OSTEOLOGY AND EVOLUTIONARY RELATIONSHIPS OF THE STERNOPTYCHIDAE, WITH A NEW CLASSIFICATION OF STOMIATOID FAMILIES

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ABSTRACT

NEW PRIMARILY OSTEOLOGICAL EVIDENCE was collected for a reinterpretation of the phylogenetic interrelationships of the teleost fish suborder Stomiatoidei, especially the nominal families Sternoptychidae and Gonostomatidae. Basic differences were found dividing the suborder into two sister groups (proposed as new infraorders), the Gonostomata and the Photichthya. Evidence indicates that the Gonostomata consists of two sister-group families, the Gonostomatidae with six of the 20 genera formerly assigned to this family and the Sternoptychidae including seven genera formerly considered as maurolicin gonostomatids and the three hatchetfish genera, which previously constituted the Sternoptychidae. A hypothesis concerning the phylogenetic interrelationships of the 10 sternoptychid genera is proposed. The genera *Thorophos* and *Araiophos* are closely related and proposed as a sister group of the remaining eight genera. The relationships of *Maurolicus* are unclear,

but apparently it forms a sister group of the remaining seven genera. *Danaphos* and *Valenciennellus* are closely related and form a sister group of the remaining five genera. *Argyripnus* and *Sonoda* form a sister group of the three hatchetfish genera, *Polyipnus*, *Argyropelecus*, and *Sternoptyx*. *Argyropelecus* and *Sternoptyx* form a sister group of *Polyipnus*. Of all the genera, *Thorophos* is the most primitive, *Sternoptyx* the most advanced. Evidence was also found demonstrating that the Photichthya consists of two sister groups (proposed as new superfamilies), the Photichthyoidea and the Stomiatoidea. The Photichthyoidea contains one family, the Photichthyidae, including seven of the genera formerly ascribed to the Gonostomatidae. The Stomiatoidea were not investigated in detail at the family or generic level, but it was found that the interrelationships, validity, and contents of the currently accepted families are questionable.

INTRODUCTION

HISTORICAL REVIEW

THE INTERRELATIONSHIPS of the nominal stomiatoid fish families Gonostomatidae, Maurolicidae, and Sternoptychidae have been subject to considerable differences of opinion and no stomiatoid family group had been reasonably defined until Baird (1971) proposed a definition for the Sternoptychidae (in the restricted sense, including only *Sternoptyx* Hermann, *Argyropelecus* Cocco, and *Polyipnus* Günther). Günther (1864) recognized two families of stomiatoids, the Sternoptychidae and Stomiatidae. In the Sternoptychidae he established three subgroups (1) the Sternoptychina (including *Sternoptyx* and *Argyropelecus*), (2) the Cocciina (including *Ichthyococcus* Bonaparte and *Maurolicus* Cocco [the latter containing *Maurolicus* as currently understood as well as species which today are placed in *Vinciguerria* Jordan and Evermann]), and (3) the Chauliodontina (including *Chauliodus* Bloch and Schneider and *Gonostoma* Rafinesque). Gill (1893) established the name Maurolicidae (misspelled Maurolocidae) and ascribed its authorship to Gill (1884). But Gill (1884) did not refer to the Maurolicidae and only remarked that the

Cocciina of Günther were distantly related to the Sternoptychidae when the latter name is restricted to *Sternoptyx* and *Argyropelecus*. Goode and Bean (1896) were the first to define the Maurolicidae in print but ascribed the name and the definition to a manuscript of Gill's. At this time Goode and Bean considered the Maurolicidae equivalent to Günther's Cocciina. Slightly later Jordan and Evermann (1896) described *Valenciennellus* and included it in the Maurolicidae. Gilbert and Cramer (1897) described *Argyripnus* and placed it in the Maurolicidae without comment. Brauer (1906) was the first clearly to consider the maurolicids as distinct from the gonostomatids and to exclude the nonmaurolicid genus *Vinciguerria*. Brauer did not place the maurolicids at the family level but grouped them in his key with *Argyropelecus*, *Polyipnus*, and *Sternoptyx* on the basis of light organ arrangement partially elucidated in his anatomical work of 1908. He further separated the maurolicids from the three sternoptychid genera on the basis of body form. Brauer was the first clearly to exclude *Ichthyococcus* from the the sternoptychid-maurolicid line. Regan (1923)

published a synopsis and key to the families of stomiatoids and recognized the gonostomatids and sternoptychids as families. He did not mention the maurolicids as a group and included maurolicid genera in the Gonostomatidae. Norman (1930) monographed the family Gonostomatidae, briefly defined the family, and separated the Gonostomatinae and Maurolicinae on the basis of photophore arrangement, following Brauer (1906). Subsequently a few new maurolicid genera were described, *Thorophos* Bruun (1931), *Neophos* Myers (1932), *Araiophos* Grey (1959), and *Sonoda* Grey (1961). These three authors recognized the maurolicids as a subfamily, Maurolicinae, of the Gonostomatidae and allied the new genera with the known maurolicid genera on the basis of Brauer's and Norman's work. Grey (1960a, 1964) discussed the difficulties in separating the Gonostomatidae and Maurolicidae as families and remarked that the only valid character separating maurolicid fishes from the gonostomatids was that "at least some and usually most" of the photophores are separated into groups.

Hubbs (1953) suggested that the Sternoptychidae (in the restricted sense) and Gonostomatidae (including the Maurolicidae) be reunited under the earliest available family name, the Sternoptychidae. This opinion was followed by Rechnitzer and Böhlke (1958) but other subsequent authors, for example Schultz (1964), Grey (1964), Berry and Perkins (1966), and Baird (1971) have preferred to recognize two distinct families. An attempt to distinguish the Sternoptychidae from the Gonostomatidae (including Maurolicidae) by Regan (1923) failed because he examined only the skeleton of *Argyropelecus*, and the single character of several used by Regan that applies to all three sternoptychid genera is "body deep, strongly compressed." Schultz (1964) and Morrow (1964a) defined the family Sternoptychidae in an abbreviated manner based on Regan's findings. Baird (1971) reviewed part of the above history with specific reference to the Sternoptychidae. Baird concluded that "there has been a failure to achieve a stable classification of the Sternoptychidae [in the restricted sense]," citing the "lack of detailed morphological studies using osteological or other acceptable criteria, and subjective conceptual differences concerning family rank." Baird (1971) then investigated the osteology of *Sternoptyx*, *Argyropelecus*, and

Polyipnus and compared his findings with the osteology of two maurolicid genera, *Valenciennellus* and *Maurolicus*, and the gonostomatid *Vinciguerria*. Baird (1971) then redefined the Sternoptychidae in some detail. His is by far the best definition we have to date.

