, *Grammatostomias*, *Leptostomias*, *Malacosteus*, *Melanostomias*, *Odontostomias*, *Opostomias*, some derived *Stomias* species, and *Thysanactis*, the anterior parapophysis bears two elongate processes (or more, see Character 208). Because of its peculiar distribution in *Stomias* (Fink and Fink, in press), I am unable to assign polarity for this character in that genus, and the character is coded as "missing." (CI = .25)

In other stomiids, only one process is present on the first parapophysis.

206. In *Aristostomias*, *Bathophilus*, *Eustomias*, *Grammatostomias*, *Malacosteus*, and *Pachystomias*, the anterior parapophysis is fused to its contralateral in the midline. In *Eustomias* and *Grammatostomias*, the parapophyses are fused together only posteriorly; in the other genera the fusion is complete along the ventral midline. (CI = .5)

In other stomiids, the parapophyses are separate.

207. In *Aristostomias*, *Malacosteus*, and *Pachystomias*, the fused parapophysis element of the anterior centrum (see Character 206) has a single ventral apex from which the pleural ribs of each side extend. (CI = .5–1.0)

In *Bathophilus*, *Eustomias*, and *Grammatostomias*, the anterior parapophysis element is a fusion of the primitive pair, but the conjoining of the pair is less developed, and the pleural ribs extend from the lateral borders of the parapophysis rather than from a single apex. (See also Character 206). In other stomiids, there are two autogenous parapophyses on the anterior centrum.

208. In *Eustomias* (Fig. 33), *Malacosteus*, and some species of *Stomias*, the anterior parapophysis bears a multifurcate process. This character is coded as "missing" in *Stomias* (see Character 205). (CI = .5)

In other stomiids, the process is double or single.

209. In *Photostomias*, the pleural ribs, the parapophyses, and the neural arches are not ossified between about the seventh (pleural ribs and parapophyses) or the tenth (neural arches) vertebra and the region of the vertical-fin origins (where ossification reappears in the form of neural and hemal spines). (CI = 1.0)

In other stomiids, all neural arches, parapophyses, and pleural ribs are ossified.

210. In members of Clade E, except for *Chauliodus*, the epineurals are fused to the neural arches for most of the body length, from the anterior region of the vertebral column to the region of the anal-fin origin. (CI = .5)

In other stomiids, fusion of the epineurals to the neural arches ends well anterior to the anal-fin origin.

211. In stomiids, with the exception of *Astronesthes*, the epineurals are fused to the neural arches for more than half the body length. (CI = .5)

In other "photichthyans", the epineurals are fused for about half (*Astronesthes*) or less than half (most "photichthyans") the body length. The epineurals are fused for more than half the body length in *Ichthyococcus*; this character may actually be a synapomorphy of stomiids plus that genus.

212. In *Aristostomias*, *Bathophilus*, *Echiostoma*, *Eustomias*, *Grammatostomias*, *Idiacanthus*, *Malacosteus*, *Melanostomias*, *Pachystomias*, and *Photostomias*, the epipleurals are fused to the pleural ribs for most of the body length. (CI = .5)

In other stomiids, the epipleurals, when present, are autogenous for most of the body length.

213. In *Heterophotus*, there are no epipleurals. (CI = 1.0)

In other stomiids, epipleurals are present.

214. In members of Clade J, the caudal vertebral centra are reduced in size so that the second preural centrum (PU2) is half or less the length and height of the anteriormost fully developed vertebral centrum. (CI = 1.0)

In most other "photichthyans", the caudal centra are not so reduced in size. In *Stomias*, PU2 is less than half the height, though not less than half the length, of the anterior centrum; this reduction is hypothesized to have evolved independently in *Stomias*.

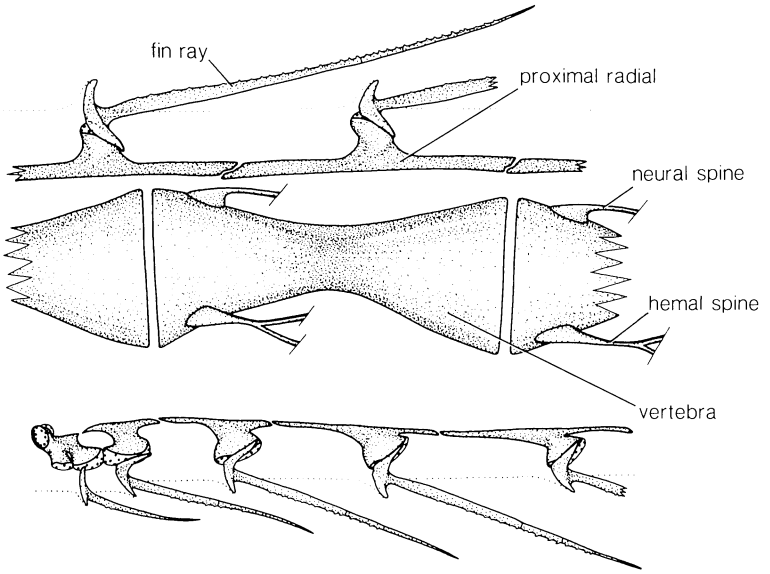

FIG. 35. Section of the axial and vertical-fin skeleton of *Idiacanthus fasciola* (ZMUC, DANA st. 3784 VIII), including the origin of the anal fin. Left side, lateral view. Dotted line indicates margin of body wall.

215. In members of Clade E, the anteriormost fully developed vertebral centrum and the posteriormost symmetrical centrum (PU2) are approximately two-thirds or less the length and height of the largest centra (those in roughly the midlength of the body). (CI = 1.0)

In other "photichthyans", the anterior and posterior centra are only slightly smaller than the largest ones.

VERTICAL FINS

216. In members of Clade E, with the exception of *Chauliodus*, the posterior end of the dorsal-fin base approaches the caudal peduncle. (CI = .5)

In other "photichthyans", the posterior end of the dorsal-fin base lies well anterior to the caudal peduncle.

217. In *Chauliodus*, the dorsal fin lies well anterior to the midbody. (CI = 1.0)

In other "photichthyans", the dorsal fin lies close to or behind the midbody.

218. In *Idiacanthus* (Fig. 35), the dorsal- and anal-fin supports are extensively modified. The dorsal-fin base is long, extending from anterior to the pelvic-fin insertion to the caudal peduncle. In males, the paired fins are not present, so that landmark cannot be used; nevertheless, the dorsal-fin base is also longer than in other stomiids. (See Gibbs, 1964b, Figs. 137–139.)

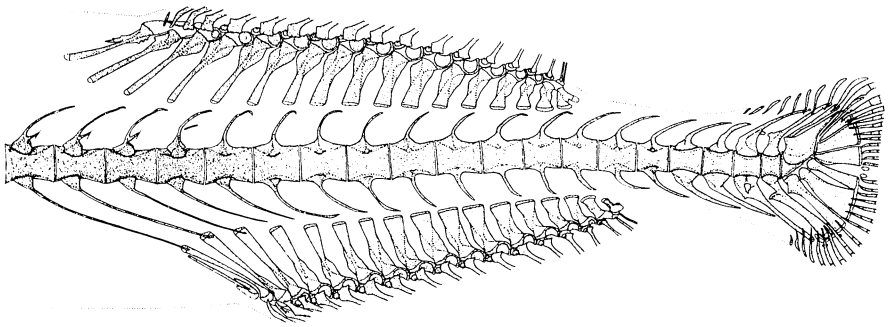

FIG. 36. Vertical-fin supports and posterior portion of axial skeleton of *Trigonolampa miriceps* (MCZ 35775). Left side, lateral view. Dotted line indicates margin of body wall.

The ray halves of most dorsal- and anal-fin rays are fused together for part or much of the length of each ray. There are no distal radials and no separate medial radial ossifications. Additionally, the proximal radials are roughly T-shaped, with a long horizontal portion, and a short vertical portion that articulates with the fin rays. The fin rays are widely spaced. (CI = 1.0)

In other stomiids, the dorsal-fin base is much shorter; all fin-ray halves are separate ossifications; distal radials are present; medial ossifications are usually present (but see Characters 222 and 226); the proximal radials are vertically elongate; and the fin-rays are more closely spaced (e.g. Figs. 36–38).

219. In *Eustomias* and *Flagellostomias*, the anal-fin origin is well anterior to a vertical from the dorsal-fin origin. See Morrow and Gibbs, 1964, Figs. 98 (*Eustomias*) and 130 (*Flagellostomias*); Regan and Trewavas, 1930, Pl. II, Fig. 2 (*Flagellostomias*) and Pl. VII, Figs. 1–4 (*Eustomias*). (CI = .5)

In other stomiids, the anal-fin origin is only just anterior to, or posterior to, a vertical from the dorsal-fin origin.

220. In members of Clade D, with the exception of *Chauliodus*, *Chirostomias*, and *Heterophotus*, the adipose fin is not present. (CI = .25)

In other "photichthyans", the adipose fin is present.

221. In *Eustomias*, the medial pterygiophore cartilage of the dorsal and anal fins is separate from that of the proximal pterygiophore, and is fused instead to that of the distal pterygiophore, and there is only one ossification on the resulting compound element. (CI = 1.0)

In other stomiids, the cartilage of the medial pterygiophore, and that of the proximal pterygiophore are fused, and the ossifications (when present) are separate (Fig. 37).

222. In *Aristostomias*, *Chauliodus*, *Heterophotus*, *Idiacanthus* (Fig. 35; see Character 218), *Malacosteus*, *Neonesthes*, *Pachystomias*, *Photostomias* (Fig. 38), and *Stomias*, no medial pterygiophore ossifications are present in the dorsal fin. (CI = .20)

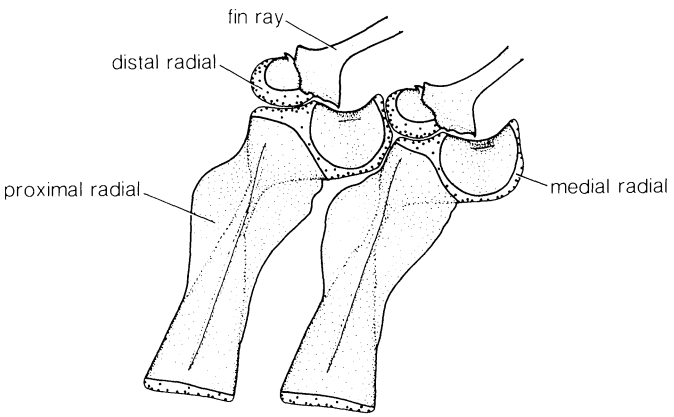

FIG. 37. Dorsal-fin pterygiophores of rays 9–10 of *Trigonolampa miriceps* (MCZ 35775). Left side, lateral view (detail of FIG. 36).

In most other "photichthyans" (except *Ichthyococcus*) such ossifications are present.

223. In *Borostomias*, *Chauliodus*, *Heterophotus*, *Neonesthes*, and *Rhadinesthes*, there is fusion between the distal cartilages of over half of the proximal pterygiophores of the dorsal fin. (CI = .25)

In most other "photichthyans", any fusion is present only between the last two or three pterygiophores (in *Polymetme*, almost half the distal cartilages are fused).

224. In *Chauliodus*, the distal cartilages of all the dorsal-fin proximal pterygiophores are fused together. (CI = 1.0)

In other "photichthyans", at least some proximal pterygiophores are completely separate.

225. In *Aristostomias*, *Chauliodus*, *Heterophotus*, *Malacosteus*, *Pachystomias*, *Photostomias*, *Rhadinesthes*, and *Stomias*, the number of medial pterygiophore ossifications present in the anal fin is reduced, so that they are absent on most (*Heterophotus* and *Rhadinesthes*) or all (all others) pterygiophores. (CI = .33)

In other "photichthyans", such ossifications are all present.

226. In *Aristostomias*, *Chauliodus*, *Idiacanthus* (Fig. 35), *Malacosteus*, *Pachystomias*, *Photostomias* (Fig. 38), and *Stomias*, the medial pterygiophore ossification is absent in the anal fin, and the medial pterygiophore cartilage is short. (CI = .33)

In most other "photichthyans", at least some medial pterygiophore ossifications are present in the anal fin and the cartilage is longer (*Ichthyococcus irregularis* lacks the ossifications).

227. In *Echiostoma*, *Idiacanthus* (Fig. 35), *Melanostomias*, and *Opostomias*, small hooks are present on the ray halves of the dorsal, anal, and pelvic fins. Hooks are present on the caudal fin rays also in *Echiostoma*, *Melanostomias*,

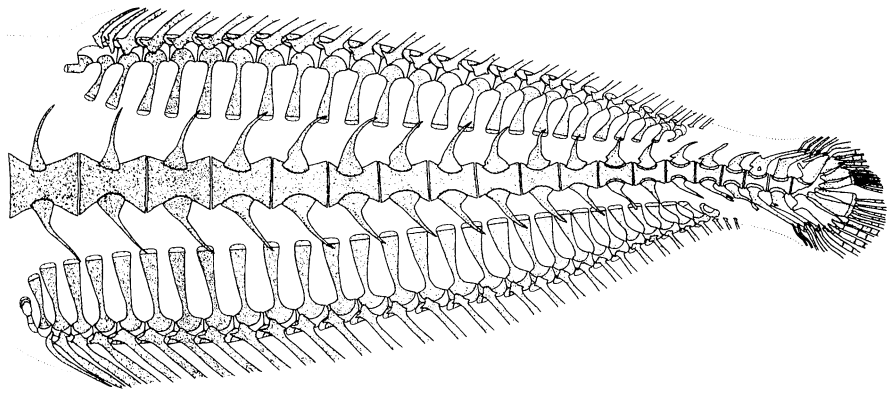

FIG. 38. Vertical-fin supports and posterior portion of axial skeleton of *Photostomias guernei* (USNM 225027). Left side, lateral view. Dotted line indicates margin of body wall.

and *Opostomias; Idiacanthus* has crenelations on the caudal rays, probably a derived condition of this character. (CI = .33)

In other stomiids, no such hooks are present.

228. In stomiids, hypural 6 is not present in the caudal skeleton (Figs. 36, 38). (CI = 1.0)

In other "photichthyans", it is present.

PECTORAL GIRDLE

229. In *Aristostomias, Bathophilus, Chauliodus, Eustomias, Grammatostomias, Malacosteus, Pachystomias,* some *Photonectes* species, *Photostomias,* and *Tactostoma* there is no extrascapular ossification. (CI = .33)

In most other "photichthyans", an extrascapular ossification is present. In *Photonectes margarita* the extrascapular is not present, but in other *Photonectes* species (such as *P. leucospilus*) there is a poorly ossified remnant of the dorsal sensory canal of the extrascapular. Evaluation of this character distribution in *Photonectes* must await hypotheses of relationship in that genus, and the character is coded as "missing."

230. In *Echiostoma* (Fig. 18), *Melanostomias,* and *Trigonolampa* (Fig. 22), the extrascapular borders are rugose or spiny. (CI = .5)

In other stomiids with an extrascapular, its borders are smooth.

231. In *Aristostomias, Bathophilus, Eustomias, Grammatostomias, Idiacanthus, Malacosteus, Pachystomias, Photostomias,* and *Tactostoma* there is no posttemporal bone. (CI = 1.0)

In other stomiids, the posttemporal is present, although it may be relatively small.

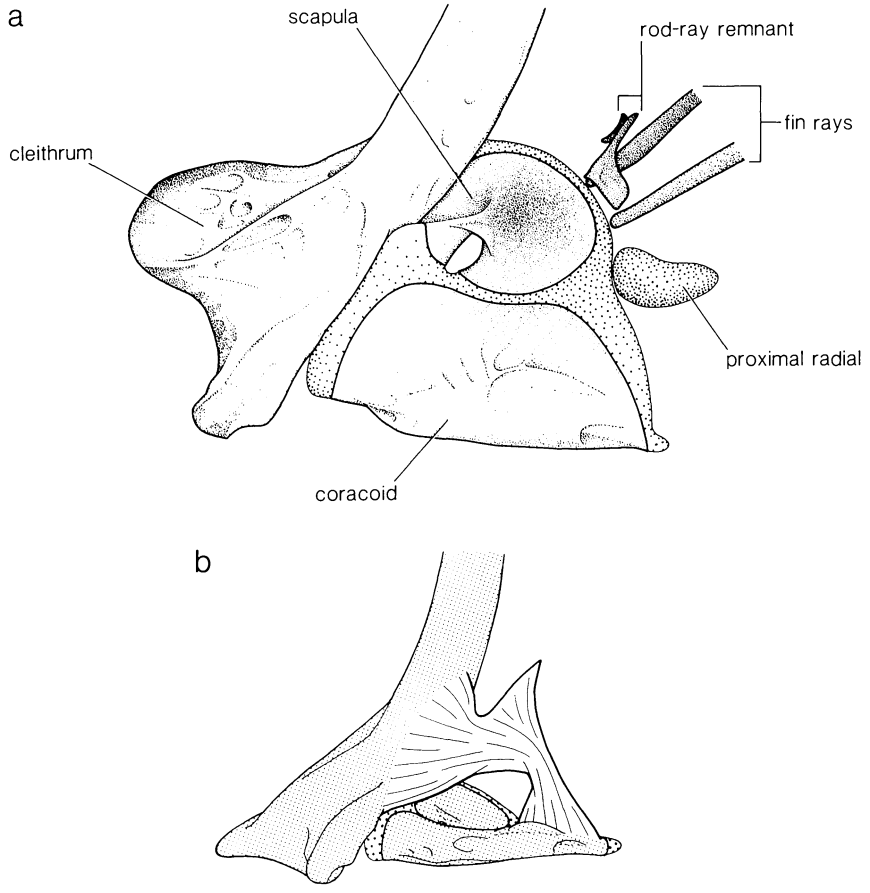

FIG. 39. Pectoral girdle of *Bathophilus pawneei* (USNM 159052), right side. a, dorsomedian view; b, median view showing connective tissue "mesocoracoid" structure.

232. In *Chauliodus*, the posttemporal is a thin disc of bone lying just anterior to the dorsal tip of the supracleithrum. (CI = 1.0)

In other stomiids, the posttemporal is represented by an elongate dorsal ramus, often with a ventral ramus, or is absent.

233. In *Heterophotus*, the dorsal ramus of the posttemporal is very thin and long and is articulated with the epioccipital by a long, very thin ligament. (CI = 1.0)

In other "photichthyans", the ramus may be elongate but never as much as in *Heterophotus*, and the attaching ligament is always much shorter than in *Heterophotus*.

234. In *Eustomias*, the supracleithrum is absent. (CI = 1.0)

In other stomiids, a supracleithrum is present although reduced in some.

235. In *Heterophotus* and *Rhadinesthes*, the dorsal tip of the cleithrum is an elongate slender spine. (CI = 1.0)

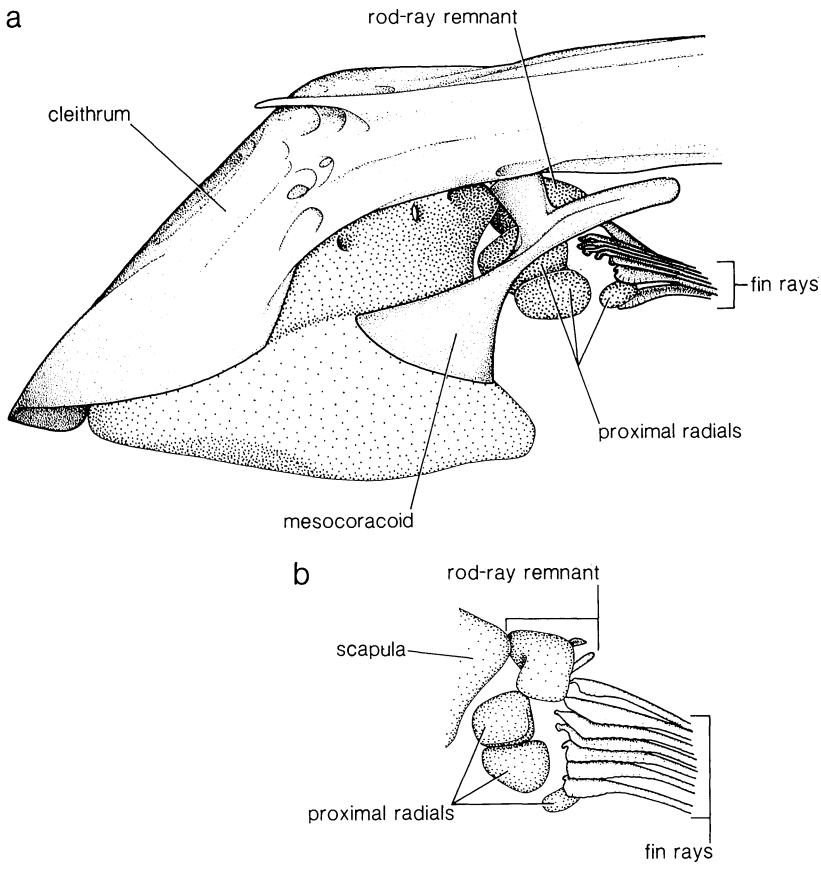

FIG. 40. Pectoral girdle of *Aristostomias xenostoma* (USNM 272943), right side. a, dorsomedian view; b, detail, dorsal view.

In other "photichthyans", the dorsal tip of the cleithrum may be blunt or pointed, but is never extended as in these two genera.

236. In *Bathophilus* (Fig. 39a) and *Grammatostomias*, the lateral wing of the cleithrum is laterally extended, somewhat thickened, and enlarged relative to the main body of the cleithrum anterior to the main curvature; the anterior termination of the main axis is somewhat to greatly foreshortened. In *Bathophilus* species the lateral wing is larger relative to the anterior main body of the cleithrum than in *Grammatostomias*. (CI = 1.0)

In other stomiids the lateral wing is not enlarged and extended as above.

237. In *Aristostomias* (Fig. 40a), *Malacosteus*, and *Photostomias*, the ventromedial surface of the cleithrum is concave near the main curvature. This concavity enfolds the cartilage of the coracoscapular plate, which is greatly reduced in *Photostomias*. (CI = .5–1.0)

In other stomiids, this ventromedial area is straight to slightly convex.