Baird (1971, p. 21) concluded from his studies that the "family [Sternoptychidae in the restricted sense] appears primitive and probably originated from a premaurolicid ancestor, possibly something between the very early *Vinciguerria* [a photichthyid genus according to the classification proposed here] and *Maurolicus*." Baird (1971, p. 15) also recognized the close relationship of the sternoptychid genera and the maurolicid genera for he stated that "The Sternoptychidae appear to be derived from some antecedent of the primitive genus *Maurolicus*," and ". . . there is little doubt that the two maurolicid genera [he only examined *Maurolicus* and *Valenciennellus*] and the Sternoptychidae are closely related." I think the evidence presented here indicates that the three sternoptychid genera (herein sometimes referred to as hatchetfishes) in the restricted sense (1) are some of the most specialized of the stomiatoids, not primitive relative to any "maurolicid" or gonostomatid; (2) are most closely related to a group of "maurolicid" genera that include *Sonoda*, *Argyripnus*, *Danaphos*, and *Valenciennellus*; (3) *Maurolicus* is not an especially primitive genus in the "maurolicid-sternoptychid" group as defined here; (4) *Vinciguerria* belongs to another evolutionary line of stomiatoids and is not closely related to the "sternoptychids" or the "maurolicids" as understood by Baird (1971).

The morphology of members of the nominal families Gonostomatidae, Maurolicidae, and Sternoptychidae has been the subject of several important investigations. Supino (1901) described parts of the cranium of *Argyropelecus hemigymnus*, and Handrick (1901) studied the distribution of the peripheral nerves and light organs of the same species. Bierbaum (1914) has investigated the stato-acoustic organ in *Gonostoma*, *Cyclothone*, *Vinciguerria*, *Argyropelecus*, and *Sternoptyx*. Günther and Deckert (1953, 1955) have described and discussed the feeding and respiratory mechanism of *Cyclothone* and *Gonostoma*. Not one of the above authors has attempted to compare the anatomy of all known living genera of stomiatoids and assemble the probable phylogenetic implications
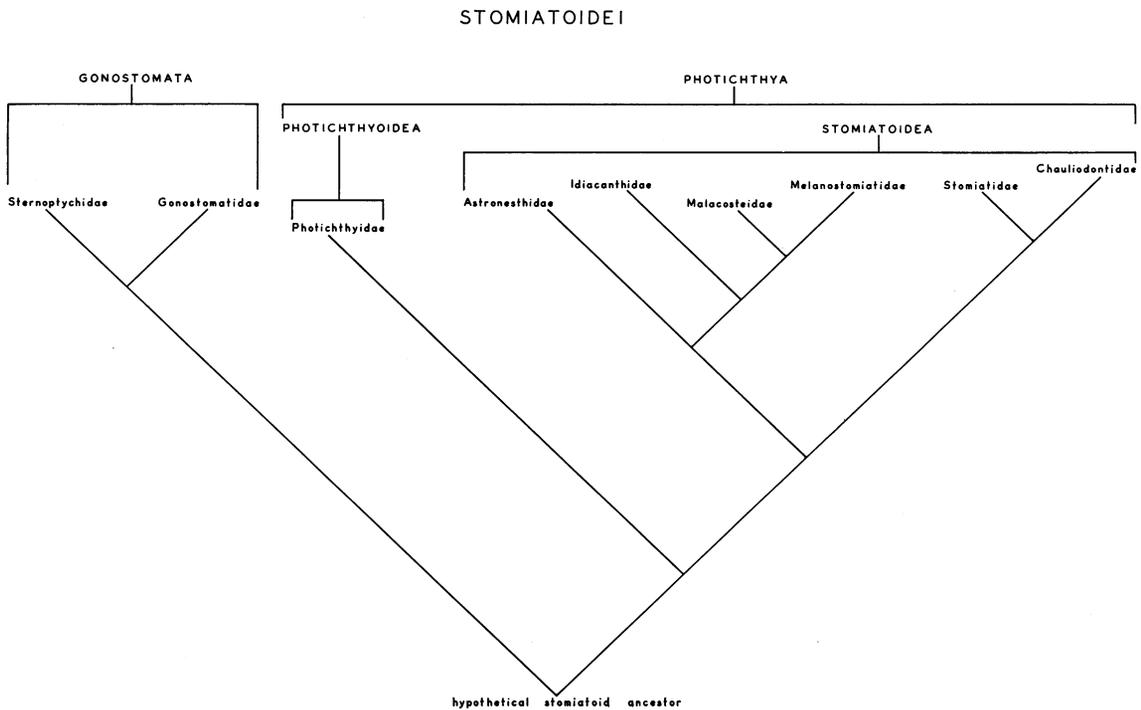
STOMIATOIDEI

FIG. 1. A phylogeny of the Stomiatoidei. Note that the sister groups suggested within the Stomiatoidea are not supported by sufficient data.

of the morphological differences and similarities.

A NEW ARRANGEMENT OF STOMIATOID FISHES

The present study attempts to outline, primarily by osteological characteristics, the phylogenetic relationships of what have been called maurolicid and sternoptychid fishes. These are *Thorophos* Bruun (two species, including *Neophos* Myers), *Araiophos* Grey (two species), *Maurolicus* Cocco (one, possibly two species), *Danaphos* Bruun (one, possibly two species), *Valenciennellus* Jordan and Evermann (one, possibly two species), *Argyripnus* Gilbert and Cramer (four or perhaps a few more species), *Sonoda* Grey (two species), *Polyipnus* Günther (about 16 species in three species groups), *Argyropelecus* Cocco (about seven species), and *Sternoptyx* Hermann (two or perhaps three species) (see figs. 2–13). Nearly all known Recent stomiatoid genera have been examined and all known Recent "gonostomatid," "maurolicid," and "sternoptychid" genera have been investigated in detail, but only those

results dealing with the "sternoptychid-maurolicid line" and certain aspects of the so-called Gonostomatidae are published here. I believe the evidence indicates that the "maurolicid" and "sternoptychid" fishes should be united into the single family Sternoptychidae, and that sternoptychids constitute one of the main lines of stomiatoid fish evolution (see fig. 1).

To treat effectively the evolutionary affinities of the genera within the Sternoptychidae it was necessary to investigate the broad general relationships of all stomiatoid genera and families, especially those genera formerly considered as constituting the Gonostomatidae. The solution of the problem of the relationships of the sternoptychids (in the expanded sense) to other stomiatoid groups required a reorganization of basic stomiatoid classification and a division of the Gonostomatidae into two families, the Gonostomatidae and a new family, the Photichthyidae.