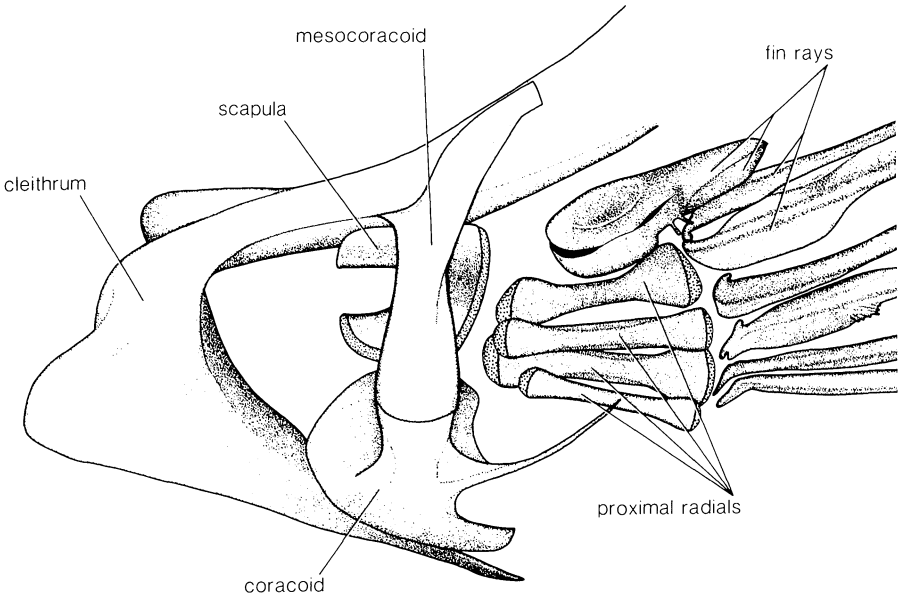

FIG. 41. Pectoral girdle of *Chirostomias pliopterus* (USNM 272907). Right side, dorsomedian view. Cartilage largely dissolved; reconstruction is approximate.

238. In *Chirostomias*, the cleithrum is bifurcated anteroventrally, with the primary axis of the girdle curving medially and terminating in a long, tapering posteroventral ramus. A ventrally-oriented lateral wing extends posteriorly from the lateral ramus. (CI = 1.0)

In other stomiids, there is a single anteroventral termination of the cleithrum. In *Bathophilus*, the lateral wing is expanded and more or less horizontally oriented, making it appear that the cleithrum is anteriorly bifurcated (see Character 236).

239. In *Odontostomias* (Fig. 42) and *Opostomias,* the cleithra are extremely fenestrated. The fenestrae are small, fairly regularly arranged and filled with oil. (CI = 1.0)

In other stomiids, the cleithra are not fenestrated but have surfaces ranging from smooth to slightly ridged. Large specimens of *Astronesthes* sometimes have a partially fenestrated cleithrum, but much less so than the two above-listed genera.

240. In *Aristostomias*, *Bathophilus*, *Echiostoma*, *Eustomias*, *Flagellostomias*, *Grammatostomias*, *Leptostomias*, *Malacosteus,* *Melanostomias,* *Odontostomias,* *Opostomias, Pachystomias, Photonectes,* and *Thysanactis,* the edge of the coracoscapular plate between the proximal part of the scapular ramus (for articulation of the rod-ray or remnant) and the medial point of articulation of the proximal radials is concave. This feature is hypothesized to be a synapomorphy for a group including the above genera plus *Idiacanthus, Photostomias*, and *Tactostoma*, all of which lack a scapula and proximal radials

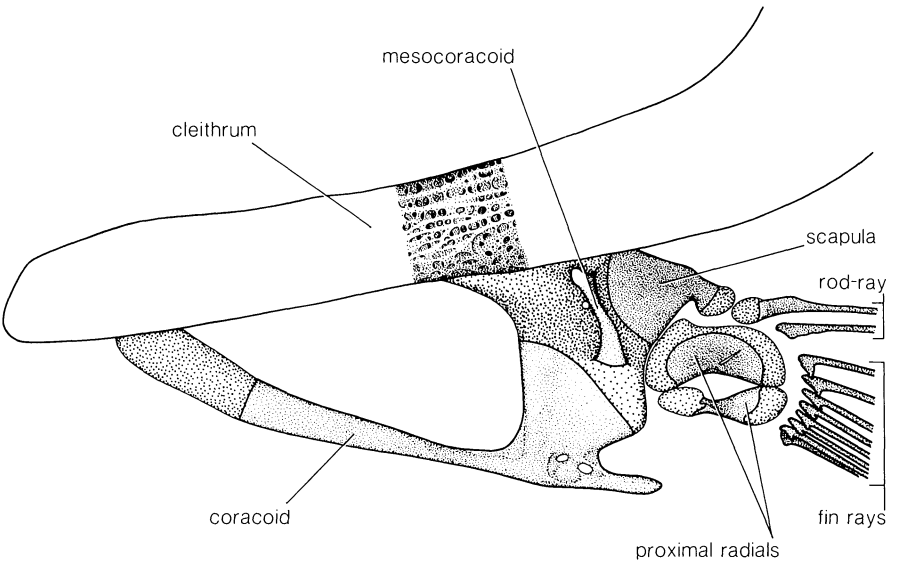

FIG. 42. Pectoral girdle of *Odontostomias micropogon* (USNM 199849). Right side, dorsomedian view.

and have the coracoscapular plate greatly reduced (this character is coded as missing in these taxa). (CI = 1.0)

In other stomiids , this border of the plate is slightly convex.

241. In *Aristostomias*, *Malacosteus,* and *Pachystomias,* the coracoscapular plate is dorsoventrally thicker relative to that of other "photichthyans," especially laterally. This is most obvious in *Aristostomias*, Fig. 40a. This feature is coded as missing in *Idiacanthus*, *Photostomias,* and *Tactostoma.* (CI = 1.0)

242. In *Idiacanthus*, *Photostomias,* and *Tactostoma,* the coracoscapular plate is greatly reduced. (CI = .5)

In other "photichthyans", the plate is more developed.

243. In *Eustomias*, the coracoscapular plates are fused to each other anteriorly (see Figs. 45, 46 and note cut surfaces). (CI = 1.0)

In other stomiids, the coracoscapular plates may be tightly bound together, but they are not fused.

244. In *Photonectes,* there is dense fibrocartilage lying between the anteromedial tip of the coracoscapular plate and the cleithrum. In some species there is a foramen formed lateral to this fibrocartilage mass. (CI = 1.0)

In other stomiids, the coracoscapular plate articulates with the cleithrum anteriorly as hyaline cartilage.

245. In *Aristostomias*, *Eustomias*, *Idiacanthus*, *Photonectes, Photostomias,* and *Tactostoma,* the scapular ossification is reduced in extent. In *Eustomias*, it consists of a small circular disc lying on either side of the coracoscapular plate (Figs. 45, 46). For conditions in the other taxa, see Characters 246 and 247. (CI = .20–.25)

In other "photichthyans", the scapular ossification is more extensive.

246. In *Aristostomias, Idiacanthus, Photonectes, Photostomias,* and *Tactostoma,*

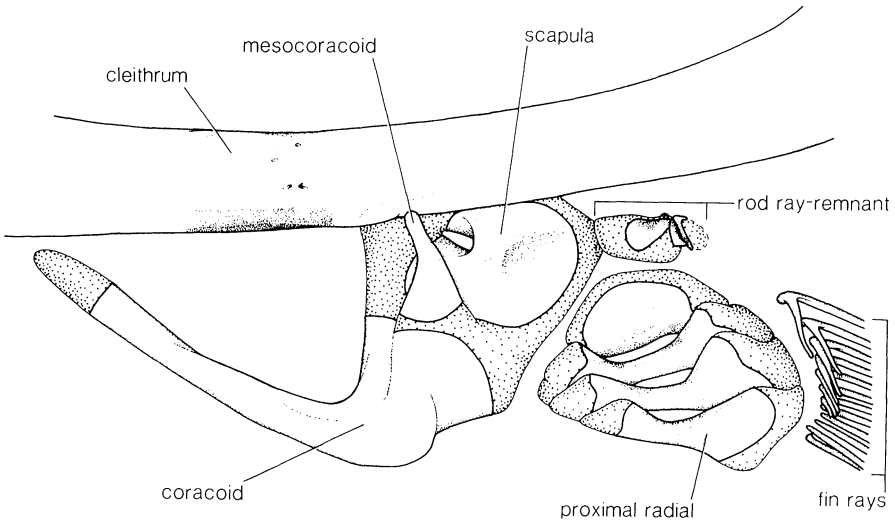

FIG. 43. Pectoral girdle of *Leptostomias gladiator* (USNM 199845). Right side, dorsomedian view. Dashed outlines indicate approximate extent of poorly preserved cartilage.

the scapular ossification is greatly reduced (*Aristostomias*, *Idiacanthus*, and *Photonectes*) or absent (the others). In *Idiacanthus*, *Photostomias*, and *Tactostoma*, this feature is associated with the great reduction in the coracoscapular plate. In *Aristostomias*, the plate is well developed but the scapular ossification consists only of a small, very thin disc on the ventral surface of the plate that wraps into the posterior foramen (ossification not visible in Fig. 40). In *Photonectes*, the coracoscapular plate is likewise well-developed but there is no scapular ossification. In large, female specimens of *Idiacanthus*, there is an ossified scapula, with a scapular foramen. (CI = .25–.33)

In other stomiids, the scapular ossification is more extensive.

247. In *Aristostomias*, *Photonectes*, and *Tactostoma*, there is no coracoid ossification. In the latter two genera this is related to the near total reduction of the coracoscapular plate. In *Aristostomias* (Fig. 40) the plate is well developed but not ossified anteriorly. (CI = .33)

In most other stomiids, the coracoid ossification is present. This character is coded as missing in *Idiacanthus* and *Photostomias*.

248. In *Chauliodus* (Fig. 48), *Leptostomias* (Fig. 43), *Odontostomias* (Fig. 42), *Opostomias*, and *Thysanactis*, the anterior coracoid ramus is slender and rounded in cross-section. (CI = .5)

In relatively primitive "photichthyans" such as *Polymetme* (Fig. 49), in relatively primitive stomiids, and in some relatively derived stomiids such as *Eustomias* (Figs. 45, 46) and *Flagellostomias*, the anterior coracoid ramus is oblong in cross-section, usually in a more or less dorsoventral plane. In most phylogenetically derived stomiids, the anterior ramus is either broad

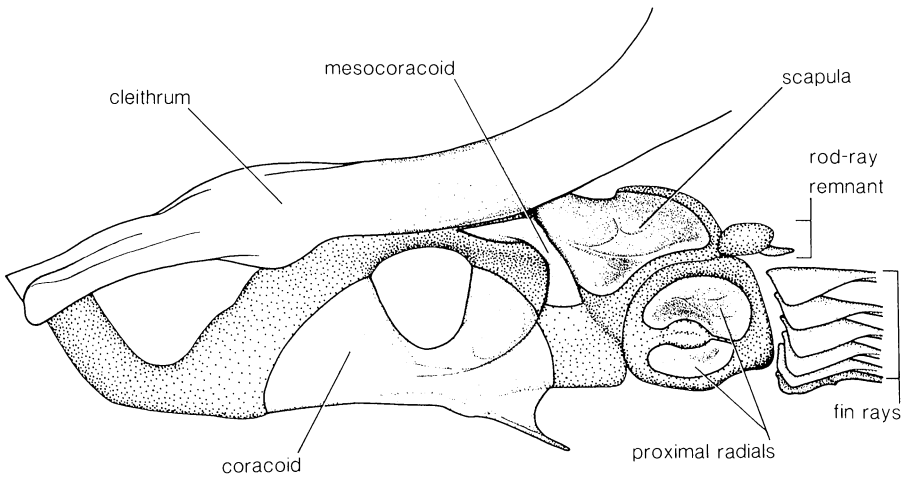

FIG. 44. Pectoral girdle of *Melanostomias tentaculatus* (USNM 199848). Right side, dorsomedian view. Proximal radials II and III are separate in some *Melanostomias* species.

(see, e.g., *Pachystomias*, Fig. 47) or reduced or otherwise modified (see *Bathophilus*, Fig. 39a; *Stomias*, Fig. 50).

249. In *Aristostomias* (Fig. 40a), *Bathophilus* (Fig. 39a), *Chirostomias* (Fig. 41), and *Grammatostomias*, the coracoid cartilage extends as far posteriorly as the scapular cartilage, so that the posterior margin of the coracoscapular plate is approximately perpendicular to the long axis of the fish. (CI = .33)

In other "photichthyans" (except those in which the plate is greatly reduced), the scapular cartilage extends well posterior to the coracoid cartilage and the posterior margin of the plate is at an angle relative to the long axis of the fish.

250. In *Aristostomias* (Fig. 40a), *Bathophilus* (Fig. 39a), *Echiostoma*, *Grammatostomias*, *Malacosteus*, *Melanostomias* (Fig. 44), *Pachystomias* (Fig. 47), *Photonectes*, and *Trigonolampa*, the coracoid portion of the coracoscapular plate is expanded anteriorally, and the coracoid aperture is reduced or absent. (CI = .33)

In most other stomiids, the coracoid portion of the plate is relatively smaller and the coracoid aperture is correspondingly larger (see, e.g., Fig. 49 of the primitive "photichthyan" *Polymetme*). This character is coded as missing in *Idiacanthus*, *Photostomias*, and *Tactostoma*.

251. In *Chirostomias* (Fig. 41), the coracoid is a more or less "disc"-shaped ossification lying ventral to the mesocoracoid and articulating fully with the ventral termination of that bone. (CI = 1.0)

In other stomiids, the coracoid ossification, when present, is longer than wide and lies anterior to the base of the mesocoracoid, when present.

252. In *Melanostomias* (Fig. 44), *Photonectes*, and *Trigonolampa*, there are two coracoid apertures, one lying lateral to and bordered by the coracoid

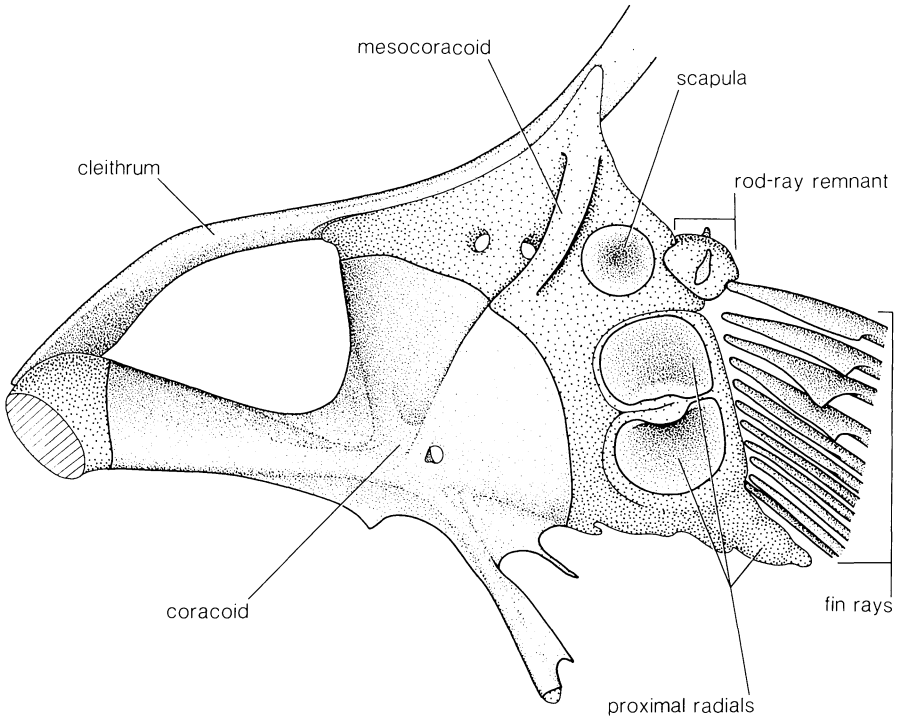

FIG. 45. Pectoral girdle of *Eustomias* cf. *macrurus* (USNM 292913). Right side, dorsomedian view. Hatched area indicates cut surface at midline.

ossification and one more anterior and bordered by the coracoscapular cartilage and cleithrum. (CI = .33)

In other stomiids either a single coracoid aperture is present or none at all.

In some species of *Photonectes,* the anterior aperture is bordered medially by the fibrocartilage extending between the coracoscapular plate and the cleithrum.

253. In *Bathophilus, Eustomias, Grammatostomias,* and *Photonectes,* the mesocoracoid is an unossified cartilage or fibrocartilage column (Figs. 39b, 45, 46). (CI = .5)

In other stomiids with a mesocoracoid there is ossification surrounding a cartilage core.

In some more specialized species of *Eustomias* and *Photonectes,* the mesocoracoid is entirely lacking. This character is coded as missing in *Idiacanthus, Malacosteus, Pachystomias, Photostomias, Stomias,* and *Tactostoma.*

254. In *Bathophilus* (Fig. 39b), *Grammatostomias,* and *Photonectes,* the mesocoracoid is represented by fibrous connective tissue. (CI = .5)

In other stomiids, the mesocoracoid, when present consists of hyaline cartilage (usually covered by bone). This character is coded as missing in *Idiacanthus, Malacosteus, Pachystomias, Photostomias, Stomias,* and *Tactostoma.*

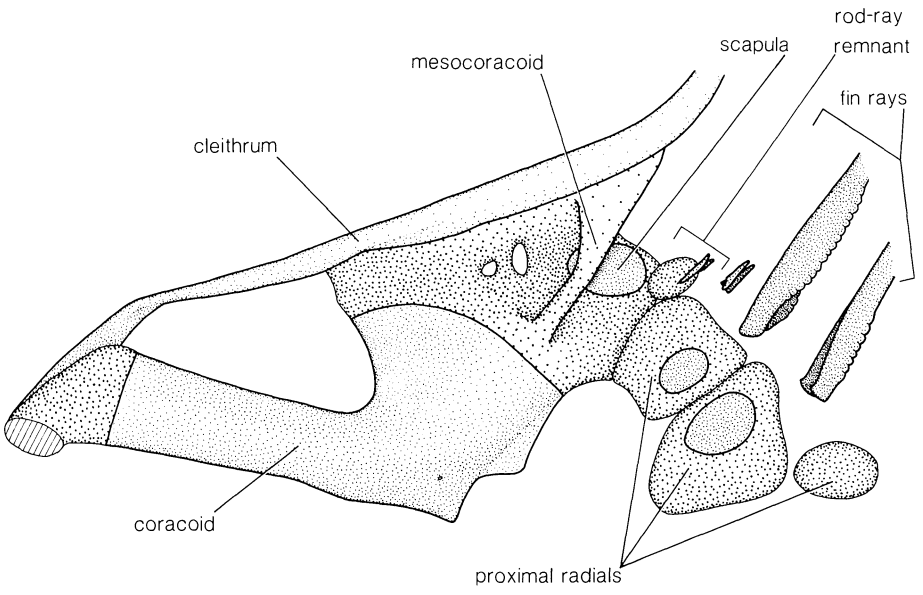

FIG. 46. Pectoral girdle of *Eustomias* cf. *brevibarbatus* (USNM 199843). Right side, dorsomedian view. Hatched area indicates cut surface at midline.

255. In *Grammatostomias*, the fibrous remnant of the mesocoracoid extends from the medial margin of the coracoscapular plate. (CI = 1.0)

In other stomiids, the mesocoracoid cartilage or its fibrous remnant extend from the coracoscapular plate lateral to the medial margin of the plate.

256. In *Idiacanthus, Malacosteus, Pachystomias* (Fig. 47), *Photostomias, Stomias* (Fig. 50), and *Tactostoma,* there is no mesocoracoid. (CI = .25)

In other stomiids a mesocoracoid is present, although it may be reduced (see also Characters 253–255).

257. In *Echiostoma, Eustomias* (Fig. 45), *Melanostomias* (Fig. 44), *Pachystomias* (Fig. 47), and *Photonectes,* at least the lateral two proximal radials are tightly articulated in a posterior deep concavity of the coracoscapular plate. This feature is hypothesized to be a synapomorphy for Clade O, including the above genera plus *Aristostomias, Bathophilus, Grammatostomias, Idiacanthus, Malacosteus, Photostomias,* and *Tactostoma,* in which the proximal radials either are lost (and the plate greatly reduced: *Idiacanthus* plus *Tactostoma, Photostomias*) or articulate in a shallow concavity associated with reduction in size of the proximal radials (*Aristostomias* plus *Malacosteus,* see Character 258) or posterior position of the coracoid (*Bathophilus* plus *Grammatostomias,* see Character 249). The deepness of the concavity is also reduced in some *Photonectes* species (e.g., *P. leucospilus*). This character is coded as missing in *Aristostomias, Bathophilus, Grammatostomias, Idiacanthus, Malacosteus, Photostomias, Tactostoma.* (CI = 1.0)

This feature is secondarily modified in some *Eustomias* also (see Fig. 46), in which a posteromedial portion of the coracoscapular plate is absent, al-

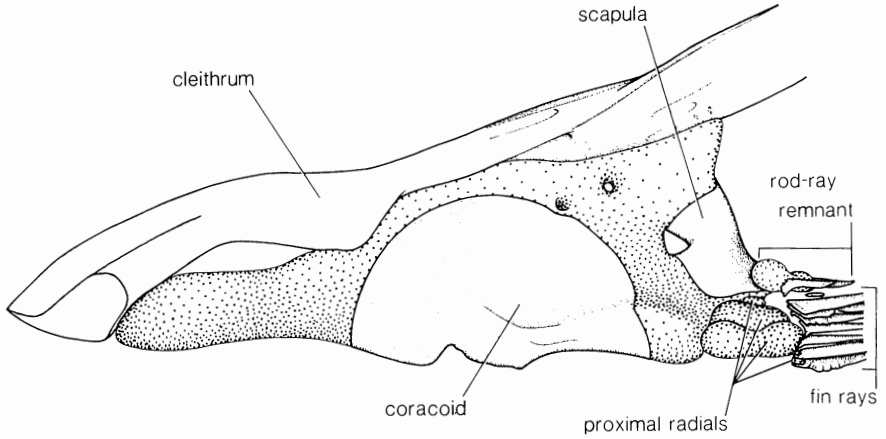

FIG. 47. Pectoral girdle of *Pachystomias microdon* (USNM uncat. DANA st. 4591). Right side, dorsomedian view.

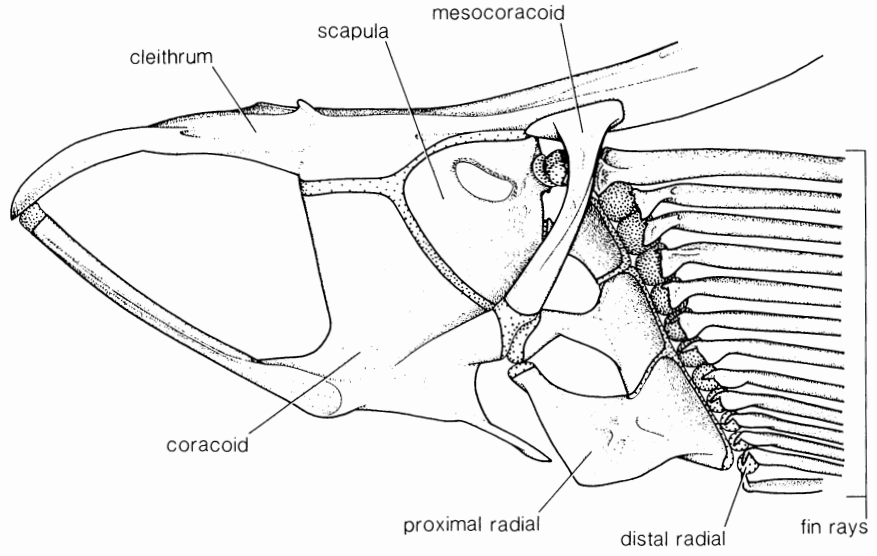

FIG. 48. Pectoral girdle of *Chauliodus schmidti* (USNM 225045). Right side, dorsomedian view.

though the position of the proximal radials remains unchanged (compare with Fig. 45).

In other "photichthyans", the proximal radials are more loosely articulated to a slightly concave or slightly convex border of the coracoscapular plate.

258. In *Aristostomias* (Fig. 40), *Malacosteus,* and *Photonectes,* the proximal radials are greatly reduced in size relative to the size of the first distal radial. (CI = .33–.5)

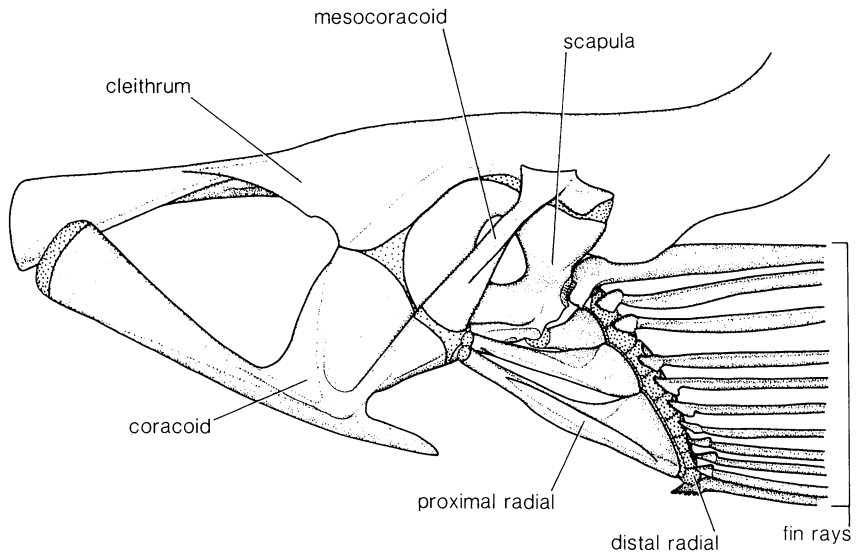

FIG. 49. Pectoral girdle of *Polymetme corythaeola* (USNM 199507). Right side, dorsomedian view.

In other stomiids, the proximal radials are proportionally larger. In *Pachystomias,* the first distal radial is also relatively reduced, but the other two radials are relatively larger.

259. In *Aristostomias*, *Bathophilus*, *Echiostoma*, *Eustomias*, *Flagellostomias*, *Grammatostomias*, *Leptostomias*, *Malacosteus, Melanostomias, Odontostomias, Opostomias, Pachystomias, Photonectes,* and *Thysanactis,* the first proximal radial has a cartilaginous lateral border. This is hypothesized to be a synapomorphy for a group comprised of the above genera plus *Idiacanthus*, *Photostomias,* and *Tactostoma,* all of which lack proximal radials, and in which this character is coded as missing. (CI = 1.0)

In other "photichthyans", the lateral border is bony.

260. In *Aristostomias*, *Malacosteus,* and *Pachystomias,* proximal radial III lies between the fin-ray halves of the ventral ("posterior") fin ray (Figs. 40a,b). This character is coded as missing in *Idiacanthus*, *Photostomias,* and *Tactostoma.* (CI = 1.0)

In other stomiids, the radial, if present, does not lie between the fin-ray halves, but is usually proximal to the fin rays.

261. In *Aristostomias* (Fig. 40), *Eustomias* (Figs. 45, 46), *Grammatostomias*, *Malacosteus,* and *Pachystomias,* the third proximal radial is positioned posteromedial to the other radial(s). This feature is hypothesized to be a synapomorphy for a group including the above genera plus *Bathophilus*, in which the third radial is absent. This character is coded as missing in *Bathophilus*, *Idiacanthus*, *Photostomias* and *Tactostoma.* (CI = 1.0)

In other stomiids, the third radial is aligned medial to the others.

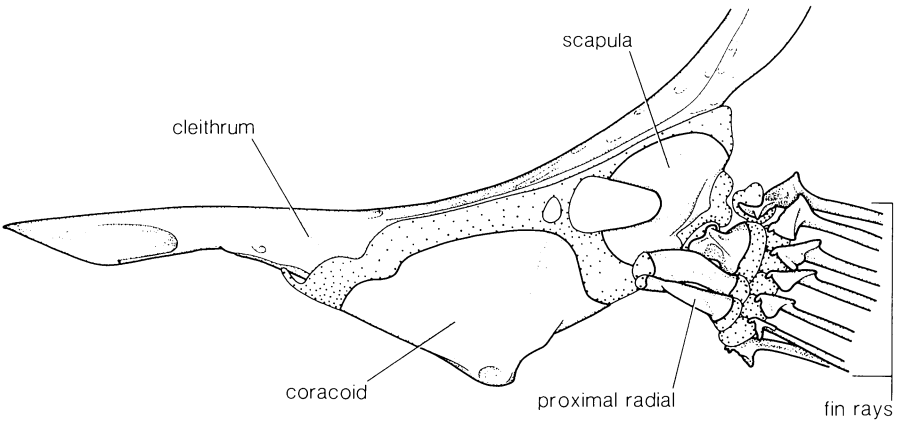

FIG. 50. Pectoral girdle of *Stomias lampropeltis* (USNM 199857). Right side, dorsomedian view.

262. In *Bathophilus*, there is only one proximal radial. (CI = 1.0) In other stomiids, two or more are present.

263. In *Leptostomias* and *Thysanactis,* the middle two proximal radials are approximately square in cross-section, the first radial is squared in shape along its medial border, and the fourth radial is squared along its lateral border (Fig. 43). (CI = 1.0)

In other stomiids, the proximal radials are less regularly shaped in cross-section, usually being approximately rectangular (but not square) or ovoid.

264. In *Leptostomias* (Fig. 43), *Odontostomias* (Fig. 42), *Opostomias,* and *Thysanactis,* the proximal radials are dorsoventrally expanded distally and proximally, so that the cartilaginous terminations are almost as deep as they are broad (or deeper). (CI = 1.0)

In other stomiids, the proximal and distal ends of the radials are not expanded dorsoventrally.

265. In *Chirostomias*, *Heterophotus*, *Leptostomias*, and *Thysanactis,* there are four proximal pectoral-fin radials. In *Heterophotus*, the fourth radial is very small (less than half the length of radial III), and its distal cartilage is continuous with the distal cartilage of radial III. In the other genera, the fourth radial is a complete, independent element (though the form is somewhat different in *Chirostomias* than in the other two genera; see Figs. 41, 43). (CI = .33)

In other "photichthyans", there are only three radials. The presence of four in these stomiids may be an atavistic feature since non-"photichthyan" stomiiforms (with the exception of *Cyclothone*) have four radials.

266. In *Rhadinesthes,* the distal radials are irregularly subdivided both horizontally and vertically into cartilage bodies of various sizes and shapes. (CI = 1.0)

In other non-Clade F stomiids and in other "photichthyans", there is a regular series of block-like distal radials, (one per fin ray).

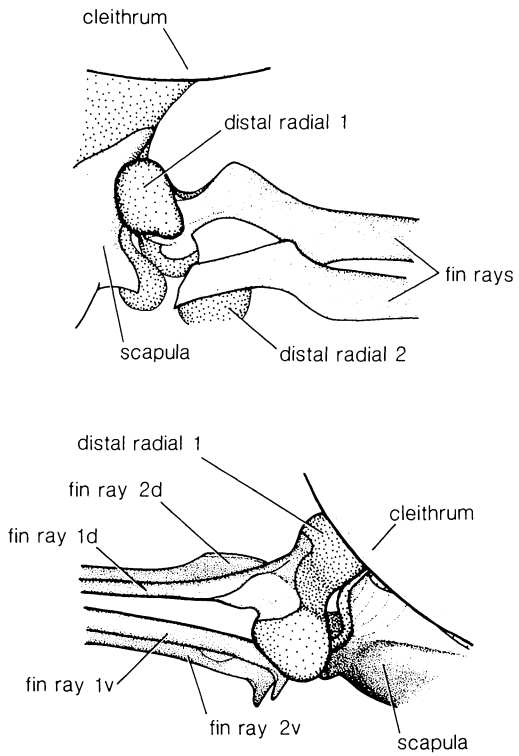

FIG. 51. Region of anterior pectoral-fin ray articulation of *Heterophotus ophistoma* (USNM uncat. DANA st. 3751-VIII), right side. a, dorsal view (anterior to left); b, lateral view.

267. In members of Clade F, all distal radials but the anterior one are reduced to small, oblong or round cartilages or are absent. When present, the radials do not articulate or barely articulate with each other. (CI = 1.0)

In other stomiids, the distal radials are larger cartilages, usually block-like, which articulate more fully with each other.

268. In members of Clade (B,C), the distal radial of the first pectoral-fin ray (the propterygial element, see Jessen, 1972), when present, remains at least partially unossified anterodorsally, so that cartilage emerges on the anterodorsal surface of the element even in adults (this cartilage forms part of the radial element and is not the articular cartilage on the surface of the radial-scapular joint). See Fig. 51 of *Heterophotus*. (CI = 1.0)

In other stomiiforms, the distal radial is ossified anterodorsally (only articular cartilage is present). See Fig. 52 of *Polymetme*.

269. In adult stomiids, the ventral cartilaginous portion of the first pectoral distal radial projects anterolateral to the lateral margin of the ventral ray half. See Fig. 51 of *Heterophotus*. (CI = 1.0)

In other stomiiforms, any cartilaginous portion projects no further laterally than the lateral margin of the ventral ray half. See Fig. 52 of *Polymetme*.

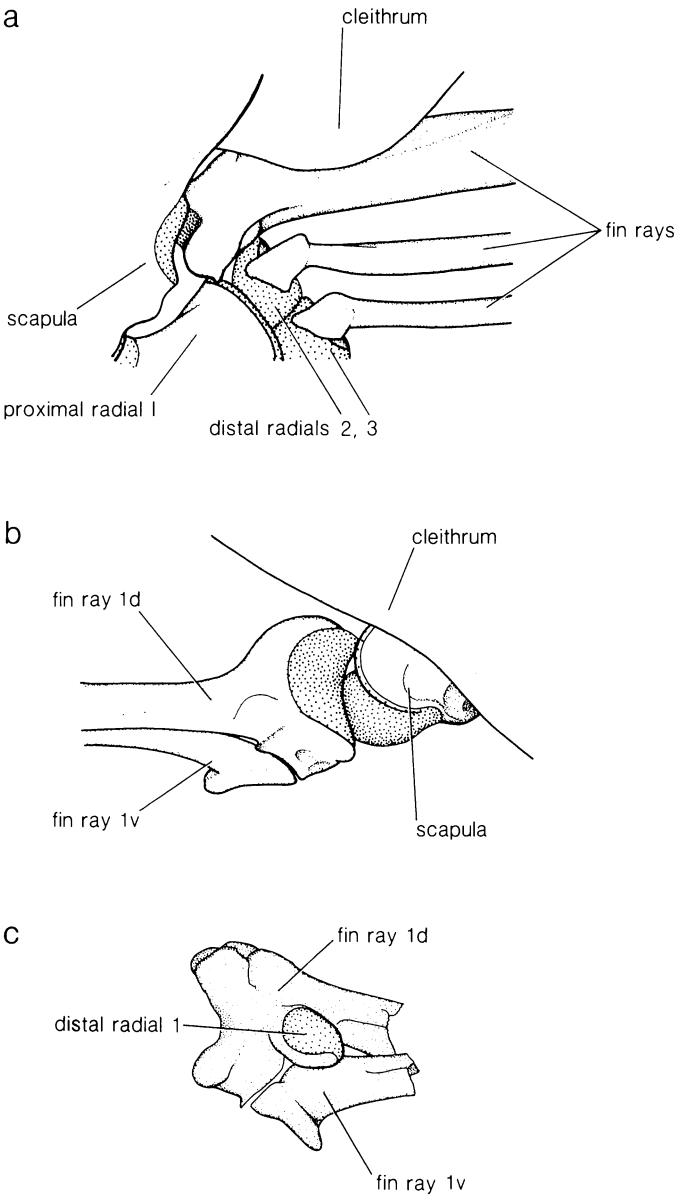

FIG. 52. Region of anterior pectoral-fin ray articulation of *Polymetme corythaeola* (USNM 199507), right side. a, dorsal view (anterior to left); b, lateral view; c, medial view of base of anterior ray.

270. In members of Clade J, there are three or fewer distal radials. These distal radials are associated with the "rod-ray" complex (see Character 271). See Figs. 42 (*Odontostomias*), 43 (*Leptostomias*), and 53 (*Thysanactis*). (CI = 1.0)

In other stomiids, there is at least one distal radial associated with each fin ray. See Fig. 48 of *Chauliodus*.

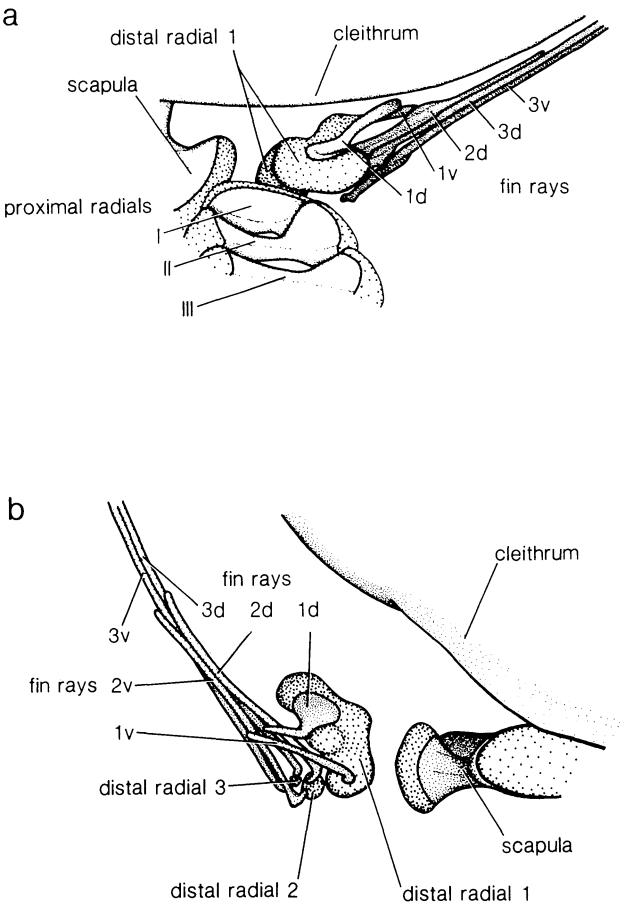

FIG. 53. Region of "rod-ray" of *Thysanactis dentex* (USNM 206704), right side. a, dorsomedian view (anterior to left); b, lateral view.

One possible exception to the character as found in stomiids is *Chirostomias*. My specimens are in poor condition and I am unable to confirm just what the radial configuration is in them. The character is coded as missing in this taxon.

271. In members of Clade J, with the exceptions noted below, the anterior one or two fin rays are reduced in length, and the anterior two to four fin rays are tightly bound together and associated with the anterior distal radial. This structure is termed herein the "rod-ray" complex and is hypothesized to be a synapomorphy of Clade J, including *Idiacanthus*, *Photostomias*, and *Tactostoma*, which have greatly reduced pectoral girdles and have entirely lost all fin rays and radial elements (this character is coded as missing in these three taxa). (CI = 1.0)

In its primitive form, (e.g., Figure 53 of *Thysanactis*), the rod-ray complex

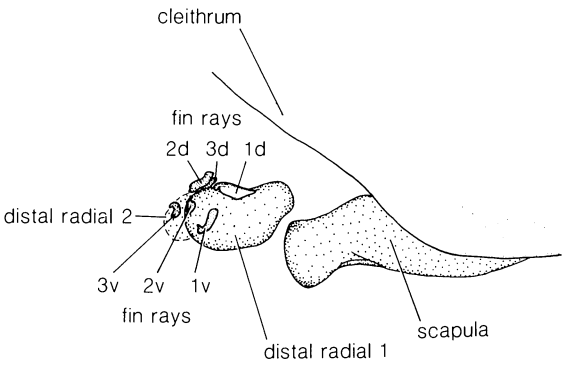

FIG. 54. Region of "rod-ray" remnant of *Leptostomias gladiator* (USNM 199845). Right side, lateral view.

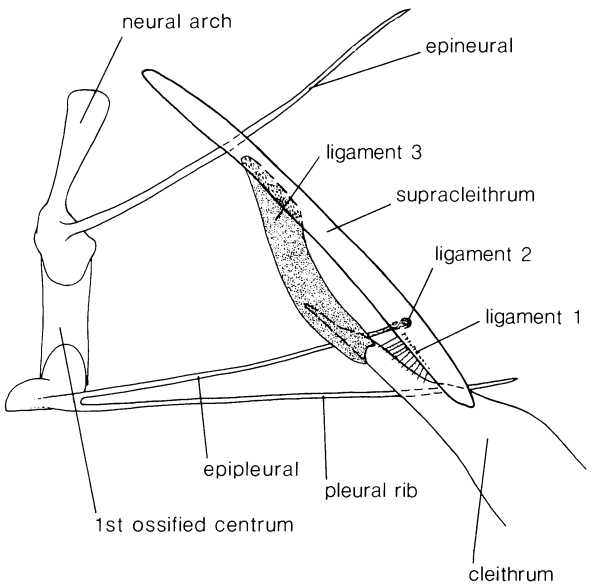

FIG. 55. Ligaments of the pectoral girdle suspensorium of *Odontostomias micropogon* (USNM 199849). Left side, lateral view.

involves a greatly enlarged distal radial 1, which has a wide articulation with the scapula and with proximal radial I, and one or two associated distal radials. Rays 1 and 2 are reduced in length and serve as muscle attachment sites. Ray 3 is stiff and elongate, and is tipped by luminous tissues. A hiatus is present between the rod-ray and the other fin rays. Similar morphology is present in *Echiostoma*, *Flagellostomias*, *Opostomias* (in which the complex includes the anterior four fin rays), and some *Photonectes* species. In some *Odontostomias* specimens (Fig. 42), and *Photonectes* specimens, the rod-ray complex includes only two fin rays, a short anterior and a longer adjacent ray. (Contrary to Norman, 1930, *Odontostomias* does have an "isolated ray",

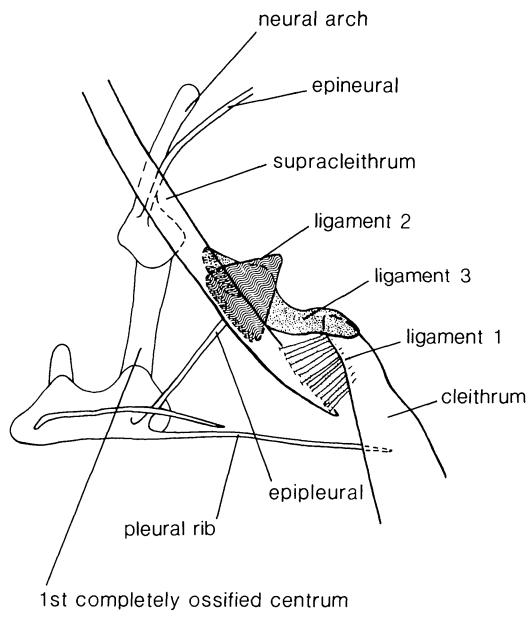

FIG. 56. Ligaments of the pectoral girdle suspensorium of *Thysanactis dentex* (USNM 206704). Left side, lateral view.

although it is rather small; this feature was found to be present in all specimens examined, including the holotype of the type species of the genus, *O. micropogon*.)

In *Aristostomias* (Fig. 40b), *Bathophilus* (Fig. 39a), *Eustomias* (Figs. 45, 46), *Grammatostomias*, *Leptostomias* (Figs. 43, 54), *Malacosteus*, *Melanostomias* (Fig. 44), *Pachystomias* (Fig. 47), and some *Photonectes* species, the rod-ray complex has been reduced, and is usually represented by an enlarged distal radial (sometimes subdivided into dorsal and ventral spheroid cartilages) plus much reduced fin-ray remnants. In *Bathophilus* specimens examined, the distal radial is also absent. In all these genera but *Leptostomias*, the hiatus between the reduced rod-ray complex and the other fin rays is small or nonexistent.

In other stomiids the anterior distal radial may be specialized as described in Characters 268 and 269, but in these and other "photichthyans", there is no abbreviation and binding together of the anterior fin rays, no hiatus between the anterior and more posterior rays, and no broad articulation with proximal radial I.

272. In *Flagellostomias*, *Leptostomias*, and *Thysanactis*, there are 13–14 pectoral-fin rays (including rod-rays and rod-ray remnants). (CI = .5)

In most other "photichthyans", there are fewer than 13 rays, usually less than 10. In *Bathophilus*, pectoral-fin ray numbers range from 1 to nearly 40. Estimates of the primitive number for the genus are difficult without hypotheses of relationship of the species in the genus. Nevertheless, species placed by Regan and Trewavas (1930) in the subgenus *Gnathostomias* appear

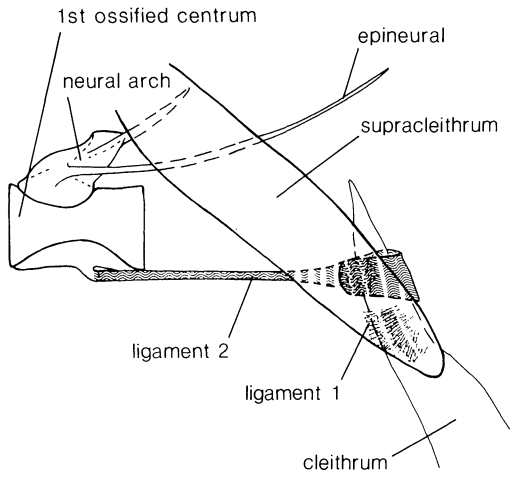

FIG. 57. Ligaments of the pectoral girdle suspensorium of *Polymetme corythaeola* (USNM 199507). Left side, lateral view.

relatively more primitive than other *Bathophilus*, and these species have pectoral-fin ray numbers of 4–8 (externally visible). In *Aristostomias polydactylus* Regan and Trewavas, there are 10–17 pectoral-fin rays. I suggest that high pectoral-fin ray counts have evolved independently in the group including the three above-mentioned genera, within *Bathophilus*, and in *A. polydactylus*.