Weitzman (1967a, 1967b) proposed a possible origin of stomiatoid fishes and briefly discussed a basic division of the suborder into two groups,
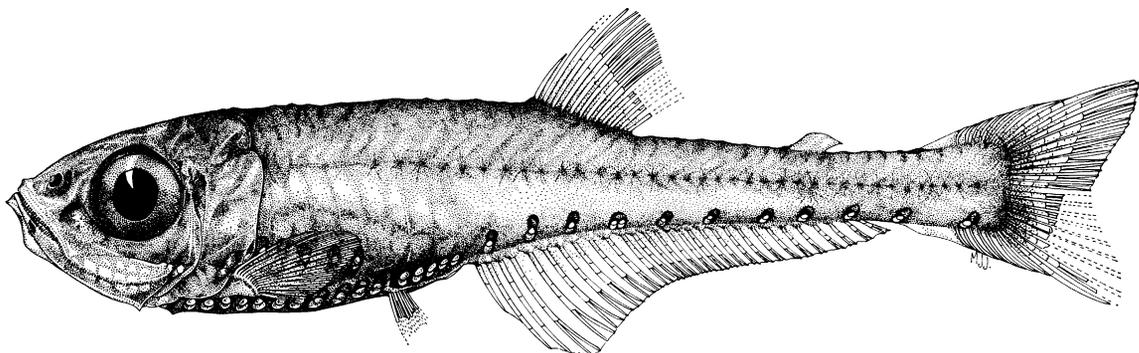
FIG. 2. *Thorophos euryops* Bruun, SL 44.7 mm., DANA 3736-VI.
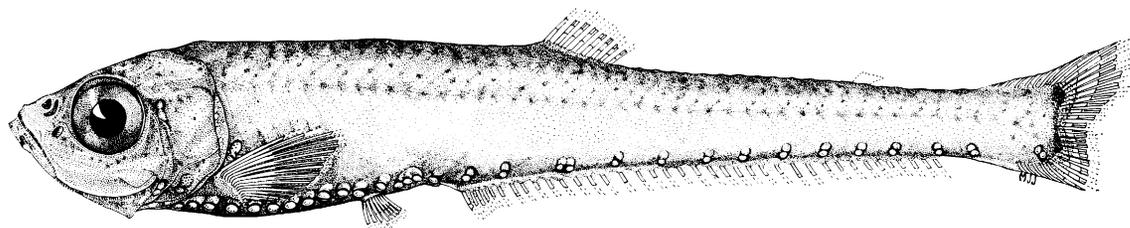
FIG. 3. *Thorophos nexilis* (Myers), SL 57.0 mm., USNM 151400.
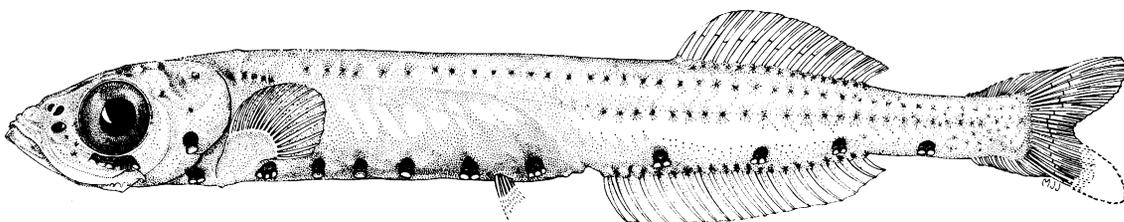
FIG. 4. *Araiophos eastropas* Ahlstrom and Moser, SL 31.5 mm., USNM 203239.
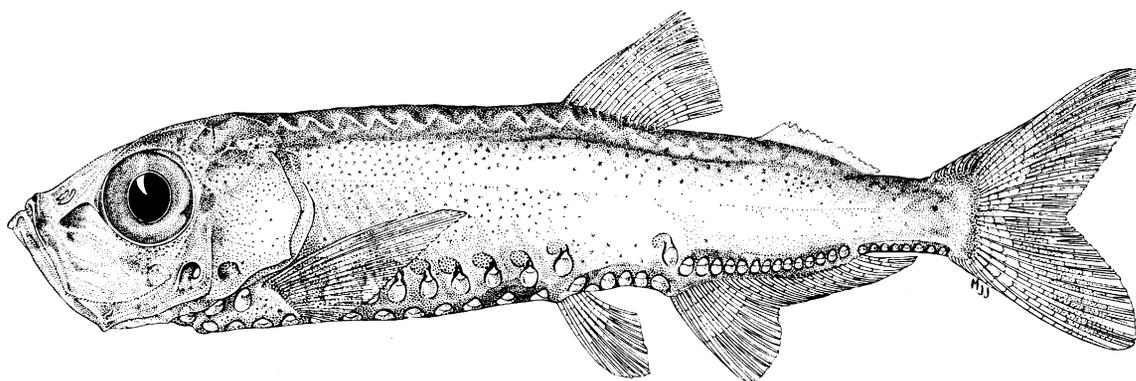
FIG. 5. *Maurolicus muelleri* (Gmelin), SL 45.5 mm., USNM 201138.
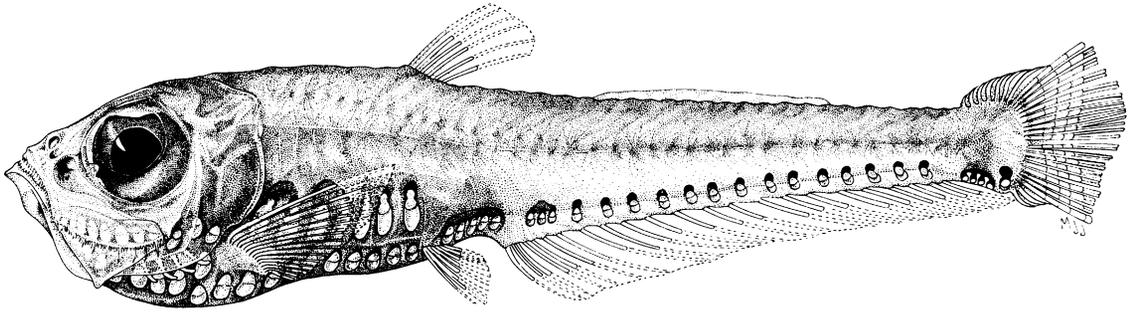
FIG. 6. *Danaphos oculatus* (Garman), SL 36.9 mm., USNM 203264.
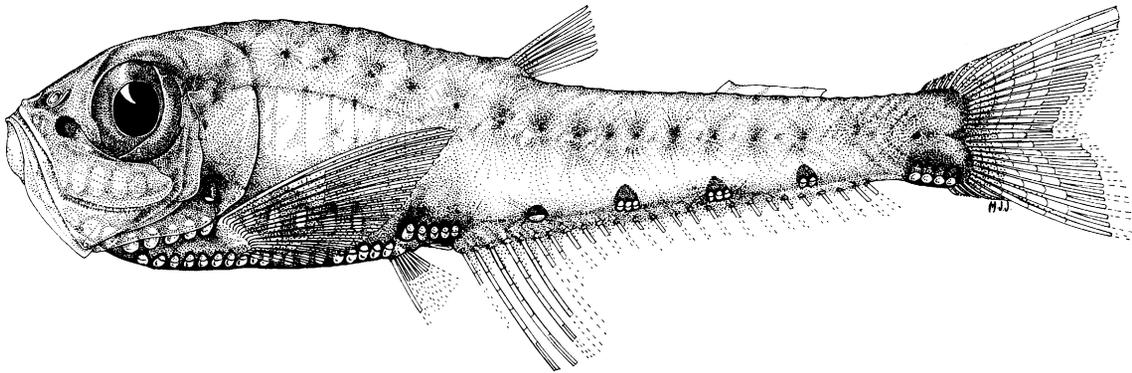
FIG. 7. *Valenciennellus tripunctulatus* (Esmark), SL 25.0 mm., USNM 201141.
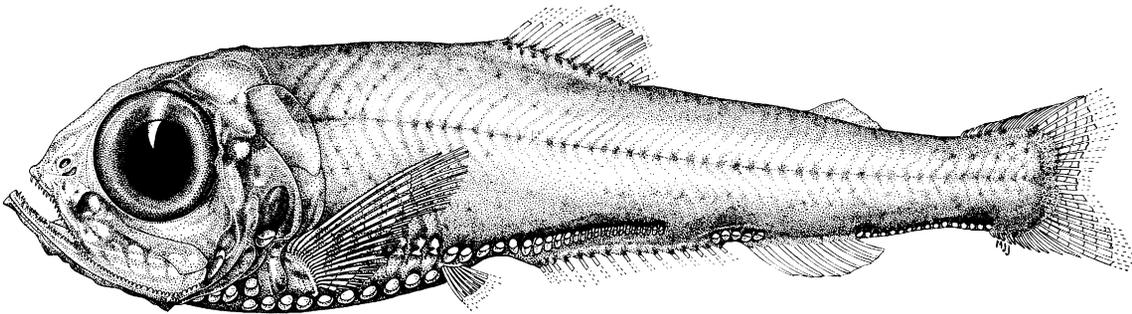
FIG. 8. *Argyripnus atlanticus* Maul, SL 67.0 mm., FMNH 65693.
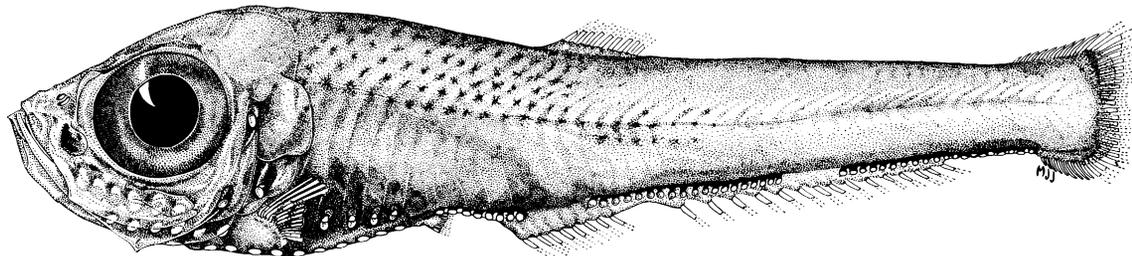
FIG. 9. *Sonoda megalophthalma* Grey, paratype, SL 53.5 mm., FMNH 65982. (Nostril reconstructed.)