273. In *Leptostomias* and *Thysanactis* there are 14 pectoral-fin rays (including rod-rays and rod-ray remnants. (CI = 1.0)

In other "photichthyans", there are 13 or fewer pectoral-fin rays. For further comments on pectoral-fin ray numbers, see the previous character.

274. In *Flagellostomias*, *Leptostomias* (Fig 43), *Odontostomias* (Fig 42), *Opostomias*, and *Thysanactis*, the flanges for muscle attachment on the dorsal halves of the more lateral non-rod ray fin rays form slender, pointed processes which project from near the proximal termination of the ray. Because of the perspective, this character is less apparent in Fig. 42 than in Fig. 43. (CI = 1.0)

In other stomiids, the flanges are blunter and project from a much more elongate basal portion of the rays.

275. In *Flagellostomias*, *Leptostomias* (Fig. 43), and *Thysanactis*, the flanges for muscle attachment on the dorsal halves of the more lateral non-rod ray fin rays are greatly elongate in an axis roughly perpendicular to the axis of the fin rays, so that the flanges overlap more than one adjacent fin ray. (CI = .5)

In other stomiids, the more lateral flanges are shorter and do not overlap more than the adjacent fin ray. (In *Melanostomias*, Fig. 44, the more medial flanges overlap more than one adjacent fin ray).

276. In *Bathophilus* (Fig. 39a), *Grammatostomias*, and *Eustomias* (Figs. 45, 46), the flanges for muscle attachment on the dorsal halves of the non-rod

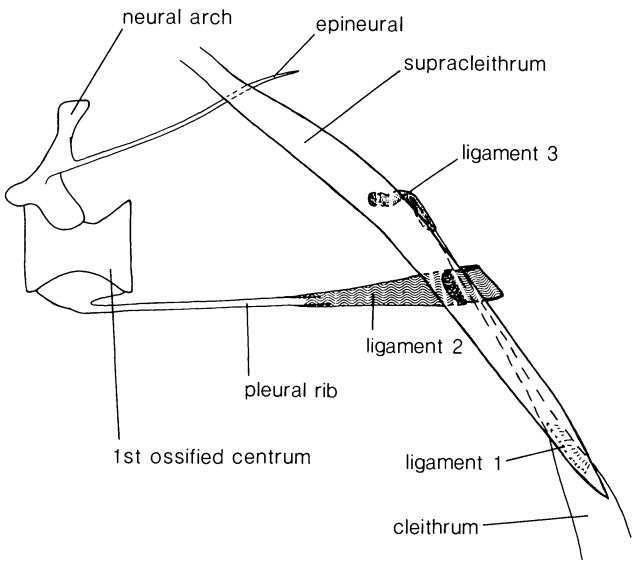

FIG. 58. Ligaments of the pectoral girdle suspensorium of *Borostomias elucens* (USNM uncat. DANA st. 486/71 15 G). Left side, lateral view.

ray fin rays are greatly reduced in breadth (i.e., in the axis perpendicular to the axis of the rays). (CI = 1.0)

In other stomiids, such flanges are more developed.

277. In *Aristostomias* (Fig. 40), some species of *Eustomias* (e.g., *E. cf. brevibarbatus,* Fig. 46), *Malacosteus,* and *Pachystomias* (Fig. 47), fine crenelations are present on the flanges of the fin rays. This character is coded as missing in *Eustomias* and *Photostomias.* (CI = 1.0)

In other stomiids, such crenelations are not present.

278. In *Flagellostomias*, *Leptostomias*, *Opostomias,* and *Thysanactis,* the non-rod ray fin rays do not articulate with the first or second proximal radials. This feature is hypothesized to be a synapomorphy for a group comprised of the above genera plus *Odontostomias;* its absence in *Odontostomias* may be associated with the reduced development of the rod-ray (see Character 271). (CI = .5)

(In Fig. 43 of *Leptostomias*, the appearance of articulation between a fin ray and the second proximal radial is due to the view being dorsomedial rather than strictly dorsal).

In other stomiids with a rod-ray or rod-ray remnant, the non-rod ray fin rays articulate with the second, and sometimes also the first, proximal radial.

279. In *Idiacanthus*, *Photostomias,* and *Tactostoma,* there are no pectoral-fin rays (or ray remnants). (CI = .5)

In other stomiids, at least some pectoral-fin rays are present, although they may be extremely reduced.

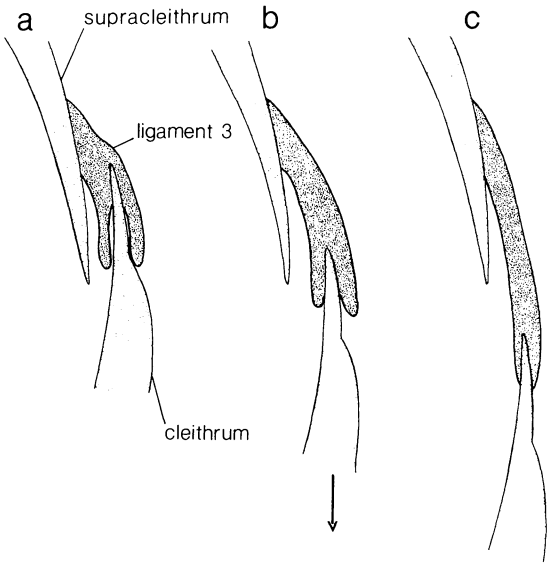

FIG. 59. Diagrammatic representation of dorsoventral movement of the cleithrum of *Idiacanthus fasciola*, showing extension of ligament 3. a, cleithrum at rest; b, cleithrum partially extended; c, cleithrum fully extended.

280. In *Echiostoma*, *Leptostomias*, *Melanostomias*, *Odontostomias* (Fig. 55), *Opostomias*, *Tactostoma*, and *Thysanactis* (Fig. 56), Baudelot's ligament (Ligament 2) extends dorsolaterally from the anterior parapophysis to the supracleithrum. In all these genera but *Tactostoma*, the ligament is associated with an epipleural bone. (CI = .33)

In other "photichthyans", Baudelot's ligament extends posterolaterally or posteroventrally to the supracleithrum (Figs. 57, 58). In some, such as *Photostomias* and *Idiacanthus*, the ligament extends as a broad sheet of connective tissue.

281. In *Echiostoma* and *Melanostomias*, the supracleithrum-cleithrum ligament (Ligament 3) is proximally adherent to almost the entire anteromedial surface of the supracleithrum. (CI = 1.0)

In other stomiids in which ligament 3 is well developed, its attachment is much more restricted (see, e.g., Figs. 55, 56, 58).

In *Echiostoma* and *Melanostomias*, Ligament 3 forms an extremely thick fibrous sheath around the dorsal tip of the cleithrum, as in Fig. 59. This allows the cleithrum to move rather substantially in a dorsoventral plane.

282. In *Stomias* (Fig. 60), Baudelot's ligament (Ligament 2) is looped just proximal to its attachment on the supracleithrum. The sheath-like supracleithrum-cleithrum ligament (Ligament 3) passes through the loop. (CI = 1.0)

In other "photichthyans", Baudelot's ligament is not looped. See Figs. 55, 56.

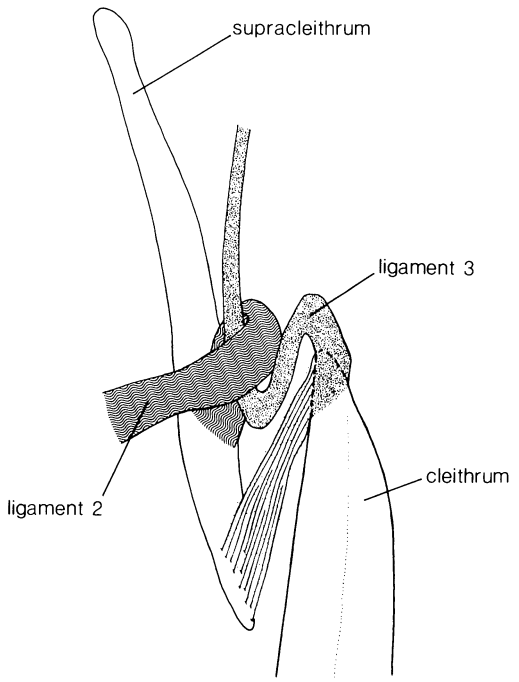

FIG. 60. Ligaments of the pectoral girdle suspensorium of *Stomias longibarbatus* (USNM 225035). Right side, medial view.

PELVIC GIRDLE

For pelvic girdle terminology, refer to Fig. 61 of *Neonesthes*.

283. In *Bathophilus*, the pelvic girdles are widely separated along most of their length, with only the medial projections of the posterior cartilaginous processes approaching each other closely. (CI = 1.0)

In other stomiids, the girdles are adjacent to the ventral midline and at least their medial plates articulate with each other.

284. In *Astronesthes*, *Heterophotus*, *Odontostomias*, *Opostomias*, *Rhadinesthes*, and members of Clade O (Figs. 62, 63), the anterior cartilaginous processes bear lateral projections. (CI = .25)

In other "photichthyans", no such projections are present

285. In members of Clade (B,C), the anterior cartilaginous process is enlarged, extending as an elongate conical cartilage primitively and elaborated extensively in most more specialized genera. See for example *Trigonolampa* (Fig. 64), *Melanostomias* (Fig. 62), and *Bathophilus* (Fig. 63). (CI = 1.0)

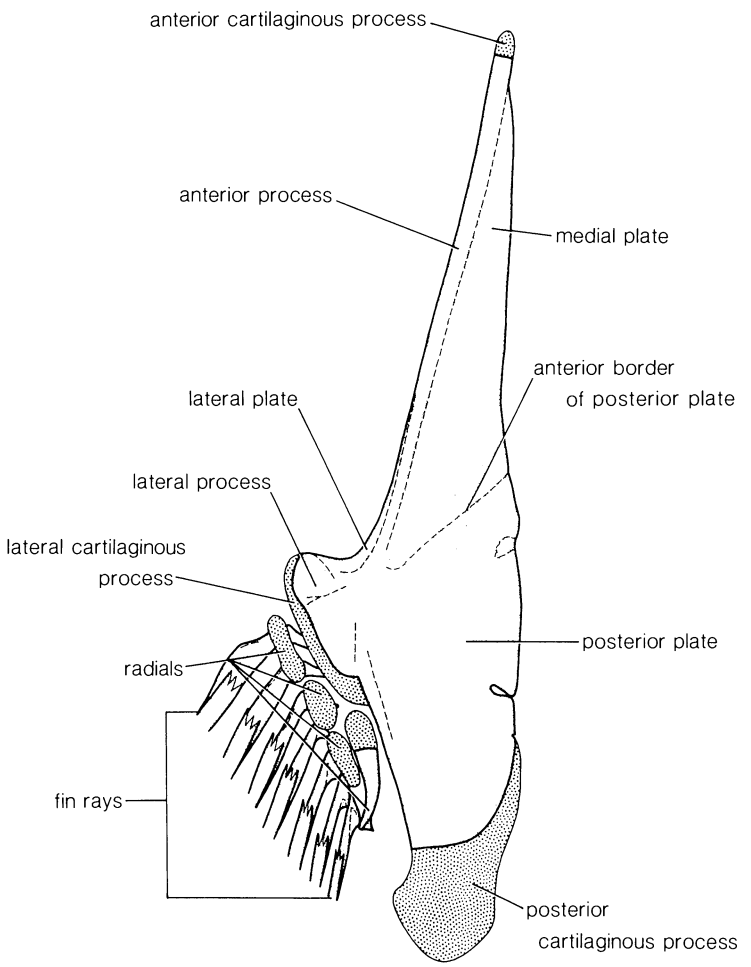

FIG. 61. Pelvic girdle of *Neonesthes capensis* (USNM 199823). Right side, ventral view. Ventral ray-halves cut and removed proximally, as indicated by broken edge.

In *Neonesthes* (Fig. 61) and other "photichthyans" (e.g., Fig. 66), the anterior cartilaginous process is a small, simple "cap" on the anterior process of the pelvic girdle.

286. In *Aristostomias*, *Bathophilus*, *Eustomias*, *Grammatostomias*, *Malacosteus*, *Melanostomias*, *Pachystomias*, *Photonectes*, *Photostomias*, and *Tactostoma*, the anterior process is expanded distally. In all but *Bathophilus*, this expansion can be characterized as resulting in the greatest width of the ossified portion of the anterior process being roughly half or more of the greatest width of the posterior plate (excluding the lateral process; e.g., Fig. 62). In *Bathophilus* (Fig. 63), the anterior process is clearly expanded, but this expansion cannot be described with reference to the posterior plate since the latter is also greatly expanded. (CI = .33)

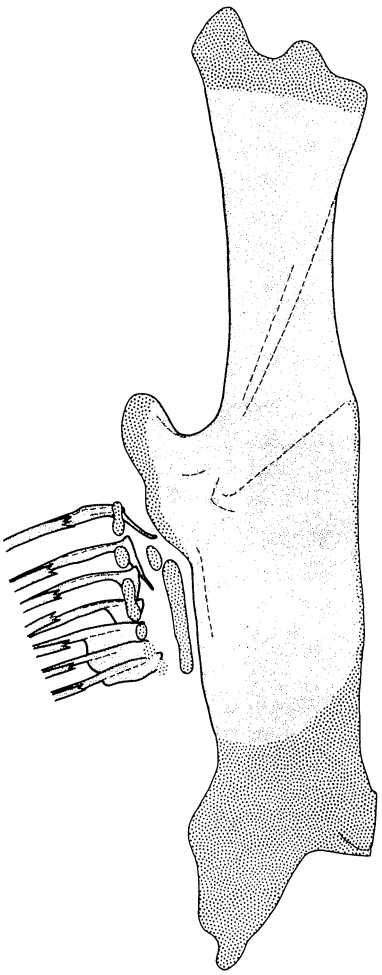

FIG. 62. Pelvic girdle of *Melanostomias tentaculatus* (USNM 199848). Right side, ventral view.

In other "photichthyans", the anterior process is less than half the width of the posterior plate.

287. In *Eustomias*, *Melanostomias* (Fig. 62), some *Photonectes* species, *Photostomias,* and *Tactostoma,* the width of the anterior process at the anterior margin of the ossification is almost equal to the width of the posterior plate. (CI = .25)

In other "photichthyans", the process is roughly half or less the width of the plate.

288. In members of Clade O, the length of the anterior process is roughly equal to or less than the length of the posterior plate. (CI = 1.0)

In other stomiids, the anterior process is longer than the posterior plate.

289. In *Aristostomias*, *Bathophilus* (Fig. 63), *Echiostoma*, *Grammatostomias*,

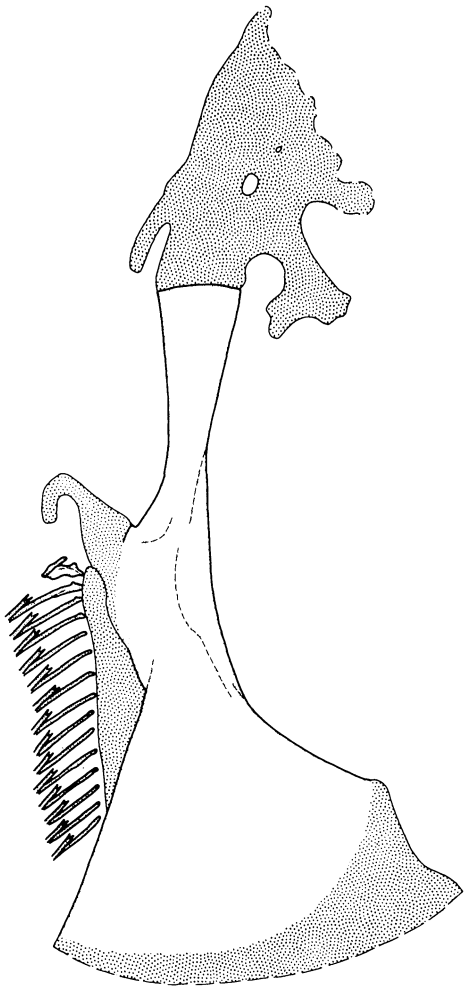

FIG. 63. Pelvic girdle of *Bathophilus pawneei* (USNM 159052). Right side, ventral view.

Idiacanthus, *Malacosteus*, *Pachystomias*, *Photonectes*, and *Photostomias*, the lateral cartilaginous process has an anterodorsal extension. (CI = .25)

In other stomiids, no such extension is present (the cartilage present in this position in some *Astronesthes* species is a separate element).

290. In stomiids, the posterior pelvic plate is enlarged anteriorly and posteriorly, relative to other "photichthyans". Additionally, the cartilaginous core of the plate extends posteriorly well beyond the plate ossification as a posterior cartilaginous process. Compare *Neonesthes* (Fig. 61) with *Polymetme* (Fig. 66) and *Diplophos* (Fink and Weitzman, 1982, Fig. 20). In many derived stomiids these posterior cartilaginous processes are elaborated (e.g., Figs. 67–69). (CI = 1.0)

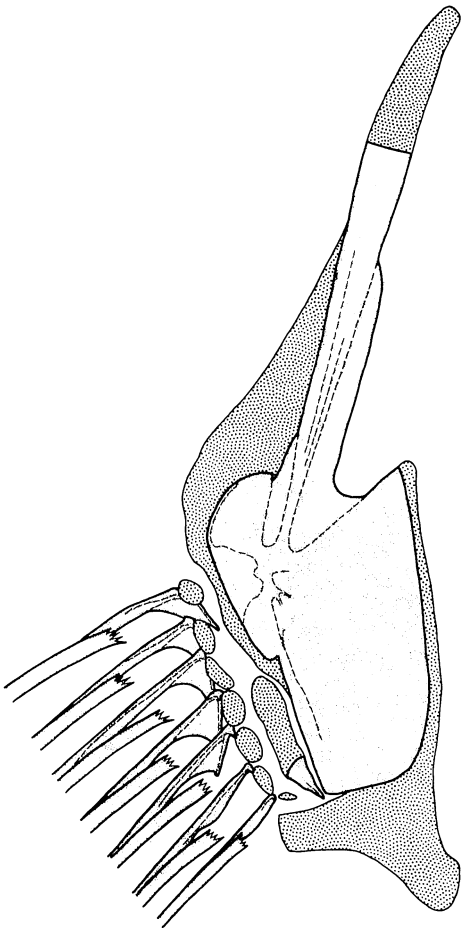

FIG. 64. Pelvic girdle of *Trigonolampa miriceps* (USNM 206683). Right side, ventral view.

291. In members of Clade O, the posterior cartilaginous process is longest near its lateral margin, so that the posterior margin of the girdles in situ forms a relatively broad inverted "U"-shape (e.g., Figs. 68b,c). (CI = 1.0)

In other stomiids, the posterior cartilaginous process extends furthest posteriorly near the midline.

292. In *Rhadinesthes* (Fig. 69c), the posterior cartilaginous process is narrow and extremely elongate along the main axis of the girdle. (CI = 1.0)

In other stomiids, the process is not so narrow and elongate (although it may bear elongate projections laterally; see Character 291).

293. In stomiids, with the exception of *Aristostomias*, *Bathophilus*, *Chauliodus*, *Flagellostomias*, and *Photostomias,* there are more than three pelvic-fin radials (e.g., Figs. 61, 62, 64, 65). (CI = .167–.20)

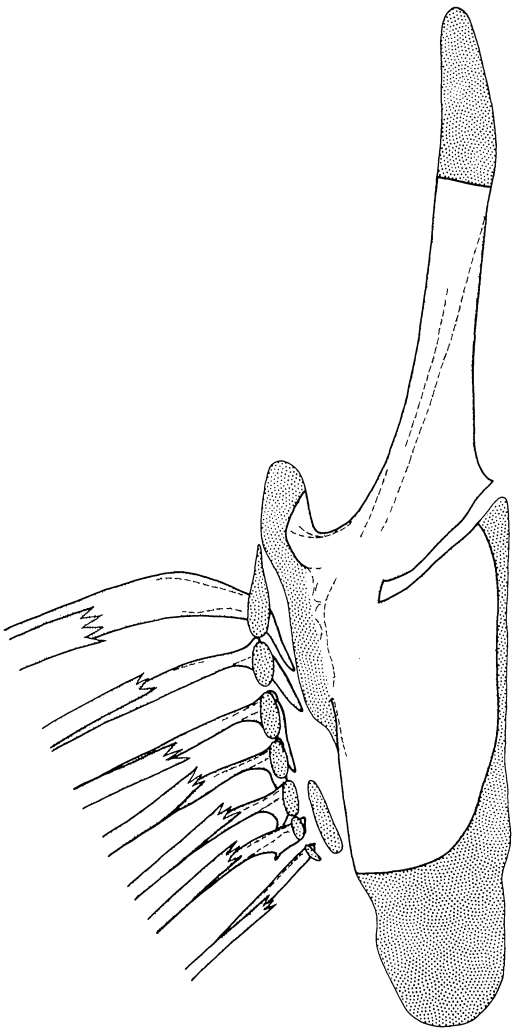

FIG. 65. Pelvic girdle of *Leptostomias gladiator* (USNM 199845). Right side, ventral view.

In *Chauliodus*, most specimens have three radials, although one individual was found with four on one side. Nevertheless, this taxon is coded as having the primitive condition. For the morphology of the other listed genera, see Characters 294–295.

In other "photichthyans" and primitive stomiiforms, there are three radials (see Fig. 66 of *Polymetme* and Fig. 20 in Fink and Weitzman, 1982, of *Diplophos*). In *Triplophos* and in some sternoptychids there are more than three radials (see Figs. 107–110 in Weitzman, 1974), and this is considered an independent acquisition in those groups.

In stomiids, the increase in pelvic radials appears to be accomplished by fission, initially, of radials 1 and 2 (the anterior two; see Fink and Weitzman,

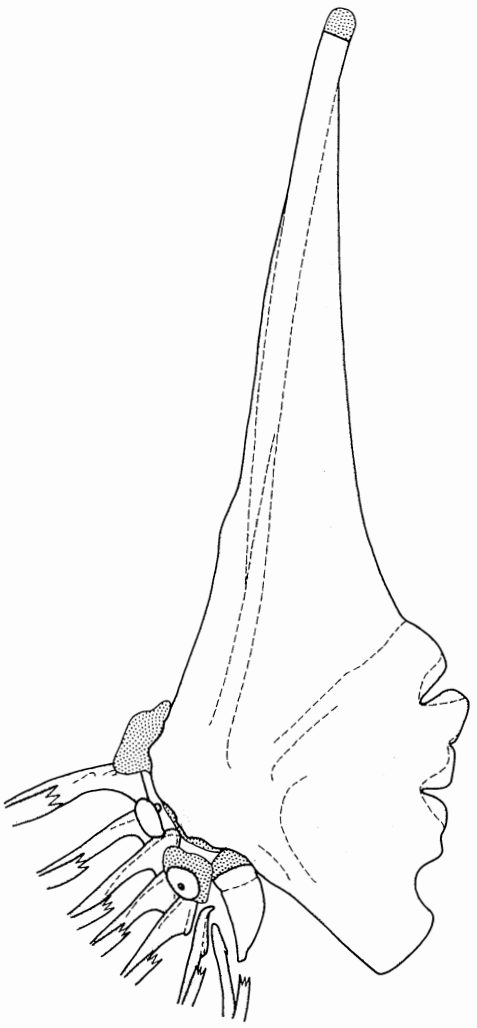

FIG. 66. Pelvic girdle of *Polymetme corythaeola* (USNM 199507). Right side, ventral view.