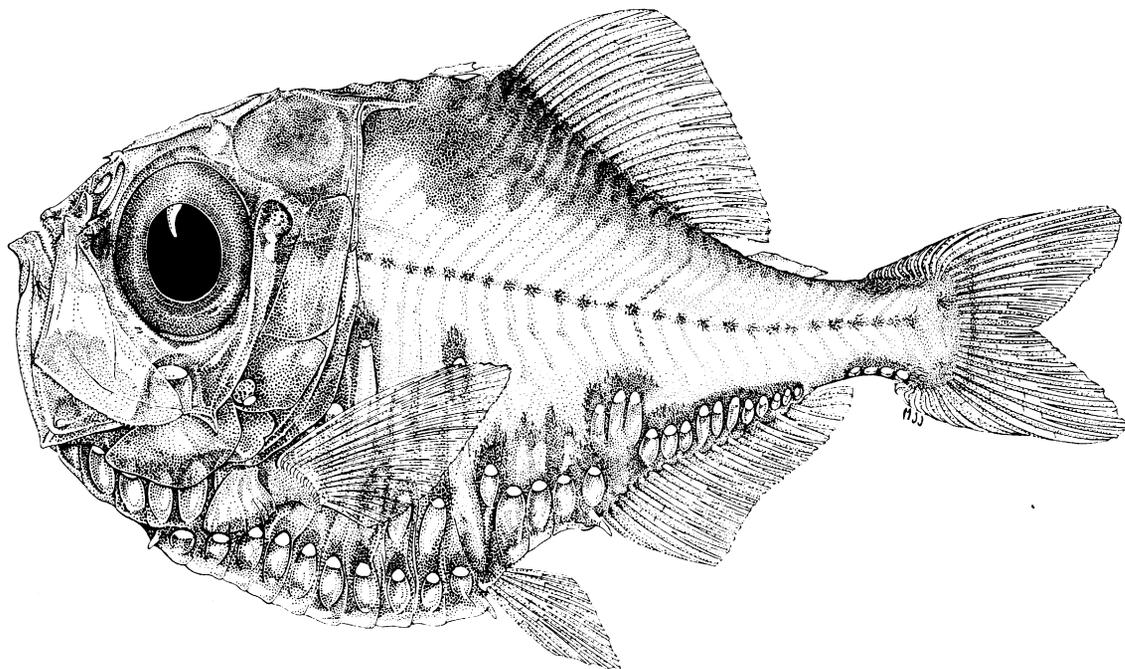
FIG. 10. *Polyipnus laternatus* Garman, SL 36.0 mm., USNM 179050.
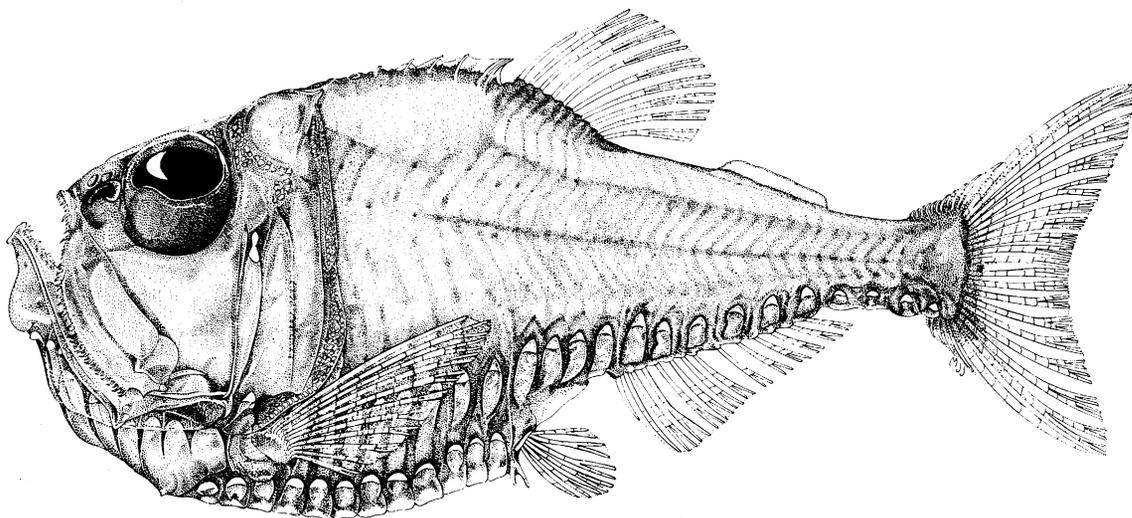
FIG. 11. *Argyropelecus affinis* Garman, SL 56.5 mm., USNM 203258.
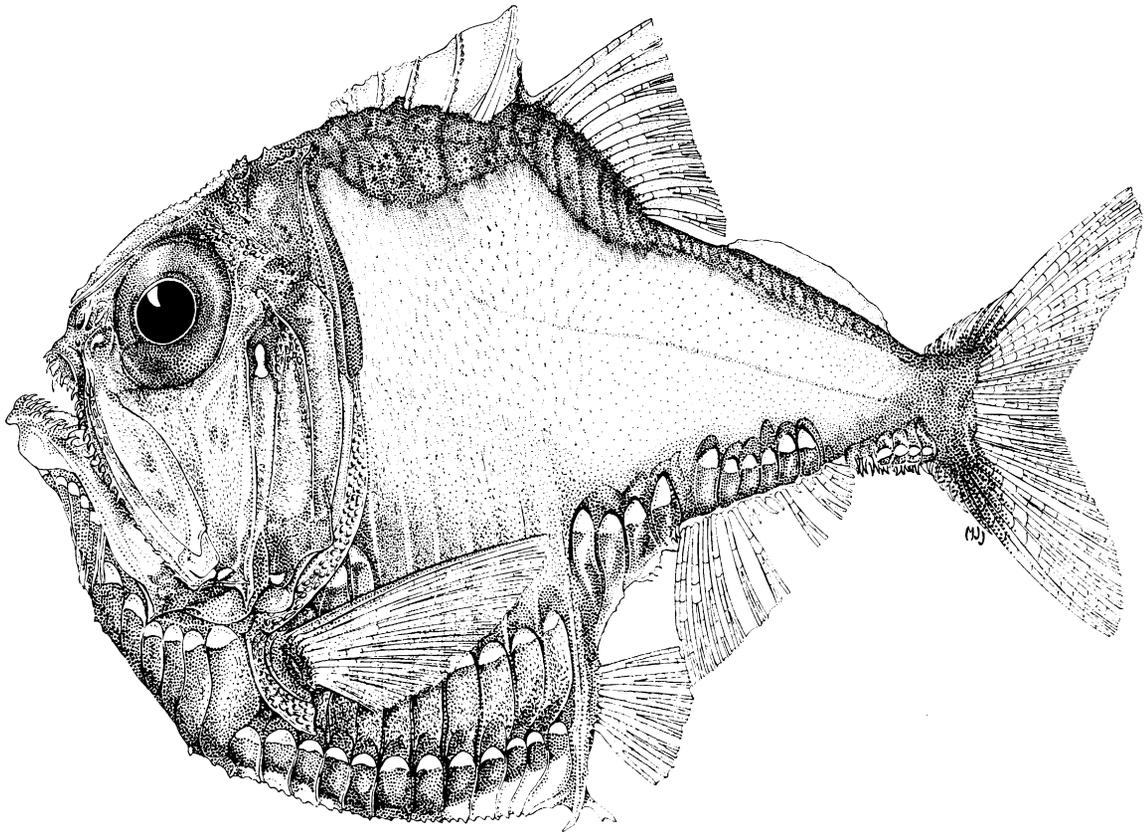
FIG. 12. *Argyropelecus aculeatus* Cuvier and Valenciennes, SL 62.0 mm., USNM 196700.
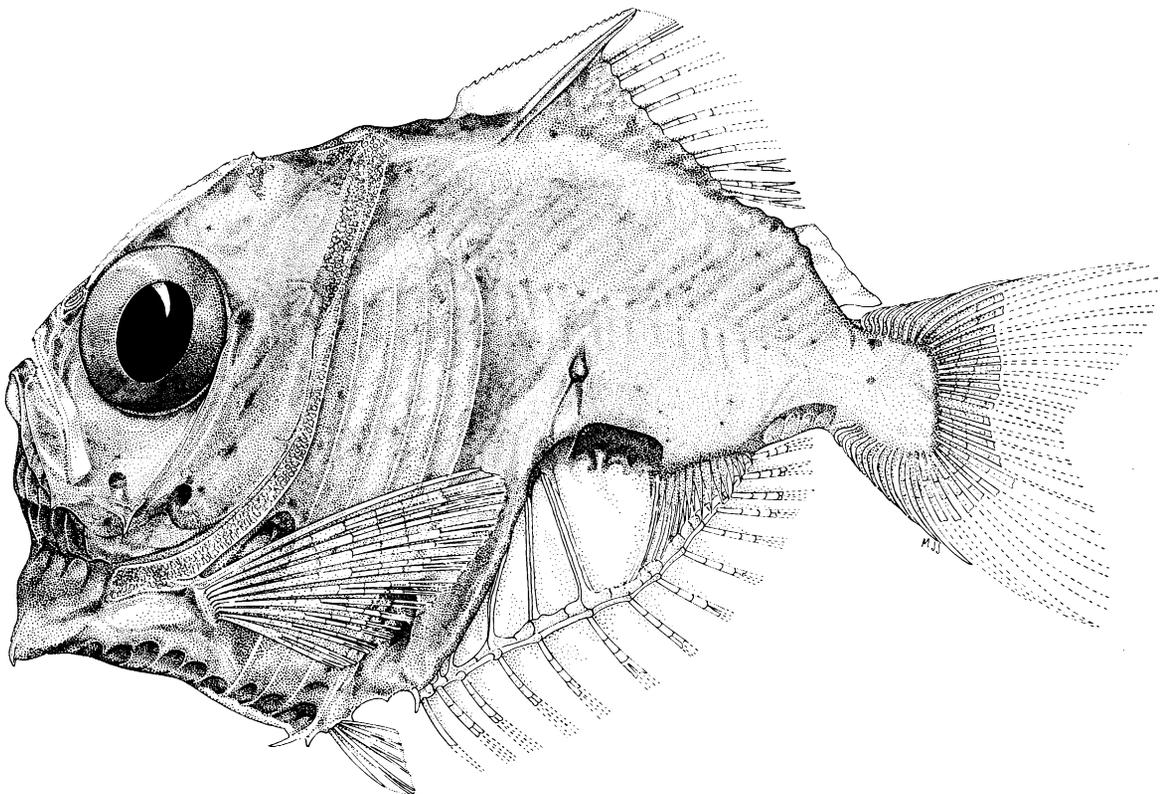
FIG. 13. *Sternoptyx diaphna* Hermann, SL 37.5 mm., USNM 203390.