1982, for nomenclature). This assumption is based on morphology as illustrated by *Neonesthes* (Fig. 61) and *Melanostomias* (Fig. 62) in which there are elongate dumbbell-shaped radials shared by two fin rays. Such shared radials are found occasionally in other stomiids, although usually there is a radial associated with each fin ray. The posterior radial (3 of Fink and Weitzman, 1982) lies medial to the other radials and does not articulate with fin rays except in *Bathophilus*.

294. In *Aristostomias* and *Flagellostomias*, there are two pelvic-fin radials. (CI = .5)

In other stomiids there are four pelvic-fin radials, except as noted in Characters 293 and 295.

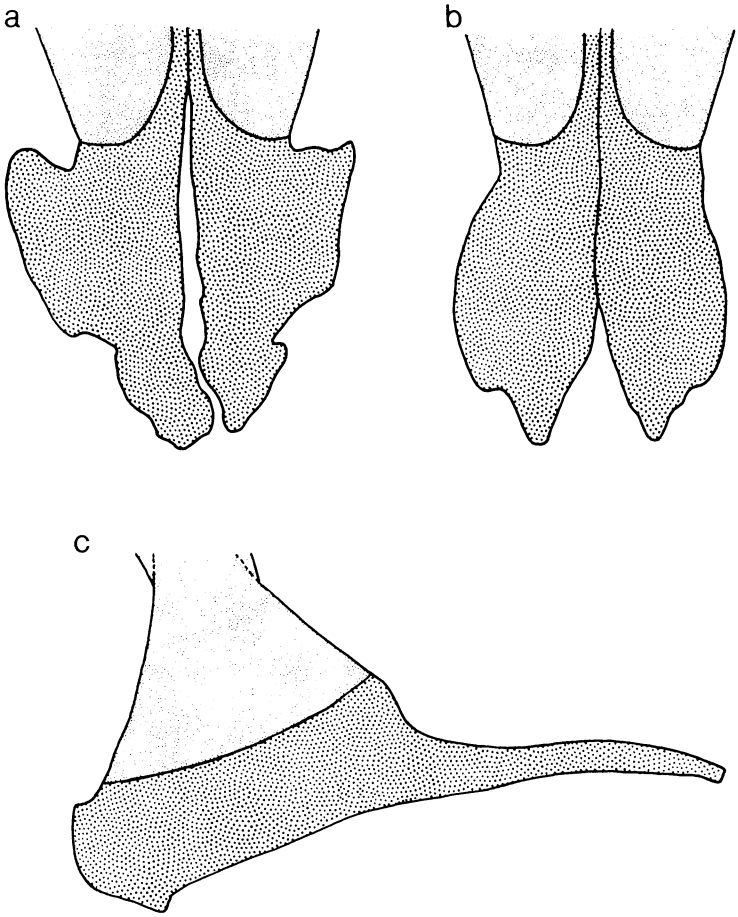

FIG. 67. Posterior cartilaginous processes of pelvic girdles, ventral view. a, *Astronesthes*; b, *Borostomias*; c, *Bathophilus* (right side only).

295. In *Bathophilus* (Fig. 63) and *Photostomias,* there is a single pelvic radial. (CI = .5)

In other stomiids there are four pelvic-fin radials, except as noted in Characters 293 and 294.

296. In members of Clade J and *Stomias,* there is no ossification on the medial pelvic radial (see Figs. 65 of *Leptostomias* and 62 of *Melanostomias*). In *Stomias,* the medial radial is reduced in primitive species and absent in derived ones; loss of ossification is considered independently acquired in *Stomias* and Clade J members. (CI = .5)

In other "photichthyans", the medial radial has a posterior, usually conical or hook-like ossification (see Figs. 66 of *Polymetme,* 61 of *Neonesthes,* and 64 of *Trigonolampa*).

297. In *Aristostomias*, *Grammatostomias*, some specimens of *Malacosteus, Melanostomias* (Fig. 62), *Pachystomias, Photonectes,* and *Tactostoma,* there are

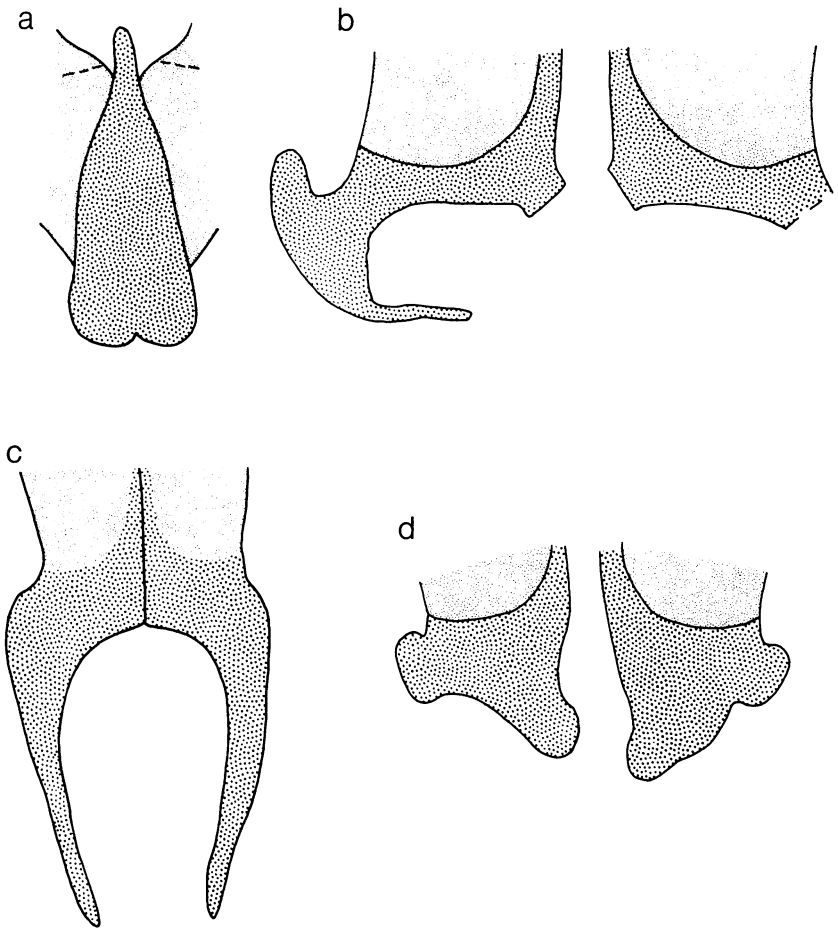

FIG. 68. Posterior cartilaginous processes of pelvic girdles, ventral view. a, *Chauliodus* (processes fused in midline); b, *Echiostoma* (left process broken); c, *Eustomias*; d, *Flagellostomias*.

two medial pelvic radials. The anterior of the pair is relatively small in *Aristostomias*, *Melanostomias* and *Photonectes*, and relatively large (approaching the size of the posterior one) in *Grammatostomias*, *Malacosteus*, and *Tactostoma*. (CI = .167–.20)

In other stomiids, there is either one or no medial radial.

298. In *Bathophilus* (Fig. 63), the elongate medial pelvic radial is very tightly bound to the lateral border of the lateral cartilaginous process. (CI = 1.0)

In other stomiids, the medial radial is not as firmly attached to the pelvic plate.

299. In members of Clade O, the medial pelvic radial is anteriorly elongate, extending at least as far anterior as between the articulations of the third and fourth fin rays. (CI = 1.0)

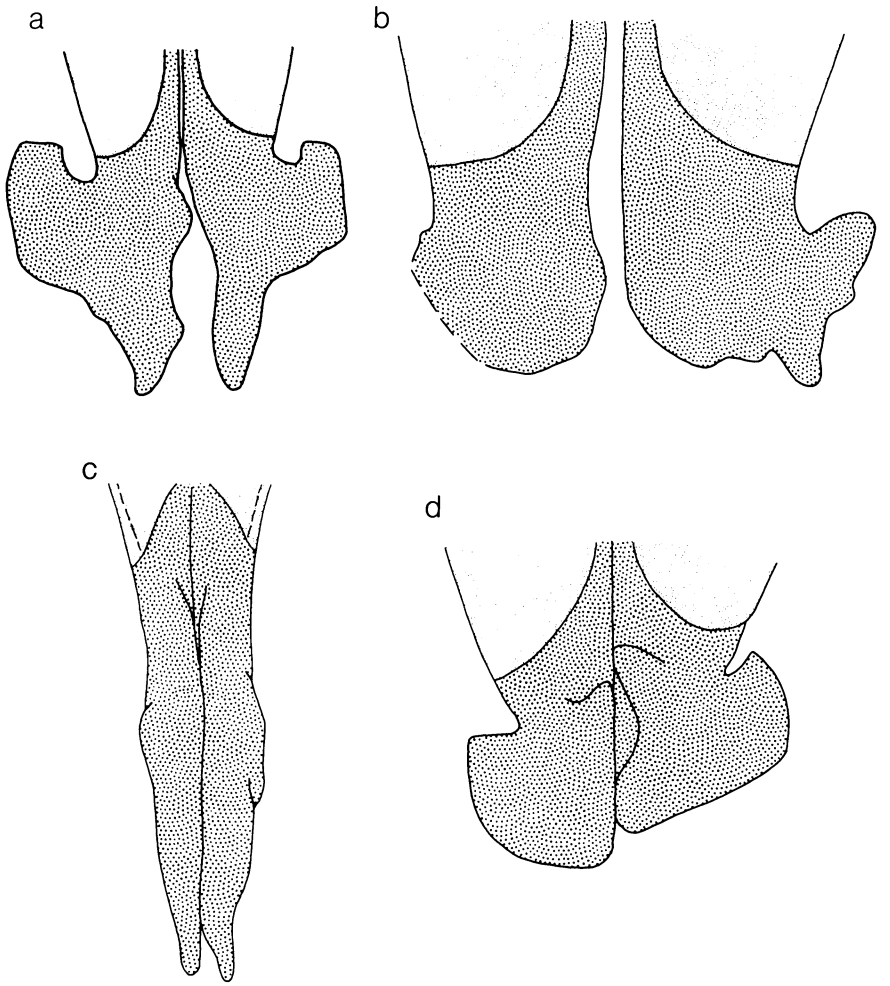

FIG. 69. Posterior cartilaginous processes of pelvic girdles, ventral view. a, *Heterophotus*; b, *Opostomias* (right process broken); c, *Rhadinesthes;* d, *Thysanactis.*

In other stomiids, it extends no further anteriorly than the articulation of the fourth fin ray.

300. In *Aristostomias*, *Bathophilus*, *Grammatostomias*, *Malacosteus*, *Melanostomias,* and *Photostomias,* the medial pelvic radial element or elements (see Character 297) are anteriorly elongate, extending forward to the articulation of the second fin ray. (CI = .25–.33)

In other stomiids, any medial radial elements extend no further anteriorly than between the articulations of the second and third fin rays.

301. In *Bathophilus* (Fig. 63), *Grammatostomias*, and *Photostomias,* the medial pelvic radial element or elements are anteriorly elongate, extending just anterior to the articulation of the first fin ray. (CI = .5)

In other stomiids, any medial radial elements extend no further anteriorly than the articulation of the second fin ray.

302. In *Photostomias,* the medial pelvic radial is abbreviated posteriorly, extending no further back than the articulation of the fourth fin ray. The lateral process of the pelvic girdle is also abbreviated posteriorly, and the fin rays are bunched anteriorly, articulating in the region of the short lateral process (the fin rays are also reduced in number, see Character 304). (CI = 1.0)

In other stomiids, the medial radial extends posterior to the articulation of the last fin ray, the lateral process is more elongate, and the rays are not bunched together.

303. In *Bathophilus* and *Photostomias,* there are no pelvic-fin distal radials. (CI = .5)

In other stomiids, there is at least one distal pelvic radial.

304. In *Aristostomias,* some *Bathophilus* species, *Idiacanthus, Malacosteus, Photostomias,* and *Stomias,* the number of pelvic-fin rays is six or fewer (four or five in *Stomias,* four to six in some *Bathophilus,* six in all others). (CI = .25–.33)

In other stomiids, there are at least seven fin rays.

305. In some *Bathophilus* species, *Echiostoma,* some *Eustomias* species, some *Opostomias* species (*micripnus,* Gibbs, pers. comm.), and *Tactostoma,* the number of pelvic-fin rays is consistently more than seven (8–26 in *Bathophilus,* eight in *Echiostoma,* 7–9 in *Opostomias,* 8–10 in *Tactostoma*). (CI = .5)

In other stomiids, with the exceptions noted in Character 304, there are seven rays.

306. In *Stomias,* there are 4 or 5 pelvic-fin rays. (CI = 1.0)

In other stomiids and "photichthyans" there are 6 or more pelvic-fin rays.

307. In *Photostomias,* the halves of each pelvic-fin ray are fused together along their anterior margins for most of their length, both halves of the anterior ray have an expanded flange with a wavy posterior edge for about half its length, and the anterior two rays are tightly bound together for most of their lengths. (CI = 1.0)

No such modifications are present in other stomiids.

308. In *Bathophilus,* there are no pelvic-fin interradial membranes. (CI = 1.0)

In other stomiids, such membranes are present.

Light Organs

309. In *Aristostomias, Malacosteus,* and *Pachystomias,* there is a large accessory light organ (accessory orbital photophore I [AOPI]) anteroventral or ventral to the eye, which extends medially well into the orbital cavity (Fig. 70). (CI = .5–1.0)

In other stomiids, there are usually only two light organs associated with the eye, the "suborbital organ" and the "postorbital organ". See Discussion

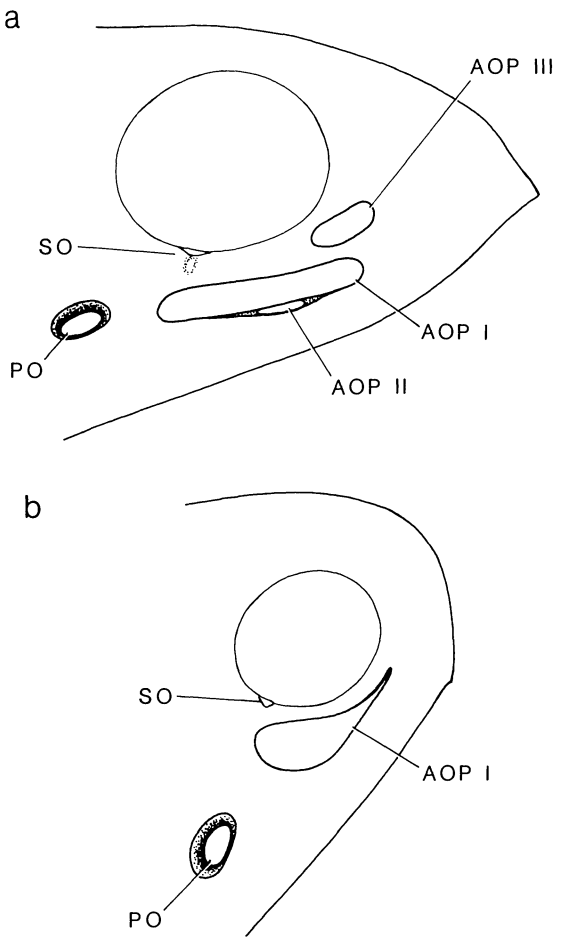

FIG. 70. Orbital photophores. a, *Pachystomias microdon* (MCZ 53256); b, *Malacosteus niger* (MCZ 53272). SO = suborbital photophore, PO = postorbital photophore, and AOP I, II, III = anterior orbital photophores.

for comments on homologies of head photophores in stomiids. *Trigonolampa* has accessory superficial patches of luminescent tissue on the head (see Character 315).

310. In *Aristostomias*, *Malacosteus*, *Pachystomias*, and *Photostomias*, the suborbital photophore is ventral or posteroventral to the eye (see Character 309). (CI = 1.0)

In other stomiids, the suborbital photophore lies anteroventral to the eye; in some phylogenetically derived species of *Eustomias*, the suborbital light organ may be absent.

311. In *Pachystomias*, there is a second accessory orbital photophore (AOPII) just ventral to accessory orbital photophore I and a third accessory photophore (AOPIII) anterior to AOPI (Fig. 70). (CI = 1.0)

In other stomiids, there is only one, or no accessory orbital photophore in this position (see Character 309).

312. In *Aristostomias*, *Malacosteus*, and *Pachystomias*, the photophores of the OA, PV, and VAV series (see Morrow, 1964b) are unevenly spaced, so that there are gaps in the rows. (CI = .5–1.0)

In *Pachystomias*, and some *Aristostomias*, the photophore rows apparently are lacking particular photophores (or they may be present but not fully developed) (see Morrow and Gibbs, 1964, Fig. 97). In some *Aristostomias*, not only are some photophores missing, but there is some "clustering" of photophores (see Morrow, 1964d, Fig. 143). In apparently derived *Aristostomias* species, this clustering is quite pronounced. In *Malacosteus*, most of the photophores are missing, and only a few, usually clustered, photophores are present.

In most other "photichthyans", the photophores are regularly spaced. See also Character 314.

313. In *Aristostomias*, *Malacosteus*, and *Pachystomias*, there are two rows of IP photophores (ventral series photophores between the isthmus and pectoral-fin insertion) (Goodyear, 1980). (CI = .5–1.0)

In other stomiids, there is but one row of IP photophores.

314. In *Heterophotus*, the photophores in the ventral series are arranged in irregular rows of 1–5 (Gibbs, 1964a; see Fig. 89). (CI = 1.0)

In most other stomiids, the ventral photophores are evenly spaced. See also Character 312.

315. In *Trigonolampa*, there is a large, multipartite superficial light organ behind the eye, extending posteriorly almost to the far edge of the operculum (Morrow and Gibbs, 1964, Fig. 96). (CI = 1.0)

In other stomiids, there is no such organ.

316. In *Thysanactis*, the rod-ray is tipped by a multi-stranded light organ (see Jørgensen and Munk, 1979, Fig. 1). (CI = 1.0)

In other stomiids with a developed rod-ray, the ray terminates in a single strand.

Miscellaneous Characters

317. In stomiids, except apparently in *Chauliodus* and *Stomias* (Morrow, 1964b,c), there are no scales. (CI = .5)

In other "photichthyans" scales are present. See Character 318.

318. In *Chauliodus* and *Stomias*, there is, in life, a gelatinous membrane over the body in which thin, non-overlapping scales are embedded (Morrow, 1964b,c). (CI = 1.0)

In other "photichthyans", there is no gelatinous membrane and scales are either absent or large and overlapping.

319. In *Chauliodus* and *Stomias*, there is a distinct hexagonal pigment pattern in the skin. (CI = 1.0)

In other stomiids, there is no such pattern. Other stomiids are usually black or otherwise darkly pigmented, and more primitive "photichthyans"

have elliptical scale-pocket patterns similar to other primitive teleosts.

320. In stomiids, except as noted below, there is a mental barbel which extends from the base of the urohyal, anteriorly in the hyoid region. In all species that have been checked, there is luminous tissue on the barbel, usually at its tip (see, e.g., Jørgensen and Munk, 1979). In *Malacosteus* (coded as missing), *Photostomias* (coded as missing), some large specimens of *Chauliodus* (coded as present), and males of *Idiacanthus* (coded as present), there is no barbel and these are considered secondary losses. (CI = .5–1.0)

For representative samples of barbel morphology, see Morrow (1964b) and Morrow and Gibbs (1964).

In other stomiiforms, there is no mental barbel.

321. In *Aristostomias*, *Malacosteus,* and *Photostomias,* there is no skin between the mandibular rami, i.e., there is no floor to the mouth. (CI = .5–1.0)

In other stomiids, there is skin between the mandibular rami.

322. In *Idiacanthus*, the larvae and postlarvae have the eyes on stalks which become shorter with age; in adults the eyes are unstalked. See Beebe, 1934. (CI = 1.0)

In other stomiid larvae, the eyes are not stalked.

323. In *Idiacanthus*, adult males retain many larval and postlarval characteristics, are much smaller than adult females, and do not feed. See Beebe, 1934. (CI = 1.0)

In other stomiids, adult males appear as developed as adult females and do feed.

DISCUSSION

Stomiid Interrelationships

In this section, I summarize and discuss the evidence presented in the Characters section for the existence of groups within the Stomiidae. Not every character mentioned above is included, partly to avoid redundancy and partly to highlight those characters that are most stable. The reader should see the legends for Figures 2 through 6 to determine which characters support each group. I also take the opportunity in this section to discuss some morphological characteristics which are relatively complex and not easily comprehensible from a reading of the character descriptions.

The term character refers to the derived state only; those wishing to know the primitive state should refer to the Characters section. This section is not designed for the identification of specimens; certain "key combinations" of primitive and derived characters are often useful for that purpose, but are not informative about relationships and are thus not discussed. Identification keys for most genera are available in Morrow (1964d), Morrow and Gibbs (1964), and Gibbs (1964a). Little effort was made to identify synapomorphies of many of the genera once their monophyly was documented

to my satisfaction; further investigations will be needed to describe more fully the features of most genera, especially since many have not been shown previously to be monophyletic.

As outlined in the Introduction, the taxa I recognize as comprising the Stomiidae historically have been relegated to several families, depending on various authors' preferences; these are Astronesthidae, Chauliodontidae, Idiacanthidae, Malacosteidae, Melanostomiidae, and Stomiidae. Inasmuch as the hypothesis of relationships generated by this study demonstrates that some of these groups are unnatural or that their continued recognition at family rank would require a radical reclassification of the entire group, the most conservative taxonomic approach appears to be to expand the Stomiidae of Regan and Trewavas (1930) to include all of the stomiiforms with barbels.