one including the Sternoptychidae and the Gonostomatidae, as constituted before the present paper, the other including all the remaining families. The classification presented by Weitzman (1967b, p. 3) was conservative, and a classification more in keeping with recently acquired facts is proposed as follows:

Suborder Stomiatoidei
    Infraorder Gonostomata, new
        Family Gonostomatidae
        Family Sternoptychidae
    Infraorder Photichthya, new
      Superfamily Photichthyoidea, new
        Family Photichthyidae, new
      Superfamily Stomiatoidea
        Family Stomiatidae
        Family Chauliodontidae
        Family Astronesthidae
        Family Melanostomiatidae
        Family Malacosteidae
        Family Idiacanthidae

The above classification divides the stomiatoids into two basic groups. (Note that throughout the present paper the adjective "stomiatoid" refers to the suborder Stomiatoidei, never to the superfamily Stomiatoidea.) These two groups, herein designated as infraorders, are based on the following analysis.

Grey (1960a, fig. 1), in conjunction with an analysis of gonostomatid generic relationships based on external characters, published a phylogenetic diagram that divides the family into three basic parts. Contrary to Weitzman (1967b, p. 49), a subsequent and more thorough osteological survey of the stomiatoids confirms the major lines of "gonostomatid" evolution proposed by Grey (1960a). Once all genera here considered sternoptychids are removed, Grey's diagram divides the Gonostomatidae into two parts that are consistent with a character that divides the entire suborder into two groups. One group is here named the infraorder Gonostomata and the other the infraorder Photichthya. All Gonostomata (including the sternoptychids) are primitive relative to the Photichthya in having four pectoral fin radials (with the exception of *Cyclothone* which has the pectoral radials reduced to one element). As is shown below the sternoptychids are a separate line of evolution and their closest relative appears to be the Gonostomatidae.

All Photichthya are advanced in having three pectoral fin radials (with the exception of some

highly derived melanostomiatid and malacosteid genera which have the pectoral fin reduced and have no pectoral radials or less than three).

Additional evidence for this division of the suborder can be found in the histology of stomiatoid photophores. The work of Bassot (1966), although not covering all stomiatoid genera, supports the classification of stomiatoids proposed here. Bassot found that the photophores in the stomiatoid genera he examined sorted into three groups based on the shape and arrangement of A-photocytes. Type Alpha photophores have relatively small A-photocytes of polyhedral form that are arranged side by side in great numbers in the photophore. These were found by Bassot in the sternoptychid genera *Maurolicus*, *Argyropelecus*, and *Sternoptyx*. In the Beta type, the A-photocytes are grouped in acini or in tubes emptying into a common collector canal. The canal may either be blind or open to the outside of the photophore. Bassot found Beta type photophores in *Gonostoma*, *Cyclothone*, *Bonapartia*, and *Diplophos* (including *Manducus*), all genera here referred to the Gonostomatidae. In the Gamma type of photophore the "deep spherical part of the photophore contains only a limited number of A-photocytes arranged radially, with their height equal to the radius of the photophore." Genera found by Bassot (1966) to have this type are *Vinciguerria* and *Ichthyococcus*, both here placed in the Photichthyidae, and *Stomias* and *Chauliodus*, both in the superfamily Stomiatoidea. All four genera with type Gamma photophores are in the infraorder Photichthya, the group with three pectoral fin radials. Although much remains to be elucidated in the study of comparative photophore histology and cytology of stomiatoids, it appears from Bassot's remarks (1966, pp. 574–576) that the type Beta photophore structure found in the Gonostomatidae is primitive relative to type Alpha found in the Sternoptychidae and type Gamma in the Photichthya, which are advanced in different directions. This concept correlates well with the relatively primitive or advanced states proposed here for other morphological features in these families and infraorders.

In the newly proposed classification the genera that constitute the family Gonostomatidae are *Diplophos* Günther, *Triplophos* Brauer, *Bonapartia* Goode and Bean, *Margrethia* Jespersen and Tåning, *Gonostoma* Rafinesque, and
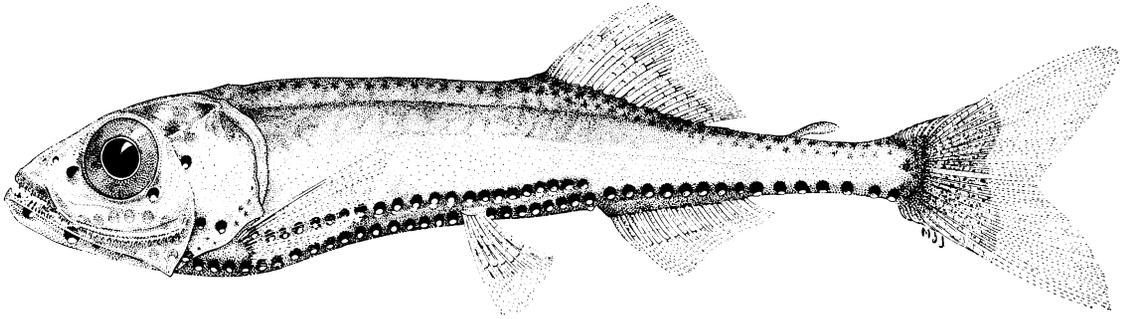
FIG. 14. *Vinciguerria lucetia* (Garman), SL 39.9 mm., USNM 203394.
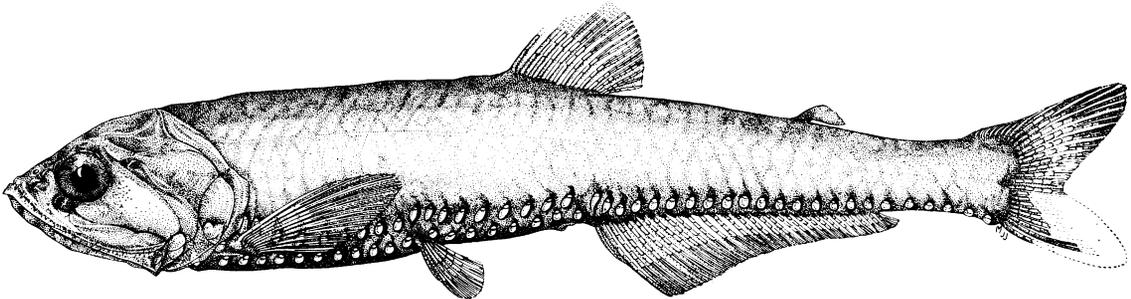
FIG. 15. *Polymetme corythaeola* (Alcock), SL 161.5 mm., USNM 203281.
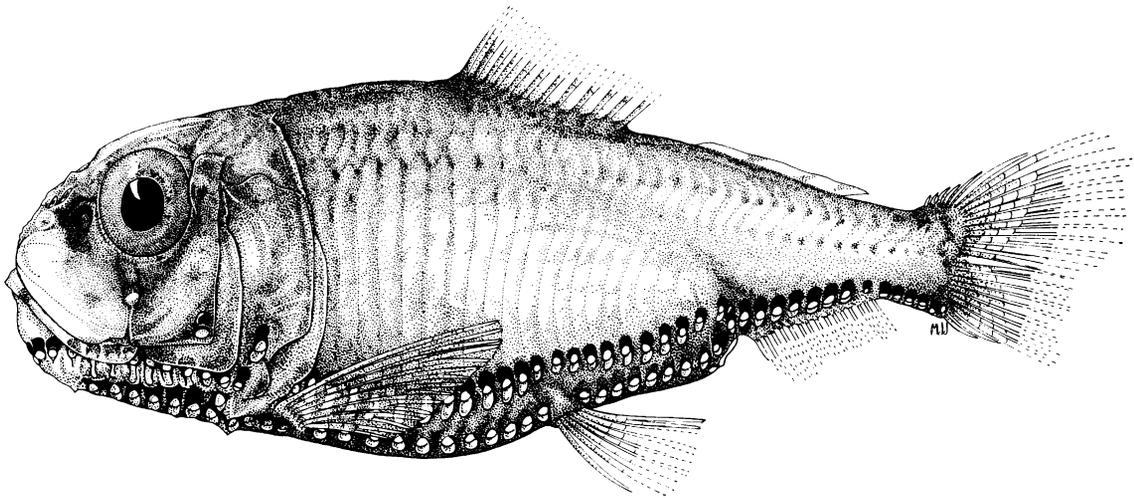
FIG. 16. *Ichthyococcus irregularis* Rechnitzer and Böhlke, SL 39.5 mm., USNM 201385.

Cyclothone Goode and Bean. Most of these genera appear to be primitive stomiatoids whose interrelationships are not treated here in detail. However, *Diplophos* appears especially primitive for a stomiatoid in its aggregate of characters which include, for example, a relatively large, toothed basihyal. *Diplophos* (including *Mandurus*) has a relatively primitive head. The most advanced genera in this group appear to be *Gonostoma* and especially *Cyclothone*, each having several advanced cranial characters. The family is recognized tentatively until an analysis of the

lines of evolution among these genera can be made.

The Sternoptychidae is the primary subject of the present report together with a detailed analysis of the family, its characters and relationships and the interrelationships of the genera. See the list of included genera above.

Weitzman (1967b) pointed out that the members of the superfamily Stomiatoidea have three or fewer pectoral radials and are apparently derived from ancestral Stomiatoidei with three pectoral radials. On other osteological grounds Weitzman (1967b) indicated that the photichthyid *Polymetme*, at least, shows affinities with astronesthid genera and therefore with the superfamily Stomiatoidea. It seems from this that all genera of the suborder Stomiatoidei with three pectoral fin radials (including derivatives of these genera with fewer than three pectoral fin radials) are interrelated and can be combined in the infraorder Photichthya.

The genera formerly in the family Gonostomatidae but which belong to the family Photichthyidae of the superfamily Photichthya are *Vinciguerria* Jordan and Evermann, *Polymetme* McCulloch, *Yarrella* Goode and Bean, *Pollichthys* Grey, *Photichthys* Hutton, *Woodsia* Grey, and *Ichthyococcus* Bonaparte. The interrelationships of these genera have not been studied in detail, but they appear to be a collection of relatively primitive Photichthya, each with possibly a few of their own advanced characters. An exception is *Ichthyococcus*, which has highly advanced mouth parts, branchial apparatus, and hearing and vestibular apparatus. The sagitta of *Ichthyococcus* in conjunction with that of *Polyipnus*, which it resembles and which it is apparently convergent in structure is described herein. The jaws of *Ichthyococcus* are beaklike, have very small premaxillaries, and a large toothed maxillary fused with the two supramaxillaries.

The family listing above under Stomiatoidea is conservative, and the relationships of these groups need considerable clarification and probably alteration. Weitzman (1967b) used two superfamilies for what is here considered the Stomiatoidea, separating the superfamily Astronesthoidea, including the Astronesthidae, Melanostomiatidae, Malacosteidae, and Idiacanthidae from the superfamily Stomiatoidea, including the Chauliodontidae and Stomiatidae.

This separation was based on the Gymnophotodermi (=Astronesthoidea of Weitzman, 1967b) and Lepidophotodermi (=Stomiatoidea of Weitzman, 1967b), both proposed by Parr (1927). The character used to separate these groups is the presence of scales in the Lepidophotodermi and their absence in the Gymnophotodermi. If numerous osteological characters of *Chauliodus* and *Stomias* Cuvier are examined and compared with those of astronesthids and melanostomiatids, it soon appears that melanostomiatids, chauliodontids, and stomiatids are closely allied and in turn are related to such astronesthid genera as *Astronesthes* Richardson and *Borostomias* Regan. The relatively primitive astronesthid genera, such as *Heterophotus* Regan and Trewavas and *Rhadinesthes* Regan and Trewavas, appear relatively far removed from the more advanced *Astronesthes* and *Borostomias*. In many ways they are more like the photichthyid *Polymetme* (see Weitzman, 1967b). The scales found in the Chauliodontidae and Stomiatidae may be atavistic characters, perhaps inherited from *Astronesthes*-like ancestors which possessed such scales. The absence of scales in other astronesthids such as *Heterophotus* and *Rhadinesthes* may be an independent loss. The loss of scales is probably a trend within the superfamily Stomiatoidea. In view of these hypotheses, which need adequate documentation, it seems wise at this point to remain "open-minded" about families of the superfamily Stomiatoidea, and realize that parts of the Astronesthidae, the Melanostomiatidae, and the Chauliodontidae might eventually be included in an expanded Stomiatidae. Therefore it seems best now to accept only one superfamily, the Stomiatoidea.

If one accepts the classification I propose here, that is of dividing stomiatoids into two separate evolutionary lines, one leading to extremely advanced morphological types such as *Sternoptyx*, the other to such highly modified genera as *Malacosteus* Ayres or *Eustomias* Vaillant, one must assume that this basic division of stomiatoids is old, probably having occurred during the Cretaceous. According to the published record one of the earliest known stomiatoids of certain identity is *Chauliodus* from the Miocene of southern California (Crane, 1966). *Chauliodus* is a highly advanced descendant of an astronesthid-melanostomiatid-like ancestor that must have had a long evolutionary history. The

referral of earlier fossils to the Astronesthidae, for example *Astronesthes simus* Arambourg from the Oligocene of Iran and *Astronesthes praevius* Danil'shenko from the Oligocene or Eocene of the Dabakhan Series of Georgia, is questionable. These fossils cannot be considered as stomiatoids with certainty (see Weitzman, 1967a).

Baird (1971) has reviewed possible Eocene or Oligocene stomiatoids in the sternoptychid line such as *Polyipnoides levis* Danil'shenko and *Polyipnus sobnioviensis* Jerzmánska. The referral of *P. levis* to the Stomiatoidei seems questionable, but *Polyipnus sobnioviensis* may be related more closely to *Danaphos* and *Valenciennellus* than to *Polyipnus*. A more complete and detailed analysis of the osteology of these fossils is needed.