The Stomiidae is documented as monophyletic based on a number of characters, including presence of a single infraorbital bone (Character 33), lack of gill rakers in adults (Character 103), presence of two main bodies of the geniohyoideus muscle (Character 168), a portion of the adductor mandibulae inserting on the postorbital photophore (Character 187), lack of hypural 6 (Character 228), and presence of a mental barbel associated with the hyoid apparatus (Character 320). This family includes some of the most morphologically specialized of teleosts, such as *Aristostomias*, *Eustomias*, and *Malacosteus*. Also of interest is the persistence of several morphologically and phylogenetically primitive representatives, such as *Astronesthes* and *Rhadinesthes,* which present a rich picture of the origins of such novelties as pectoral-fin specializations and changes in placement of the vertical fins. Some of these evolutionary changes are mentioned below in the context of various subgroups, and others are discussed in the more general summary which follows the subgroup descriptions.

Neonesthes is the sister group to all other stomiids. It is diagnosable by presence of a row of toothplates along the entire medial length of the hyoid bar (Character 73).

Regan and Trewavas (1929) originally described *Neonesthes,* placing it in the Astronesthidae. Gibbs (1964a) figured and described individuals of *N. capensis,* and Weitzman (1967b) described much of its osteology.

All other stomiids are united by such traits as presence of ventral rector gill-arch muscles attaching to the fifth ceratobranchial (Character 179), morphology of the first distal radial of the pectoral fin, including lack of complete ossification (Character 268), and enlargement of the anterior cartilaginous process of the pelvic girdle (Character 285). All of these characteristics are further elaborated within the group.

At this node of the cladogram there are two alternate hypotheses which are equally supported by the data at hand: *Astronesthes* as the sister group to either *Borostomias*, or to all remaining (i.e., non-*Neonesthes*) stomiids. For this reason, in the summary cladogram the unresolved node is noted as (B,C), representing the alternative hypotheses represented in Fig. 2.

Astronesthes is one of the most perplexing of the stomiid clades. The

morphology includes traits which appear independently in more advanced groups, and there are character transformations within the genus which mimic similar transformations in stomiids as a whole. *Astronesthes* is diagnosable by the form of the blood-vessel passage in the hypohyal element (Character 88), and the way in which the prezygapophyses of the anterior 10–20 neural arches are enlarged, closely approximated serially, and extend over the neural tube as a bony hood (Character 199).

Other traits of *Astronesthes* include "serrae"-like teeth on the maxilla, in combination with the dorsal fin near the dorsal midpoint of the body. The former is also found in the members of Clade E, and the latter is primitive for stomiids.

Within *Astronesthes*, there are morphological changes that are similar to those in other stomiids. For example, the parietal bones are absent in some more derived species (such as *A. niger*, see Weitzman, 1967b, Fig. 3), as they are in *Aristostomias*, *Echiostoma*, and some *Stomias* species (see Character 28). Body elongation, typical of many stomiids, occurs in some species, such as *A. psychrolutes* (Gibbs and Weitzman). The posterior pelvic plate ranges from a relatively simple projection to a large, single fused plate-like cartilage (Weitzman, 1967b, Fig. 18). The general phenetic "gestalt" of *Astronesthes*, particularly of the head, is suggestive of a phylogenetically more derived taxon than detailed comparisons show. In the context of all the characters, these similarities are shown to be convergently acquired, which might make further work on the genus easier and more interesting.

The characters found have not allowed a resolution of the relationships of *Astronesthes*, although its general placement near the base of the cladogram is amply demonstrable. But whether *Astronesthes* is the sister group of all stomiids but *Neonesthes* (Fig. 2a), or whether it is most closely related to *Borostomias* (Fig. 2b) is not clear. As is often so in primitive members of a large group, there are few specializations which are informative about their interrelationships. The evidence for *Astronesthes* and *Borostomias* being sister taxa is presence of a parasphenethmoid bone (Character 15), and supraneural placement (reversal of Character 193 to the primitive condition), a reversal which occurs elsewhere in the tree. The evidence that *Astronesthes* is the sister group of *Borostomias* plus the other stomiids is based on presence in the latter taxa of the rectus communis muscles extending anteriorly as far as the second hypobranchial (Character 180; this trait is not present in *Chauliodus*). Based on the unique parasphenethmoid, my inclination is to consider *Astronesthes* and *Borostomias* as sister taxa, but the alternate hypothesis is equally supported in the context of the entire stomiid lineage. Thus these taxa are left in an unresolved trichotomy in the summary cladogram.

Borostomias itself is diagnosable by virtue of such traits as extent of the palatine bone posteriorly beyond the anterior border of the quadrate (Character 50) and lack of articulation between the second epibranchial and the third pharyngobranchial (Character 151).

The remaining stomiids (Clade D) are considered monophyletic based on several characters, including position of a blood vessel in the ventral hypo-

hyal (Character 87) and attachment of the ligament between the basihyal and the hypohyal to the anterior half of the hypohyal element (Character 90).

Within the remaining stomiids, *Rhadinesthes* and *Heterophotus* are sister taxa, they then being the sister group of the rest (Clade E). The data that support the relationship of the two genera include the preopercle being very narrow near the symplectic-hyomandibular joint (Character 57), and the dorsal tip of the cleithrum forming an elongate spine (Character 235).

Rhadinesthes is diagnosed by the presence of, among other traits, a muscle between the barbel and the dentary (Character 171) and irregular subdivision of the pectoral-fin distal radials (Character 266). These distinctive fish are extremely elongate, laterally compressed, and rather delicate looking.

Heterophotus is recognizable by several traits, among them its lack of epipleurals (Character 213) and its photophores in the ventral series being arranged in irregular rows of 1–5 (Character 314).

The remaining stomiids, members of Clade E, are united by several characters, the two non-homoplasious ones being loss or reduction in the number of supraneurals (Character 194) and the size of the anterior and posterior vertebral centra compared with those in the mid-body region (Character 215).

Stomias plus *Chauliodus* form the sister group of remaining stomiids, represented by Clade F. These two genera are placed together on the basis of numerous traits, including the distinctive cup-like nasal bones (Character 16; Figs. 17a,b), palatine tooth placement into two groups (Character 51; Fig. 21), deeply bifurcated branchiostegals (Character 167; Fig. 31a), and hexagonal pigmentation pattern in the skin (Character 319). Both of these taxa are morphologically highly specialized, and the "morphological gaps" between them and other stomiid taxa have been interpreted as "family" level in the past, a policy not followed herein.

Chauliodus is diagnosed by many features, including the anterior location of the dorsal fin (Character 217), fusion of the distal cartilages of all dorsal-fin proximal pterygiophores (Character 224), and the posttemporal bone in the form of a thin disc of bone (Character 232). *Chauliodus* specimens are fairly common and have elicited studies like that of Tchernavin (1953), on the "functional morphology" of the rather impressive feeding structures—the anterior mandibular teeth extend dorsally up over the snout and the head is often "cocked" at an angle to the body in preserved specimens. Crane (1966) presented a non-phylogenetic analysis of *Chauliodus*, including description of a Miocene species.

Stomias is diagnosed by such features as maxillae that closely approach each other at the midline (Character 38), an elongate cartilage-tipped posterior ramus of the posterior ceratohyal which articulates with the interhyal (Character 102; Fig. 31a), a greatly enlarged anterior supraneural (Character 197; Fig. 34), a loop in Baudelot's ligament (Character 282; Fig. 60), and presence of only 4 or 5 pelvic-fin rays (Character 306). No attempt was made to investigate the protrusion mechanism of the upper jaws, but the

associated morphology is distinctive within stomiids. The maxillae are loosely joined to each other medially and to the premaxillae anteriorly. In the protruded position, the premaxillae are nearly separated from the maxillae (the jaws are partialy protruded in Fig. 21). The only other stomiids with greatly protrusible jaws are *Eustomias*, which have very different morphology, including maxillae and premaxillae tightly bound together. *Stomias* specimens also have the dorsal and anal fins well posterior on the elongate slender body, but whether this fin placement was acquired from an ancestor shared with the more derived stomiids and reversed in *Chauliodus*, or was acquired convergently in *Stomias* and more derived stomiids is not differentiable on the cladogram, since both hypotheses are equally supported by the character data. Mention is made here of *Macrostomias* only to repeat that that genus is not recognized since Fink and Fink (in press) found that the species are the sister group to some phylogenetically derived species within *Stomias*. It is best to think of *S. longibarbatus* and *S. pacificus* as simply somewhat elongate and differentiated members of a rather specialized group of stomiids. Gibbs (1969) presented a non-phylogenetic revision of *Stomias*.

The members of Clade F are united by such characters as having no more than one pair of toothplates associated with any basibranchial ossification (Character 105), and reduction or loss of all pectoral-fin distal radials except the anterior, propterygial element (Character 267). Most of the taxa included in this group were previously placed in the Melanostomiidae, but it also includes the former Malacosteidae and Idiacanthidae.

Chirostomias and *Trigonolampa* are sister taxa, themselves the sister group of the remaining stomiids. Although other workers have suggested a relationship between the above two genera, the data have been primitive traits. For example, Regan and Trewavas (1930) used as their main evidence of relationship the presence of a posttemporal bone joining the "pectoral arch" to the neurocranium, a primitive condition in this context. Beebe and Crane (1939) also united the taxa on exclusively primitive characters. It came as somewhat of a surprise to me to find that although their relationship has historically been unsupported by relevant data, the genera are linked by several characters, including having the ligament between the posterior ceratohyal and the posteroventral process of the mandible attaching anterior to the posteroventral point of the mandible (Character 63) and having the bilateral toothplates associated with basibranchials 2 and 3 usually fused to those basibranchials (Character 120).

Chirostomias has an adipose fin, a structure lacking in other members of Clade F. Derived, unreversed characters that differentiate *Chirostomias* include presence of ventral processes on the urohyal that are longer than the anterior margin of the basihyal (Character 83), an anteriorly bifurcated cleithrum with its primary axis curving medially and terminating in a long, tapering posteroventral ramus (Character 238), and a "disc"-shaped coracoid ossification that lies ventral to the mesocoracoid and articulates fully with that bone (Character 251) (Fig. 41). Additionally, and not included in

the Characters list, is the unique morphology of the external pectoral-fin rays and associated luminous tissues (for which see Morrow and Gibbs, 1964, Fig. 95).

Trigonolampa is diagnosable by means of such characters as fusion of the third hypobranchial with the third basibranchial (Character 136), having the adductor mandibulae portion which inserts on the PO photophore forming the posterior muscular border of the eye (Character 188), and a distinctive, multipartite superficial light organ behind the eye (Character 315).

The remaining stomiids form Clade J, characterized by numerous features, including the spinous portion of most of the neural arches not meeting in the midline (Character 200), reduction in the size of the caudal centra (Character 214), and reduction in the number of pectoral-fin distal radials to three or fewer, these being associated with the innovative rod-ray complex (Character 270). This clade is divided into two large subgroups, one of which comprises *Flagellostomias* and its relatives, and the other the remaining stomiids.

Clade K includes *Flagellostomias*, *Leptostomias*, *Odontostomias*, *Opostomias*, and *Thysanactis*, all of which share an elongate opercular process of the hyomandibula (Character 56), a distinctive interopercular shape (Character 59) (see Fig. 28), and slender flanges on the pectoral-fin rays that lie perpendicular to the axis of the fin rays (Character 274; Fig. 43). Regan and Trewavas (1930) considered these taxa (with the exception of *Odontostomias*, which had not yet been described, but which was considered related to *Opostomias* by Norman, 1930) to form a "natural group", based on general similarity of the skull, jaws, and intestine, although none of the characters as described is unique to these genera. The members of this group were considered the "base for the remaining melanostomiatids" by Beebe and Crane (1939), and their "phylogeny" shows the genera as sister taxa to various other melanostomiids. For example, *Thysanactis*, *Leptostomias*, and *Odontostomias* are shown in a trichotomy which is itself the sister group to an unresolved group consisting of *Eustomias*, *Melanostomias*, *Photonectes*, and *Tactostoma*. *Flagellostomias* and *Opostomias* are shown as the "sister group" to *Eustomias*, these together forming the sister group to *Bathophilus* and *Grammatostomias*. This interpretation of Text-figure 12 of Beebe and Crane assumes that the "phylogeny" can be interpreted as a genealogy, although relationships are not interpreted explicitly in that way in their text.

Flagellostomias is the sister group to other group members. The genus itself is recognizable by the anal-fin origin being in advance of a vertical from the dorsal-fin origin (Character 219, a trait shared with *Eustomias*), and having but two pelvic-fin radials (Character 294, a trait shared with *Aristostomias*). Although little effort was made to find unique traits for this genus, it is apparently monophyletic and clearly separable from the remaining members of the group. The latter taxa share numerous characters, including relatively short and deep jaws (Character 41), the hyomandibula nearly perpendicular to the long axis of the fish (Character 55; Fig. 28), the anterior few vertebrae being very narrow (Character 191), and dorsoventral

expansion of the pectoral-fin proximal radials distally and proximally (Character 264; Figs. 42, 43). In addition, there is only a single tooth attached to ceratobranchial 5 (Character 141), a character whose significance is ambiguous in the context of absence of teeth on that bone in many other stomiids (see Characters 140, 141).

Within this group, at Clade L, the data support two sister groups, *Leptostomias* plus *Thysanactis* (Clade M), and *Odontostomias* plus *Opostomias* (Clade N). The former group is supported by such characters as the square shape in cross-section of the pectoral-fin proximal radials (Character 263), and presence of 14 pectoral-fin rays (Character 273; Fig. 43). The latter group is supported by the extremely fenestrated cleithrum (Character 239; Fig. 42).

Leptostomias is an elongate fish usually with an elongate barbel; there is no evidence of a rod-ray complex externally, although the skeletal remnants are there. The genus is diagnosable on the basis of reduction of the toothplates along the posterior edge of ceratobranchial 4 to tiny, toothless plates of bone (Character 139). *Thysanactis* is diagnosable based on the presence of a multistranded putative light organ distally on the rod-ray (Character 316). *Thysanactis* is not as elongate as *Leptostomias*. Regan and Trewavas (1930) were so impressed by the overall morphological similarity and thus apparent close relationship of these two genera that they considered the "rod-rays" to have evolved convergently in *Thysanactis* and in *Opostomias*. That hypothesis is rendered unnecessary since *Leptostomias* has remnants of that system.

The original description of *Odontostomias* (Norman, 1930) contains no characters unique to the genus, and both the generic and species descriptions contain errors of observation that have not been corrected by subsequent workers. Examination of the holotypes of *O. micropogon* and *O. masticopogon* shows that there is a small and poorly developed "rod-ray complex" rather than none as Norman implied in suggesting lack of an "isolated ray". In addition, *O. masticopogon* has a PO photophore, contrary to Norman. I have not done a comprehensive search for characters to diagnose the genus and have found only two traits, both reversals, which separate it from its close relatives: presence of a toothplate on the third hypobranchial (see Character 137) and articulation of the non-rod ray fin rays with the second proximal pectoral-fin radial (Character 278; Fig. 42). Any future work on the genus will have to be based on a better substantiated hypothesis of monophyly than I have found.

Opostomias is diagnosable by virtue of the large foramen passing vertically through the premaxilla, just lateral to the symphysis, into which a mandibular tooth fits (Character 36). It also has a well developed rod-ray.

The remaining stomiids form a group (Clade O) based on the interhyal articulating along or anterior to the front margin of the cartilage between the hyomandibular and symplectic bones and attached by ligament to the metapterygoid (Character 70), the size of the pelvic girdle anterior process relative to the posterior plate (Character 288), and the anterior extent of the medial pelvic radial (Character 299). The best hypothesis of relationships

within this group places *Photonectes* as the sister group to all the rest. An alternative hypothesis will be discussed below.

Photonectes is an interesting genus that encompasses a surprising amount of morphological diversity. Attempts to communicate this diversity have been made by various workers, most notably Regan and Trewavas (1930), through the erection of subgenera. Most of these subgroups are based on combinations of characters, and it is likely that some are not monophyletic. The characteristics marking the subgenera include skin covering the dorsal and anal fins, lack of external pectoral-fin rays, and location of the pelvic fins on the body (a summary is available in Morrow and Gibbs, 1964). An understanding of interrelationships within *Photonectes* will require a critical survey of these, and other traits. I have not attempted such a survey, but my work has shown some trenchant osteological differences even among specimens recognized on standard external characters as conspecific. In short, an understanding of this genus is barely sketched out at this point. Nevertheless, the genus can be diagnosed by presence of the elongate posterior process of the anguloarticular (Character 46; Fig. 30), the elongate hypohyal (Character 100), and dense fibrocartilage lying between the anteriomedial tip of the coracoscapular plate and the cleithrum (Character 244).

The remainder of this large group (Clade P) is documented by no unique characters. One trait, which is reversed in *Tactostoma,* allows diagnosis of the clade: epipleurals fused to the pleural ribs for most of the body length (Character 212). Another trait, fewer than five branchiostegals articulating with the posterior ceratohyal ossification (Character 163), is reversed in *Aristostomias* and *Pachystomias,* and is present in only some *Eustomias.*

Within this clade, however, relationships of most of the subclades are fairly well documented. In the simplest hypothesis, the pair *Echiostoma* plus *Melanostomias* form the sister group to the remaining genera, represented by Clade Q. These two genera are united by presence of a small conical bone in a pocket on the ventrolateral surface of the ethmoid cartilage (Character 9), a robust posterior process on the pterotic (Character 24; Figs. 14b, 15b), and ligament 3 forming a thick sheath around the dorsal tip of the cleithrum and adhering to almost the entire anteromedial surface of the supracleithrum (Character 281). These genera have not been considered formally as sister taxa before, although previous authors have considered them together with *Photonectes* and *Tactostoma* (see e.g., Beebe and Crane, 1939). Externally, the species are relatively similar, the greatest difference being in the well developed rod-ray of *Echiostoma* and the almost total reduction of that complex in *Melanostomias.* Both genera share with *Trigonolampa* a somewhat spinous extrascapular bone (Character 230).

Echiostoma is distinctive, with large rugosities on the frontal sensory canals and antorbital (Characters 26 and 58; Fig. 14).

Melanostomias is characterized by presence of several characters, all of which appear elsewhere among stomiids. Fusion of the distal cartilage tips of the lateral ethmoid and supraethmoid (Character 11) is found in the members of Clade K as well as in *Melanostomias.* Anterior elongation of the

medial pelvic radial (Character 300) is also found in several genera and has evolved at least three times within stomiids. Further work is needed to establish that this genus is monophyletic.

The remaining stomiids (Clade Q) can be placed together based on their possession of such traits as lack of a mesopterygoid (Character 54), and lack of a posttemporal bone (Character 231). *Idiacanthus* and *Tactostoma* form the sister group of the other members of this group. The former two share a palatine bone which has its ventral border dorsally arched from lateral view (Character 49; Fig. 19), a reduced, cylindrical basihyal (Character 77), a combined tendinous and musculous insertion of the dorsal portion of the geniohyoideus muscle on the dentary (Character 170), and the dorsal section of the medial division of the adductor mandibulae muscle with its origin anterior or anteromedial to the insertion of the levator arcus palatini (Character 189). These genera include the most elongate, anguilliform-shaped of the stomiids. Both have a number of specializations, and those of *Idiacanthus* have led some workers to place it in a monogeneric family.

Idiacanthus is diagnosed by the presence of numerous traits, including fusion at the midline of the toothplate pair associated with basibranchial 1 (Character 114), highly modified dorsal- and anal-fin supports (Character 218; Fig. 35), stalked eyes in larvae (Character 322), and retention of larval and postlarval characteristics in adult males (Character 323).

Tactostoma is somewhat less distinctive than *Idiacanthus*, but the presence of Type 4 teeth in adults as well as juveniles is unique within the family (Character 35; Fig. 19).

The remaining stomiids (Clade R) are united by having a looped ligament in the floor of the mouth that attaches to the dentaries at the symphysis (Character 45), a relatively long basihyal (Character 74), and no branchiostegals articulating on the ventral hypohyal near its anterior border (Character 161). There are two subgroups in this clade, one consisting of the members of Clade U and the other including the members of Clade W.

Clade U includes *Bathophilus*, *Eustomias* and *Grammatostomias*, a combination which has not been recognized by previous authors, probably because the numerous autapomorphic specializations in *Eustomias* caused it to be considered by authors with a gradal viewpoint as "an isolated genus" (e.g., Regan and Trewavas, 1930). Nevertheless, there are a number of features which document monophyly of this group, including several from the branchial basket, from the vertebrae, and from the pectoral girdle. In all members of the group the hypohyal bone is twice as long as its dorsoventral height (Character 96), the third epibranchial articulates with the third pharyngobranchial anterior to the posterior border of the ossification of the latter bone (Character 152), and the proximal flanges of the pectoral-fin rays are greatly reduced in breadth (Character 276; Figs. 39, 45 and 46). Within this group, *Eustomias* is the sister taxon to the other two genera.

Eustomias is distinctive and in many ways is among the most unusual of teleosts. Because of a fair degree of morphological differentiation within the

genus, there have been attempts to partition its more than 100 species into subgenera (this history was recently reviewed by Gibbs et al., 1983). However, these attempts have been largely unsuccessful because there have been no explicitly phylogenetic analyses, and characters purporting to diagnose most groups are usually combinations of primitive and derived traits. The task of detecting relationships among the many included species will not be easy, but there are many traits examined during this study that are suggestive of major lineages.

Among the characters that uniquely diagnose *Eustomias* are the structure of the jaw suspensorium, and of the anterior vertebral column, and several modifications of the fin skeletons. The ectopterygoid and palatine are largely separate from the other bones of the suspensorium, the only attachment being by a thick ligament between the posterior tip of the ectopterygoid and the ventral, articular process of the quadrate. The ectopterygoid and palatine articulate with the maxilla to form a rigid structure that posteriorly bifurcates and extends bilaterally around the mandible. In addition, the anterior portion of the palatine is enlarged and projects well dorsal to the margin of the maxilla. These specializations (Character 52, see Fig. 24), together with the extreme dorsal expansion of the interopercle and its associated opercular-interopercular ligament (Character 60), are part of the protrusion mechanism which gives *Eustomias* the most protrusible jaws of any stomiids. Another feature of the genus, one that was discussed at length by Regan and Trewavas (1930), is the extreme modification of the anterior region of the vertebral column (Character 192). In this area, the notochord is nearly bared of centra and is greatly curved, forming an almost sigmoid structure clearly resembling a spring (Fig. 33).

The internal skeleton of the anal and dorsal fins is specialized in *Eustomias,* with the medial pterygiophore being fused to the distal pterygiophore, rather than the proximal pterygiophore (Character 221) as in all other stomiids. *Eustomias* has two unique pectoral-girdle specializations, one being lack of a supracleithrum (Character 234) and the other being the medial fusion of the coracoscapular plate cartilages (Character 243; see Figs. 45, 46).

Bathophilus and *Grammatostomias* have been placed together before, primarily on the basis of general similarity of skull morphology (Regan and Trewavas, 1930). I have also found several features which support their monophyletic relationship, including the ventrally produced ethmoid region (Character 8; Fig. 13), presence of only 3 branchiostegals on the posterior ceratohyal (Character 164), and the morphology of the cleithrum, in which the lateral wing is laterally extended and somewhat thickened, and the cleithrum is foreshortened anteriorly (Character 236; Fig. 39a).

Bathophilus specimens are quite distinctive, the most obvious features being the wide separation of the pelvic fins (Character 283) and the elongate pelvic-fin rays lacking interradial membranes (Character 308). Other unique features include presence of but a single proximal pectoral-fin radial (Character 262; Fig. 39a) and a process on the premaxilla which articulates

along the anterodorsal margin of the maxilla (Character 37; Fig. 20).

Grammatostomias species are characterized by such features as lack of a levator internus muscle to the posterior pharyngobranchial toothplate (Character 177) and the mesocoracoid being reduced to a fibrous body which extends from the medial margin of the coracoscapular plate (Character 255).

Clade W includes the old Malacosteidae, comprising *Aristostomias*, *Malacosteus*, and *Photostomias*, plus *Pachystomias*, formerly considered a melanostomiid "close to" but not in the former family (Goodyear, 1980, considered these taxa as "malacosteid-grade stomiatoidei"). The "malacosteids" include some of the most bizarre members of a generally unusual group of fishes, with blunt heads, large jaws, and no "floor" to the mouth. Their neurocrania are among the most specialized I have seen. These fishes, like *Chauliodus*, inspired a "functional morphological" analysis (Gunther and Deckert, 1959, which includes numerous, often somewhat inaccurate drawings of the anatomy). Characters supporting this group are numerous, including posterior termination of the parasphenoid well anterior to the posteroventral margin of the basioccipital (Character 18), projection of the cartilage of the exoccipital posterior process anterodorsal to the posterodorsal bony border of the process (Character 30), interruption of the cartilage of the palatine arch and posterior termination of the palatine as a bony point (Character 47), and location of the suborbital photophore ventral or posteroventral to the eye (Character 310).

Characters diagnostic of *Aristostomias* include extension of the ventral portion of the neurocranium well ventral to its position in other stomiids (Character 19) and extension of the sphenotic spine as far posteriorly as the pterotic process and the posterior border of the prootic (Character 21); these characters give the neurocranium a very distinctive look (Fig. 9b). *Malacosteus* is diagnosed by such features as the convex margin of the anterodorsal portion of the neurocranium (Character 1, Fig. 7a), a completely unossified palatine element (Character 48, Fig. 26), and a median toothplate associated with basibranchial 4 (Character 131). *Pachystomias* is characterized by three accessory orbital photophores (Character 311). *Photostomias* has the anterior half of the neurocranium greatly foreshortened (Character 2, Fig. 8), the rector communis muscle attaching anteriorly solely on the ventral hypohyal (Character 184), and highly specialized pelvic fin morphology including fusion of the pelvic ray fin halves to each other (Character 307).

Interrelationships within Clade W are not resolved in this study, as the phylogenetic analysis has provided several alternate hypotheses of equal length. The set of shortest trees (Fig. 1) place all four taxa as an unresolved polychotomy at Clade W.

Unique characters that support *Pachystomias* in a sister group relationship with *Malacosteus* and *Aristostomias* include neurocranium depth being greater than its length (Character 3), a laterally produced pterotic which does not bear a sensory canal (Character 23) (Figs. 7b, 9b, 10b), a fused single parapophysis of centrum one which has a single ventral apex and

from which the pleural ribs of each side extend (Character 207), a large accessory light organ which extends medially well into the orbital cavity (AOPI) (Character 309), ventral photophores that are unevenly spaced (Character 312), and IP photophores in two rows (Character 313).

Unique characters supporting the alternative hypothesis of *Photostomias* in a sister group relationship with *Aristostomias* and *Malacosteus* include a concave ventromedial surface of the cleithrum (Character 237, Fig. 40a), and lack of skin between the mandibular rami (Character 321). It is on the basis of this last, rather striking morphology that these genera have been placed together at family rank. For other resolutions and the characters supporting them, see Fig. 6.

There are some other alternative cladograms that deserve discussion here. In the aforementioned relationships of *Photonectes,* the best hypothesis regarding the membership of Clade O places *Photonectes* as the sister group to those remaining. An alternative hypothesis is that *Idiacanthus* plus *Tactostoma* are the sister group of *Echiostoma* plus *Melanostomias,* these together forming the sister group of *Photonectes* and the more derived stomiids. The single unique trait in the matrix which supports a monophyletic arrangement of these four genera (not including *Photonectes*) is the anterior projection of the toothplates associated with the first basibranchial (Character 113), but this feature also occurs in some *Photonectes* species. It was not entered into the matrix as derived for that genus for the reasons discussed in the Methods section. All of the remaining 6 characters supporting this four-taxon grouping have CI's of .25 or .33. The single unique trait that supports placement of *Photonectes* as sister group of the remaining stomiids is the concave dorsal border of the foramen magnum (Character 32); the remaining 10 characters have an average CI of .36.

Other cladograms were examined for length and character distributions. These alternatives included trees in which the various "astronesthid" genera, *Stomias,* and *Chauliodus* were arranged in different ways, in which *Photonectes* was moved into several positions in the tree, and in which the *Idiacanthus—Tactostoma* and *Echiostoma—Melanostomias* clades were broken up and moved to several places in the tree. There are several alternative arrangements which are within 5 or so steps of the most parsimonious tree. None of these is presented or discussed, partly for reasons of economy, and partly because it does not seem profitable since I do not know how many such trees are possible.

Character Evolution

Stomiids present an amazing array of specializations and a degree of morphological differentiation virtually unequaled in a group of its size within the teleosts. The differences in, for example, skull morphology between primitive taxa such as *Neonesthes* and *Rhadinesthes* and the highly derived *Malacosteus* and *Photostomias* are impressive. Some casual ichthyological viewers of the neurocranium figures included herein were un-

certain whether those drawings were even actinopterygian. The evolutionary processes "driving" these morphological changes are unknown. Speculations on the functional significance of some of the structures, based on comparisons with other animals for which we have behavioral observations are useful to a degree, but given the dearth of reasonable hypotheses about evolutionary processes, it would not be profitable at this time to construct an intricate scenario about stomiid evolution.

On a more limited scale, however, given the phylogenetic hypotheses discussed above and the character optimizations chosen, it is possible to examine in some detail several of the transformations in morphology that have occurred during the evolutionary history of stomiids. In this section, I will discuss some of those transformations and mention some implications of alternative hypotheses of relationships.

NEUROCRANIUM.—Stomiiforms primitively have a typical primitive euteleostean neurocranium. Fink and Weitzman (1982) have described the morphology of the primitive *Diplophos* in detail. Within stomiids, however, there are some major innovations in morphology including loss (sometimes multiple) of several bones (e.g., parietals, rostrodermethmoid) and changes in the relative sizes and shapes of some bones which result in significant morphological specializations not found elsewhere. The most modified neurocrania occur in *Aristostomias* (Fig. 9), *Malacosteus* (Fig. 7), and *Photostomias* (Fig. 8), but a perusal of the figures of skull morphology will show the reader that other stomiids are also quite distinctive. Compared with the most primitive stomiiforms, stomiids have rather foreshortened skulls, as seen by comparison of the included figures with Figure 3 of Fink and Weitzman (1982). Loss or reduction of skull ossification includes loss of the rostrodermethmoid in *Heterophotus* and in members of Clade F (Character 5), reduction of the lateral ethmoid in several genera (Character 12) and loss of that bone in *Eustomias* and *Malacosteus* (Character 13), loss of vomerine teeth in a large number of genera (Character 17), and loss of the parietal in several genera and within *Astronesthes* and *Stomias* (Character 28). Innovations in bone architecture include ventral extension of the ethmoid region in *Bathophilus* and *Grammatostomias* (Character 8), presence of a small, conical bone in a pocket on the ethmoid cartilage in *Echiostoma* (Fig. 14) and *Melanostomias* (Character 9), presence of a parasphenethmoid in *Astronesthes* and *Borostomias* (Character 15), formation of a cup-like nasal bone in *Chauliodus* and *Stomias* (Character 16; Fig. 17), elongation of the basisphenoid in *Aristostomias* (Fig. 9b) and *Pachystomias* (Fig. 10b) (Character 20), presence of rugosities on the frontals in *Echiostoma* (Fig. 14), *Melanostomias,* and *Trigonolampa* (Character 25), fusion ontogenetically of the parietals with the epioccipitals in several genera (see Character 27), and a major rearrangement of the posterodorsal area of the skull in several genera such that the internal walls of the braincase are visible from dorsal view, through the foramen magnum (Character 32; see for example, Fig. 16a, of *Photonectes*). See the discussion of each of these characters for descriptions of morphology and their distributions.

SUSPENSORIUM AND JAWS.—As with the neurocrania, the suspensorium and jaws of stomiids are distinctive. The most obvious specializations are those of the enlarged, fang-like teeth, often barbed distally. However, there are also specializations of the palatine arch, the opercular/mandibular linkage for opening the jaws (see Lauder, 1982), and a surprising degree of reduction compared with more primitive stomiiforms (of, for example, the infraorbitals).

Although it is a stomiiform trait to have Type 3 teeth (hinged teeth with an anterior axis of rotation; Fink, 1981 and Fink and Weitzman, 1982), several stomiids secondarily have the more primitive Type 1 (fully ankylosed to the jaws) in the adult (Character 34). The taxa that have Type 1 teeth include the members of Clade W (see Figs. 25, 26), *Astronesthes*, and *Chauliodus*. In one genus, *Tactostoma*, juvenile tooth morphology (Type 4, a neoteleostean trait according to Fink and Weitzman, 1982) is retained in adults (Character 35, Fig. 19). In several stomiids, the jaw teeth are extremely long and extend either up and over the head, as in *Chauliodus*, or fit into foramina in the premaxillae, as in *Opostomias*. Another specialization of the dentition found in some stomiids is the presence on the maxilla of regularly and closely set teeth (Character 39), giving the maxilla a characteristic "serrated" look (see, e.g., Figs. 18, 20, 22). This morphology has evolved within stomiids twice: in *Astronesthes* and in the members of Clade E. Primitively there are teeth of more than one size on the maxilla, but in *Astronesthes*, *Stomias* plus *Chauliodus*, and in the members of Clade R, the teeth are uniformly small (Character 40). *Stomias* and *Chauliodus* also have among their many shared features a unique distribution of palatine teeth, with a group of teeth anteriorly, near the articulation of the bone with the neurocranium and another group well posterior (Character 51, Fig. 21).

Predacious fishes such as these might be expected to have this region highly developed, but stomiids have many features of the palatine region reduced. The mesopterygoid is reduced (Character 53), and in *Thysanactis* and members of Clade Q, the mesopterygoid is absent altogether in adults (Character 54). In members of Clade W the cartilage core of the palatine arch is interrupted, separating the palatine from the posterior portion of the arch (Character 47), and in *Malacosteus* the palatine is cartilage only (Character 48, see Fig. 26). In *Eustomias*, the suspensorium is extremely specialized, with the ectopterygoid and palatine largely separated from the other bones of the suspensorium, connecting with the maxilla instead and forming part of the complex for jaw protrusion (Character 52; Fig. 24); in this morphology, *Eustomias* is unlike any other teleost. *Idiacanthus* and *Tactostoma* have a distinct dorsal arching of the palatine arch, when viewed from a lateral perspective (Character 49, Fig. 19).

The Characters section lists numerous specializations of the ligaments associated with the suspensorium and jaws, as well as certain osteological features associated with the opening and closing of the impressive jaws of these fishes. An attempt to correlate this complex of traits in an analysis of function seems premature at this point, but the reader is referred to such

attempts for the "malacosteids" (Gunther and Deckert, 1959) and *Chauliodus* (Tchernavin (1953).

BRANCHIAL BASKET AND HYOID.—These two intimately connected morphological structures are complex and details of their features should be sought in the Characters section. Many of the characters used in the analysis of relationships involve the shapes and interconnections via ligaments of the many bony and cartilaginous elements of these structures. That these areas are complex should not be surprising since much of the head morphology in these fishes is also specialized, apparently for the acquisition of food, and the hyoid and branchial basket are functionally associated with mouth opening and food processing, respectively. A few of the more significant specializations are briefly mentioned below.

Stomiids lack gill rakers as adults (Character 103), although they may be present in juveniles. In *Neonesthes* the medial surface of the hyoid bar bears a row of toothplates (Character 73). *Stomias* has an interesting specialization of the hyoid in that the posterior ceratohyal has an elongate posterior ramus which articulates with an elongated interhyal (Fig. 31a); a remnant of the primitive interhyal-ceratohyal articulation point is often retained in a more anterior position on the dorsal border of the ceratohyal, and this indicates that in *Stomias* the articulation has shifted well posteriorly.

MUSCLES AND LIGAMENTS OF THE HEAD.—Numerous specializations are present in this morphological complex, again probably correlated with the general specialization in this region of the body. Most of the differentiation has to do with increases in muscle complexity, changes in insertions and origins of muscles, as well as changes in tendons and ligaments. An example of these structural changes may be seen in the geniohyoideus muscle (see Characters 168–175). In stomiids the muscle primitively is divided into two bodies (in contrast to the broad single muscle of other stomiiforms), and the ventral portion is often subdivided; one part of the ventral portion extends into the barbel. Primitively, the muscle has a tendinous insertion on the dentary, but in the members of Clade R and *Photonectes,* the dorsal portion has a muscular insertion, and in *Idiacanthus* and *Tactostoma* the insertion is both muscular and tendinous. Additionally, the ventral portion of the muscle may have one (derived) or two (primitive) distal attachment sites. This part of the muscle may also be further subdivided by a tendon, forming two muscle bodies. In *Malacosteus* and *Photostomias,* the ventral portion of the geniohyoideus distally overlies the dorsal portion and wraps over it dorsomedially. In a few stomiids, the dorsal portion of the geniohyoideus is subdivided into dorsal and ventral bodies.

POSTCRANIAL AXIAL SKELETON.—Many of the specializations occurring in stomiids represent "reduction," with loss of bones or reduction in ossification, compared with outgroups. Such specializations include a reduced number of supraneurals (Characters 193–196), decrease in the size of the spiny portions of the neural arches (Character 201), and reduction in size of the caudal vertebral centra (Character 214; compare the relative sizes of these centra in Fig. 36 of *Trigonolampa* and Fig. 38 of *Photostomias*). However,

a surprising number of features of this part of the body involve increases in complexity. These include the specialized hood-like prezygapophyses of *Astronesthes* (Character 199), the greatly enlarged anterior neural arch of *Chauliodus* and *Stomias* (Character 202; Fig. 34), and the various specializations and elaborations of the anterior parapophyses in numerous genera (Characters 203–208).

Also among the several interesting features of the axial skeleton are the reduction of centra in the anterior of the body in *Leptostomias*, *Odontostomias*, *Opostomias*, and *Thysanactis* (Character 191), and the striking multi-curved notochord of *Eustomias*, with its various centra and neural arches (Character 192, see Fig. 36), which resembles a spring mechanism.

VERTICAL FINS.—One striking aspect of the morphology of most stomiids is vertical-fin position. Most members of the group have the dorsal, anal, and caudal fins together at the posterior of the body. Several phylogenetically primitive members have the anal and dorsal fins, especially the latter, in the plesiomorph position near the midbody. On the hypothesis of relationships I have generated, the dorsal fin has moved posteriorly on the body at least three times in stomiids, and possibly four. Some species of *Astronesthes* have the dorsal fin somewhat posteriorly placed, although this has not been quantified; that position is clearly derived within the genus. *Heterophotus* has the dorsal-fin origin somewhat posteriorly placed, apparently an autapomorphy of the genus. In the members of Clade E, dorsal-fin position is well posterior in all members except *Chauliodus*, where the fin is well anterior on the body. Within this group, it is equally parsimonious to assume that: posterior dorsal-fin position evolved once in members of Clade E and the anterior dorsal-fin position of *Chauliodus* evolved as a reversal from the posterior state, or the posterior dorsal-fin position evolved independently in *Stomias* and in the members of Clade F, and the anterior position in *Chauliodus* evolved from the primitive midbody position.

Chauliodus is interesting for two reasons related to fin morphology. First, the adipose dorsal fin is rather large and lies dorsal to the posteriorly placed anal fin. Thus, it appears that the posterior-fin placement of other members of Clade E is achieved by *Chauliodus* as well, but with the adipose fin rather than the dorsal fin. Although any functional explanations of this posterior-fin placement would be speculative, presumably the combined fin area well posterior on the body generates a large amount of burst-speed thrust for prey capture (Webb, 1975). Second, the second dorsal-fin ray, which is long and filamentous, is supposed to be tipped with luminous tissues. Tchernavin (1953) and others have interpreted this structure to be a "lure" as is found in anglerfishes.

PECTORAL GIRDLE.—A complex series of morphological transformations appears to have taken place in the evolution of the pectoral fin and girdle in stomiids. Some of these transformations seem to be correlated with reduction of the pectoral fins as swimming organs and association of some fin rays with light organs, but they cannot be totally accounted for by such explanations.

The most complex set of transformations involves some reduction in fin size accompanied by elongation and greater mobility of the anterior fin rays, with luminous tissues in association with these rays (the "rod-ray" complex), then subsequent loss of these rod-rays, and finally some neomorph reacquisition of light organs on other rays of the pectoral fins.

The pectoral-fin rays in many stomiids are an integral part of a presumably light-organ bearing complex. In those primitive stomiids where the primary function of the fin is locomotor and it lacks organized luminous bodies, the fin rays, with the exception of the articulation of the first ray with the scapula, resemble those of *Polymetme* (Fig. 49) in general morphology. In these primitive members of the group, the rays are relatively strong and are branched. In more specialized stomiids, with the exception of the rod-rays, the relative size of the fin rays is less than in primitive genera and the rays are unbranched. It is not unusual for the ray halves to be very loosely bound together.

Associated with the alterations in fin-ray morphology is an alteration in distal radial morphology, involving specialization of the anterior one to three radials and loss of the others. In stomiids, the anterior distal radial has its cartilaginous core extending anterolateral to the lateral margin of the ventral ray-half in adults (see Character 269). In stomiids, except for *Neonesthes*, the cartilaginous core also extends dorsally (Character 268). Primitively, in stomiids other than *Neonesthes*, the anterior distal radial is somewhat to markedly bilobed ("dumb-bell") in shape and is in the position occupied in outgroups by the cartilage-lined articulation surface on the dorsal half of the first fin ray. Compare Fig. 52 of *Polymetme* and Fig. 51 of *Heterophotus* for examples of these ways in which the anterior pectoral-fin ray articulates with the scapula. In *Astronesthes*, the anterior radial is "dumb-bell" shaped only in juveniles, becoming more ossified and rather more primitive in appearance in adults. In *Borostomias*, the anterior distal radial directly touches the scapular surface and displaces the dorsal ray-half dorsally. Further, a column of the cartilage of the distal radial extends dorsally above the horizontal plane of the scapula and serves as an attachment site for muscles. Bone of the dorsal ray-half reinforces this cartilage. In *Chauliodus*, *Heterophotus*, *Stomias*, and *Trigonolampa*, the anterior distal radial clearly has a "dumb-bell" morphology. *Rhadinesthes* has the anterior distal radial somewhat cuboid in shape, but it retains the concave proximal surface. While no function can be ascribed with certainty to this bilobed radial shape, it appears to lend greater mobility to the anterior pectoral-fin ray than is present in non-stomiids. It may be significant that *Trigonolampa* has presumed luminous tissues in the anterior region of the pectoral fins, and movement of the fins would cause the lights to move as well. In *Chirostomias* (Fig. 41), pectoral radial/fin morphology is uniquely specialized, and no specimens available to me had cartilage fully intact, so I am unable to say what its distal radial morphology is like.

In the remaining stomiids, there is primitively a "rod-ray" complex involving the anterior one to three distal radials and anterior two to four fin rays.

As described under Character 271, the first and sometimes second fin rays are reduced in length, and the anterior two to four rays are tightly bound together and associated with the anterior radial(s). There is a wide articulation of the distal radial(s) with proximal radial I, the scapula, and in some cases with some of the more posterior distal radials. This morphology is well illustrated in Fig. 53 of *Thysanactis*. The anterior, shorter rays act as muscle attachment sites, and the more elongate rays, bound together as a stiff rod, carry presumed luminous tissues either at their tips (as in *Thysanactis*), or along their length (as in *Echiostoma*). In addition, there is no interradial membrane connecting the rod-ray to the more posterior fin rays. The latter lack distal radials (Character 271) and are generally somewhat reduced.

Speculations about the function of these highly mobile, sometimes rather elaborate luminous structures have included their being tactile, serving as sexual or prey attractants, and so on, but until we are able to observe the animals in captivity or in nature for long periods of time, it seems fruitless to continue this tradition of conjecture. Whatever their function, and whatever advantage they may have conferred, according to my hypothesis of relationship the majority of this group of stomiids has lost the external manifestations of the rod-ray. There are small internal remnants of the system in many, including *Aristostomias* (Fig. 40b), *Bathophilus* (Fig. 39a), *Eustomias* (Figs. 45, 46), *Leptostomias* (Figs. 43, 54), *Grammatostomias*, *Malacosteus*, *Melanostomias* (Fig. 44), *Pachystomias* (Fig. 47), and some *Photonectes*. The primary pectoral girdle is virtually absent in *Idiacanthus*, *Photostomias*, and *Tactostoma*, but presumably their ancestors also had remnants of the rod-ray complex. According to the hypothesis of choice, the rod ray has been lost externally at least four times during the course of stomiid evolution. *Leptostomias* has remnants while its sister group, *Thysanactis*, and their sister lineages have the external rays. The external system has been lost within *Photonectes*, as some species have a rod-ray, and also in *Melanostomias*, as its sister taxon *Echiostoma* has a well developed ray system. The remaining stomiids which have lost the rod-ray form a monophyletic group; loss in a single common ancestor could account for its absence in all of them.

Interestingly, in a number of genera with remnants of the rod-ray, the remaining pectoral-fin rays are specialized in various ways, often as bearers of luminous tissues. Examples include *Aristostomias*, *Bathophilus*, some species of *Eustomias*, *Grammatostomias*, *Malacosteus*, *Melanostomias*, *Pachystomias*, and some species of *Photonectes*. For instance, in *Aristostomias* the pectoral-fin rays have luminous tissues at their bases, and the anterior two rays are elongate and surrounded by luminous tissues from base to tip. All the fin rays also have well developed, serrated flanges proximally for muscle attachments. The obvious inference is that a remote ancestor of *Aristostomias* (and a more inclusive group) had a functional rod-ray complex, lost it, and subsequently, the immediate ancestor of the *Aristostomias* clade evolved a functionally similar structure from the remaining fin rays. Much the same course of events appears to have occurred in the history of *Grammatostomias*, which also has a rod-ray remnant combined with modified, posterior fin

rays which bear light organs. Additional evidence of the function of the luminous pectoral fins of *Grammatostomias* can be seen in the presence of a groove in the skin into which the fin can be placed, thereby effectively halting light emission.

Some species of *Photonectes* have evidently also reevolved a light-bearing ray complex. In *P. leucospilus,* there is a rod-ray remnant; the remaining, externally visible rays are bound together into a unit by interradial membrane and have luminous material on the anterior and posterior edges. The entire fin unit pivots around the broadly convex, posterior border of the scapula. In some other members of the genus (e.g., specimens identified as *P. margarita*), the girdle morphology is quite different and an original rod-ray is present, though possibly without luminous function (I could find no associated luminous tissues on the rod-ray, but Beebe and Crane, 1939, reported finding a bulbous terminal tip).

Many species of *Eustomias* have specialized fin rays of unknown function. The primitive condition within *Eustomias* appears to be presence of a rod-ray remnant, with the remaining fin rays relatively numerous and well developed (e.g., Fig. 45). In some presumably more derived species, shown in Fig. 46, only one or two elongate rays are present externally, with no interradial membrane, and apparently no luminescent tissues.

Another set of pectoral-girdle transformations involving several apparent reversals concerns the number of pectoral girdle proximal radials. As diagnosed by Weitzman (1974), members of the Photichthya have three proximal radials, in contrast to other stomiiforms and primitive teleosts generally, which have four. However, I have found four to be present in *Chirostomias*, *Heterophotus*, *Leptostomias*, and *Thysanactis* (Character 265). These are interpreted as neomorphic structures which have appeared independently in each of the first two genera and once in an ancestor of the latter two genera. I am unable to determine the homology of any of the radials of *Chirostomias* relative to other stomiids, primarily because of their relative placement to each other and similarity in size and shape. The fourth radial of *Heterophotus* is very small and continuous with the third radial distally, and is presumably derived ontogenetically from III. I suspect that radial IV of *Leptostomias* plus *Thysanactis* is derived by fission from radial III.

Other changes in pectoral girdle evolution include reduction of the primary girdle, with loss of ossification of the scapula (e.g. Characters 245, 246), coracoid (Characters 247–251), and mesocoracoid (Characters 253–256). The morphology of the coracoscapular plate in each stomiid genus is distinctive, and any adult or juvenile specimen can be identified to genus simply by examination of that plate, as may be seen by a perusal of the figures of pectoral girdles. I know of no other large teleost group with such morphological diversity in the pectoral girdle. Loss or reduction of the extrascapular (Character 229) and posttemporal (Character 231), are other minor but noteworthy events which mark large groups of stomiids.

Also of some functional interest is the complex of ligaments connecting the pectoral girdle to the head. These structures are involved in the rather

extensive movements the pectoral girdle must pass through as large prey items are swallowed, and they presumably help guide and limit the movement of the skeletal parts. An example is Ligament 3 in *Echiostoma* and *Melanostomias*, which forms a thick sheath between the supracleithrum and cleithrum. Another interesting morphology is that of *Stomias*, in which Baudelot's ligament is looped around the sheath-like Ligament 3. The functional significance of this loop, if any, is not currently ascertainable.

The pectoral girdle morphology of *Eustomias* is noteworthy in that the coracoscapular plates are fully fused medially.

PELVIC GIRDLE.—Also striking for their morphological diversity are the pelvic girdles of stomiids. While not quite as distinctive as pectoral girdle morphology, pelvic girdle morphology alone allows identification of quite a number of genera. The main trend in the evolution of these structures is elaboration of the anterior and posterior cartilaginous processes, expansion of the anterior process, and increase (and then reduction) of the cartilaginous radial elements. See Fig. 61 of *Neonesthes* for the terminology of pelvic girdle morphology and Fig. 66 of *Polymetme* for plesiomorph stomiiform girdle morphology.

In all stomiids except *Neonesthes*, the anterior cartilaginous process is enlarged (Character 285). There are lateral projections, in some cases rather elaborate, extending from this process in several lineages, including *Astronesthes*, the *Odontostomias* plus *Opostomias* sister group, and in the monophyletic group including *Tactostoma* through *Aristostomias* in the preferred cladogram (Character 284; Fig. 63 of *Bathophilus*). In this latter group, there is also, with the exception of *Idiacanthus* and *Echiostoma*, a distal expansion of the anterior process (Character 286; Figure 62 of *Melanostomias*) so that in most taxa the process anteriorly is about half the width of the posterior plate.

In stomiids, the posterior pelvic plate is enlarged relative to other stomiiforms, and the cartilaginous core of the plate extends posteriorly beyond the plate ossification (Character 290). Compare Fig. 66 of *Polymetme* with Figs. 61 of *Neonesthes* and 62 of *Melanostomias*. In many taxa, these posterior cartilaginous extensions are very elaborate, as can be seen by examination of Figs. 67–69. The anterior and posterior cartilaginous processes in stomiids seem to serve to anchor the pelvic girdle in the body; the posterior processes also serve as attachment sites for muscles that insert on the pelvic-fin rays.

Another major theme in pelvic girdle evolution in stomiids is the proliferation of pelvic-fin radials, as described under Character 293. Indeed, it is a stomiid trait to have more than three such radials, although there has been secondary reduction in some lineages and similar proliferation in some other stomiiform subgroups. The original source for the increased number of radials in stomiids seems to be fission of the anterior two radials (note the bilobed shape of these elements in *Neonesthes,* Fig. 61). Subsequent subdivisions result in every fin ray having its own radial in most stomiids; this is a morphology unreported in other teleosts. As far as I am aware, the

primitive ossification centers of these radials are also absent in most stomiids.

A feature of pelvic radial evolution that is of interest is the fate of the posterior, or third, radial in primitive stomiiforms. As Fink and Weitzman (1982) noted, the homology of this element with the other radials is in doubt. In any case, its evolution in stomiids differs from that of the other radials. Primitively, radial 3 lies medial or posteromedial to radial 2, is a convex cartilage anteriorly, and posteriorly terminates in a bony "hook" (see Figure 66 of *Polymetme*). Within the Stomiidae, radial 3 becomes more elongate and loses its posterior ossification. In the members of Clade J, the radial has no ossification, and in the members of Clade R (but lacking in *Eustomias*), this radial is anteriorly elongate, extending forward to the articulation of the second fin ray, and even further in some members of this group (Characters 300, 301; Figures 62 of *Melanostomias,* and 63 of *Grammatostomias*, in which the third radial is the only radial element present). In addition, the third radial is sometimes present as two cartilage bodies, presumably derived by fission from a single element (see Character 297, Fig. 62 of *Melanostomias).*

The overall picture of pelvic girdle evolution within stomiids includes complexity of the anterior and posterior cartilaginous processes, increase in relative size of the posterior plate, increase in size of the medial radial, and increase in number of distal radials such that each fin ray has its own radial. There is also increased complexity of pelvic-fin musculature in concert with the elaboration of distal radials. The functional result of this increased complexity is not certain, but, it would appear that the pelvic fins are capable of motions that those of more primitive stomiiforms (and other primitive teleosts) are unable to perform.

Before leaving the pelvic girdle, I would like to point to such specializations as the widely spaced pelvic girdles and elongate fin rays lacking interradial membranes of *Bathophilus*, and the elongate, partially fused pelvic-fin rays of *Photostomias.*

LIGHT ORGANS.—These structures are among the most distinctive features of the bodies of these teleosts. The presumably luminous chin barbel is diagnostic of the family, and many of the characters used in stomiid systematics, especially at the species level, are associated with it. But stomiids have other luminous organs, including large photophores on the head, photophore rows along the ventrolateral body (whose spacing and configurations are used in Characters 312 and 314), and bands or other masses of luminous tissues on the head (*Trigonolampa,* Character 314), dorsum, or sides of the body.

One outcome of this analysis is that the nomenclature of some light organs of the head must be modified to reflect homologies in other stomiids (see Fig. 70). Specifically, I have coined new names for some of the photophores in the genera *Aristostomias*, *Malacosteus, Pachystomias,* and *Photostomias.* The "döppelorgan" of other authors is considered the suborbital photophore (SO), due to its association with the first infraorbital in all

stomiids, including these taxa (its posterior location is considered an apomorphy of the members of Clade W, Character 310). The structure in *Aristostomias*, *Malacosteus,* and *Pachystomias* which was previously called the suborbital photophore is termed accessory orbital photophore I (AOPI). The small photophore ventral and adjacent to AOPI in *Pachystomias* is termed accessory orbital photophore II (AOPII; equivalent to the "infrasuborbital organ" of Goodyear, 1980, a name considered inappropriate since the organ adjacent to it is not the suborbital organ), and the photophore anterior to AOPI in that genus is termed accessory orbital photophore III (AOPIII). A small, organized, luminous mass anterior to the eye in subadult and adult males of *Photostomias* is called accessory orbital photophore IV. AOPIII and AOPIV were considered the "preorbital organ" by Goodyear (1980); I reject this name because it implies the homology of these organs with each other (which is possible) and with the preorbital organ of sternoptychids (which is unlikely).

The full significance of luminous tissues in the lives of these fishes, as lures, devices for intraspecific communication, or as camouflage may never be known. Most accounts of variation in luminous structures concern meristic differences in serial photophores and details of barbel structures, but little is recorded about variation in the various luminous patches, loops, and other structures on the body in some species. For a discussion of luminous structures associated with the pectoral fin, see the discussion above.

MISCELLANEOUS STOMIID FEATURES.—The following features are not clearly associated with any particular region of the body discussed above.

Stomiids, with the apparent exception of *Chauliodus* and Stomias, as mentioned below, are scaleless (Character 317). Those two genera are reported to have non-overlapping scales (not "typical" teleost scales), which are embedded in the gelatinous coverings these fishes have in life (Character 318; see Morrow, 1964b,c).

One of the most striking specializations present in stomiids is the lack of skin between the mandibular rami in *Aristostomias*, *Malacosteus,* and *Photostomias* (Character 321). The methods by which these creatures manage to get prey items into the gullet have been the source of much "functional morphological" speculation (see, e.g., Gunther and Deckert, 1959).

And, finally, *Idiacanthus* has two distinctive and interesting specializations which have also been the subject of some speculation: the paedomorphic males resemble larvae and do not feed after transformation (Character 323, Beebe, 1934), and the larvae have stalked eyes (Character 322, see Beebe's 1934 figure).

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APPENDIX 1

Data Matrix

Primitive states are coded as 0, derived states as 1. Characters coded as missing are noted by question marks. See Methods section for discussion.

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APPENDIX II

Fossil Teleosts Previously Referred to the Stomiidae

Most of the fossil teleosts which have been referred to the Stomiiformes were discussed by Weitzman (1967a); none of those are pertinent to the current work. There are five fossil taxa which have been referred to the Stomiidae as recognized herein which were not mentioned by Weitzman, since he was not concerned with stomiids. These are *Astronesthes praevius* Danil'chenko (1962), *Astronesthes simus* Arambourg (1967), *Protostomias maroccanus* Arambourg (1943), and *Pronotacanthus sahel-almae* (Davis, 1887), and *Chauliodus eximius* (Jordan and Gilbert, in Jordan, 1925).

The description of *Astronesthes praevius* includes mention of photophores, small conical teeth on the rear of the maxilla, and fairly large pelvic fins, all present in *Astronesthes*. The figure, though poor, generally resembles an *Astronesthes*. Although none of the features found herein to be diagnostic of the genus are mentioned, it is probable that this fossil represents a member of the genus. *Astronesthes simus* does not appear, however, to be an *Astronesthes*. Judging from the figures and the description, gill rakers are present, there are some large teeth on the maxilla in addition to small teeth and the prezygapophyses of the anterior neural arches are not enlarged. The latter two characters indicate the fossil is not an *Astronesthes*, and the first indicates that it is not a stomiid.

Protostomias was originally described in the Stomiatidae and then was placed in the new family Protostomiatidae by Arambourg (1954); however, the figures in both the 1943 and 1954 papers show a fish which is clearly different from any known stomiiform. Such characters as the large infraorbital bones, very slender, elongate premaxilla and maxilla, lack of a su-

pramaxilla, and greatly enlarged coronoid process of the mandible clearly indicate that *Protostomias* is not a member of the Stomiidae, and that it is probably not a stomiiform at all. The condition of the specimen and the poor quality of the photographs makes any confident assessment of the reconstructions difficult. Although Arambourg makes reference (1954:95) to the teeth (found only on the dentary) and states that they have a large "cavite pulpaire comme celles des Stomiatidae actuels," it is not possible to determine whether there are Type 3 teeth as would be expected in a stomiid. Examination of the specimen will be necessary to determine its placement.

Arambourg (1943) mentioned in passing that *Pronotacanthus* Woodward is also probably a stomiid, a suggestion that was formalized by Bertin and Arambourg (1958), without comment. *Pronotacanthus* was erected by Woodward (1901) for *Anguilla sahel-almae* Davis, which Woodward considered a notacanthid. There is a clear phenetic similarity between *Protostomias* and *Pronotacanthus* and they may be related (or the same); however, as far as can be determined from Woodward's description (pp. 169–171) and figure (Plate XV), *Pronotacanthus* also lacks any features which would place it in the Stomiidae (or Stomiiformes).

Chauliodus eximius has been discussed by Crane (1966), who reviewed its taxonomic history and provided photographs to confirm that the specimens are indeed *Chauliodus*. I have examined some fragmentary material at the MCZ.

APPENDIX III

Material Examined

The following list includes specimens which are not already listed in papers by Fink (1981), Fink and Weitzman (1982), or Weitzman (1967b, 1974). The genera and species are listed alphabetically, followed by museum number, number of specimens in parentheses, size in standard length, and whether one or more of the specimens was dissected (d), or cleared and stained (c). If more than one specimen was cleared, the number is given.

Aristostomias lunifer, MCZ 53267 (1), 40 mm.
Aristostomias tittmanni, MCZ 58811 (1), 180 mm.
Aristostomias xenostoma, USNM 272943 (1), c.
Aristostomias sp., MCZ 58795 (1), 135 mm.
Aristostomias sp., MCZ 58791 (3), 39–66 mm.
Aristostomias sp,. MCZ 58789 (2), 41–100 mm.
Astronesthes caulophorus, MCZ 58806 (1), 95 mm, d.
Astronesthes similis, MCZ 35590 (1), 105 mm.
Astronesthes sp., MCZ 58817 (1), 163 mm, d.
Bathophilus ater, MCZ 52027 (1), 150 mm.
Bathophilus brevis, USNM 206701 (1), c.
Bathophilus kingi, MCZ 49146 (1), 98 mm.
Bathophilus metallicus, MCZ 42285 (3), 53–57 mm, c.
Bathophilus pawneei, MCZ 42279 (1), 77 mm.

Bathophilus sp., MCZ 58797 (1), 94 mm.
Bonapartia pedaliota, MCZ 58794 (7), 43–61 mm, d.
Bonapartia pedaliota, MCZ 58798 (1), 74 mm.
Bonapartia pedaliota, MCZ 58818 (4), 42–65 mm, d.
Bonapartia pedaliota, MCZ 58851 (1), 64 mm, c.
Borostomias antarcticus, MCZ 42877 (1), 220 mm, d.
Borostomias elucens, MCZ 58786 (2), 74–201 mm, d.
Borostomias elucens, USNM uncat. WH. STA. 486/71 (1), c.
Borostomias sp., MCZ 58814 (2), 107–233 mm, d.
Chauliodus danae, MCZ 58784 (3), 86–128 mm.
Chauliodus macouni, LACM 37121-1 (2), 53–118 mm, c.
Chauliodus sloani, MCZ 58788 (9), 152–200 mm, d.
Chirostomias pliopterus, MCZ 42274 (1), 113 mm, d.
Chirostomias pliopterus, USNM 272907 (1), c.
Chirostomias pliopterus, USNM 272905 (1), c.
Cyclothone sp., MCZ 58808 (approx. 150), c 20-c 60 mm, d.
Diplophos maderensis, MCZ 61476 (1), 96 mm.
Echiostoma barbatum, MCZ 42203 (1), 290 mm.
Echiostoma barbatum, MCZ 58819 (3), 161–236 mm, d, 1 c.
Echiostoma barbatum, MCZ 58852 (1), 166 mm, c.
Eustomias bifilis, USNM uncat. 71-3-2 (1), c.
Eustomias binghami, USNM uncat. HMS 47, STA 66 (1), c.
Eustomias cf. *brevibarbatus*, MCZ 47789 (1), 116 mm.
Eustomias macrurus, USNM 272913 (1), c.
Eustomias obscura, MCZ 58790 (1), 158 mm, d.
Flagellostomias boureei, MCZ 58802 (1), 298 mm, d.
Flagellostomias boureei, MCZ 58813 (1), 120 mm.
Flagellostomias boureei, USNM 206681 (1), c.
Grammatostomias dentatus, USNM 272909 (1), 156 mm, d.
Grammatostomias dentatus, USNM 272903 (1), c.
Grammatostomias flagellibarba, USNM 273256 (1), 190 mm.
Heterophotus ophistoma, MCZ 42116 (1), 203 mm, d.
Idiacanthus fasciola, MCZ 42390 (3), 167–260 mm.
Idiacanthus fasciola, MCZ 58796 (1), 273 mm.
Idiacanthus fasciola, MCZ 58815 (1), 295 mm.
Leptostomias gladiator, MCZ 58793 (1), 162 mm, d.
Malacosteus niger, MCZ 53272 (1), 150 mm, d.
Malacosteus niger, MCZ 58804 (3), 105–183 mm, d.
Malacosteus niger, MCZ 58824 (1), 69 mm.
Malacosteus niger, MCZ 58825 (1), 42 mm.
Malacosteus niger, MCZ 58826 (3), c 40-c 57 mm.
Maurolicus muelleri, MCZ 58809 (29), 46–61 mm, d.
Melanostomias biseriatus, MCZ 42013 (1), 175 mm, c.
Melanostomias cf. *biseriatus*, USNM 272911, c.
Melanostomias sp., MCZ 56955 (1), 257 mm, d.
Neonesthes capensis, MCZ 58800 (1), 116 mm, d.
Neonesthes capensis, MCZ 58803 (2), 127–133 mm, d.
Neonesthes capensis, MCZ 58849 (1), 45 mm, c.
Neonesthes capensis, USNM 272906 (1), c.
Odontostomias micropogon, MCZ 58810 (1), 204 mm, d, partial c.
Opostomias micripnus, MCZ 58845 (1), 66 mm.
Opostomias micripnus, MCZ 58846 (1), 66 mm.
Opostomias micripnus, MCZ 58847 (1), 61 mm, d.
Opostomias micripnus, MCZ 58848 (2), 63–68 mm.
Pachystomias microdon, MCZ 58801 (1), 78 mm.

Pachystomias microdon, MCZ 53256 (1), 188 mm.
Pachystomias microdon, USNM uncat. Sta. 4591 (1), c.
Photonectes braueri, MCZ 54284 (4), 120–143 mm, d.
Photonectes fimbria, MCZ 55080 (1), 132 mm, d.
Photonectes gracilis, MCZ 58805 (1), 148 mm, d.
Photonectes leucospilus, USNM 272911 (1), c.
Photonectes margarita, MCZ 61477 (1), 64 mm, c.
Photonectes margarita, MCZ 53260 (1), 300mm, c.
Photonectes margarita, MCZ 53258 (1), 26 mm, c.
Photonectes margarita, USNM 272908 (1), c.
Photonectes mirabilis?, MCZ 55079 (1), 133 mm, d.
Photonectes sp., MCZ 58792 (1), 205 mm.
Photonectes sp., MCZ 58807 (1), 230 mm, d.
Photostomias guernei, MCZ 42394 (17), 79–103 mm.
Photostomias guernei, MCZ 58816 (4), 61–165 mm, d.
Photostomias guernei, USNM 272952 (1), c.
Photostomias guernei, USNM 272904 (1), c.
Polymetme corythaeola, USNM 188236 (1), c.
Polymetme corythaeola, USNM uncat. #3598 (1), c.
Rhadinesthes decimus, USNM 272910 (1), 335 mm, d.
Stomias affinis, MCZ 57655 (1), 108 mm, c.
Stomias affinis, USNM uncat. Oregon II 11215 (2), 103–181 mm, d.
Stomias affinis, USNM uncat. Oregon 4441 (1), 161 mm.
Stomias affinis, USNM uncat. Oregon 10832 (1), 106 mm.
Stomias affinis, USNM uncat. Oregon 10794 (1), 130 mm.
Stomias affinis, USNM uncat. Oregon 10834 (3), 107–146 mm.
Stomias atriventer, SIO 63–441 (8), ?133–209 mm, d, c.
Stomias atriventer, MCZ 58844 (1), 190 mm, c.
Stomias boa boa, MCZ 58820 (16), 31–154 mm, d, 4 c.
Stomias boa boa, MCZ 58821 (3), 88–110 mm, d, c.
Stomias boa ferox, MCZ 58822 (10), 90–175 mm, d.
Stomias boa ferox, MCZ 58823 (17), 86–230 mm, d, 3 c.
Stomias brevibarbatus, MCZ 58828 (1), 86 mm.
Stomias brevibarbatus, MCZ 58829 (2), 61–61 mm.
Stomias brevibarbatus, MCZ 58827 (1), 75.1 mm.
Stomias brevibarbatus, MCZ 58850 (1), 144 mm, c.
Stomias colubrinus, MCZ 58834 (21), 57–242 mm, d, c.
Stomias danae, MCZ 58785 (1), 39 mm.
Stomias danae, USNM 201830 (1), 158 mm, d.
Stomias danae, USNM uncat. "Teritu" 71-6-16 (1), mm, c. ???
Stomias gracilis, USNM 221032 (2), 223- mm, d, c. ????
Stomias lampropeltis, USNM 207500 (2), 178–220 mm.
Stomias lampropeltis, USNM 207524 (4), 94–105 mm.
Stomias longibarbatus, MCZ 58787 (2), 252–290 mm, d.
Stomias longibarbatus, MCZ 58812 (1), 279 mm.
Stomias nebulosus, MCZ 58832 (1), 156 mm, d.
Stomias nebulosus, MCZ 58835 (8), 90–136 mm, c.
Stomias pacificus, UMMZ 213426 (1), 340 mm. c.
Tactostoma macropus, LACM 33732-11 (3), 140–155 mm, d.
Thysanactis dentex, USNM 206704 (1), c.
Trigonolampa miriceps, MCZ 45959 (1), 62 mm, d.
Triplophos hemingi, USNM 20384? (2), 146–162 mm, d.
Vincigueria lucetia, USNM uncat. B6212 (9), c.
Woodsia nonsuchae, USNM uncat "from LaJolla" (1 neurocranium, branchial basket), c.
Woodsia nonsuchae, USNM 208539 (1), 50 mm, c.