Mr. John E. Fitch has kindly permitted me to use unpublished information concerning stomiatoid otoliths from the Eocene. He has found deepwater, middle Eocene deposits near La Jolla (Rose Canyon Formation), California, to contain *Ichthyococcus*-like otoliths but appearing possibly ancestral to that genus because they bear a well-defined sulcus. This same deposit has also yielded otoliths of three or four other stomiatoids, all similar to those of gonostomatids or photichthyids. Mr. Robert Lavenberg informed me that *Xyrinius houshi* Jordan and Gilbert (1919) from Miocene Monterey formations, California, and described as a labrid is actually an *Ichthyococcus*. Lavenberg and Fitch (*in litt.*) also confirm David's (1943) identification of *Rogenio* Jordan (1907) as a *Cyclothone* and note that two species of *Argyropelecus* (one similar to that described by David [1943] from Sepulveda Canyon, Santa Monica Mountains, California), two species of *Cyclothone*, and apparently one of *Sternoptyx* have been found in Miocene diatomite at Lompoc, California. These fishes are apparently identical or almost identical with modern species. Fitch also has records of *Polyipnus* otoliths from the Miocene Bowden Formation in Jamaica and a few Miocene otoliths of a large *Gonostoma*-like fish from the Temblor Formation near Bakersfield, California.

In view of the apparent presence of *Danaphos*- and *Ichthyococcus*-like stomiatoids in the Eocene and the wide variety of specialized, modern stomiatoid-like genera in the Miocene, it seems quite reasonable to assume that the evolution of major stomiatoid groups took place before the Eocene, certainly before the Miocene, and that probably much of it occurred during the Cretaceous. In numerous characters several modern stomiatoid genera are relatively primitive, far more so than the fossils discussed above (excluding consideration of those only represented by otoliths). Presumably the Recent relatively primitive stomiatoids are quite old and probably more or less unchanged since the Cretaceous. The modern, relatively primitive genera are *Thorophos* in the Sternoptychidae, *Diplophos* and *Triplophos* in the Gonostomatidae, and *Yarrella*, *Polymetme*, *Vinciguerria*, and *Photichthys* in the Photichthyidae. The photichthyid *Ichthyococcus* is highly advanced but may be related to the relatively primitive *Woodsia*. The subject of a future paper is the relationships of gonostomatid and photichthyid genera.

In the total sum of their characters, the Gonostomatidae and Photichthyidae are not remarkably distinct. This is especially true of the relatively primitive genera, all of which retain a large number of primitive stomiatoid features. There exists a practical problem in that there are no external characters easily and visibly useful for placing a specimen into one or the other of these two families. Despite this problem, if one acknowledges the basic and apparently very old division of the suborder into its two major evolutionary lines, then it is necessary and logical to recognize these two families.

METHODS

Methods of collecting data used here are conventional for studies on osteology and relationships in ichthyology. Most specimens were prepared by the enzyme technique of Taylor (1967), that is, stained with alizarin and preserved in glycerine and thymol. Specimens were subsequently dissected and drawn using a variety of optical aids and types of microscopes depending on the particular problem at hand. Several special problems arose in working with stomiatoids because of the extremely brittle, thin, delicate bones, small adult size, and rareness of specimens (one of a kind available for dissection in some instances). Care and patience in dissection is the only answer for most of these problems. Examination of the details of the skulls of very small forms, for example in *Araiophos*, sometimes required the use of a histological microscope despite the attendant lack of depth of field. Rareness of specimens forced the development of a dissection technique that allows one to prepare a fish so that all bones are

visible at least on one side and all joints, at least on one side of the body, are intact except the symphysis of the lower jaw, the interpremaxillary joint, and the joint between the anterior borders of the two coracoid bones of the pectoral girdle.

The dissection procedure is as follows. First cut the interpremaxillary joint and the joint at the symphysis of the lower jaw. Remove the eye of the right side being careful not to destroy the orbital bones. Next remove the "face" bones of the right side by cutting through the fleshy floor of the mouth between the lower jaw and basihyal bone. Continue this cut posteriorly to the joint between the dorsal and ventral hypohyals on the one hand and the basibranchial of the first arch and hypobranchial of the first gill arch on the other. Then cut the hypohyals free of the basi-branchials and hypobranchial of the first gill arch so that the hypohyals, ceratohyals, and epihyals come free of the branchial basket. Continue to cut these hyal bones free accompanied by their branchiostegal rays so that these remain attached to the opercular bones but are free of the branchial basket.

Cut the premaxillary, maxillary, and palatine bones free of the ethmoid bones and cartilages. This operation is complex and sometimes difficult to accomplish without damage to the specimen, but a careful search for, and cutting of, the cordlike ligaments in this area will greatly reduce damage. Continue this cut posteriorly between the palatine and pterygoid bones on the one hand and the parasphenoid on the other until the joint between the hyomandib-ular and the skull is reached. Be careful not to damage the orbital bones in this process. The antorbital and nasal bone of the right side should be separated from the lateral ethmoid and other ethmoid bone or bones and left attached to the orbital bones and jaw bones of the right side. If a supraorbital bone is present it can be cut free of the frontal and/or the lateral ethmoid and removed along with the "face" bones just described.

When this dissection is complete, the face bones of the right side should be almost free, being attached primarily by the capsular joint between the hyomandibular and the skull. This joint should be cut next. To do this it is often easiest to turn the specimen belly up, spread the face bones of the right side laterally, away from the branchial arches, and expose the internal

portion of the joint between the hyomandibular bone and skull (usually consisting of pterotic and prootic at this point). The capsular ligament of this joint should then be cut by running a sharp scalpel between the internal surface of the hyomandibular bone and the skull. When this ligament has been successfully cut the face bones will usually suddenly spread further under continued lateral pressure and the hyomandibular bone will "pop" out of its fossa-like joint. A pair of iridectomy scissors or a scalpel may then be used to cut the opercle, lateral part of the joint between the hyomandibular bone and the skull, and the attachment of the dermosphenotic from the skull. At this point all face bones, jaws, orbital bones, opercle bones, lower hyoid bones, and branchiostegal rays of the right side should be intact and free of the cranium. These may then be set aside for cleaning and further dissecting if necessary. All the joints thus far cut, except the symphysis of the lower jaw and the interpremaxillary joint, should remain intact on the left side.

Next remove the right pectoral girdle. With a scalpel or scissors first cut the joint between the anterior ends of the coracoid bones of each side. Free the posterior border of the pectoral girdle by removing scales and cutting skin and then muscle and fascia between the anterior pleural rib and the posterior border of the pectoral girdle of the right side. Be careful to avoid postcleithra (if present) when removing scales or cutting tissue along the posterior border of the pectoral girdle. Continue cutting dorsally along the posterior edge of the pectoral girdle, freeing the posttemporal from the skull by first detaching the upper limb from the epiotic and removing the extrascapular bone (if one is present) with the upper limb of the posttemporal. Clean the muscle tissue away from the posttemporal bone until the ligament between the ventral limb and the intercalar is found and cut. Next cut the tissues between the supracleithrum, cleithrum, and coracoid on the one hand and the esophagus and oral cavity on the other. The pectoral girdle should then come freely away and can be cleaned of soft tissues.

The branchial basket is then exposed for removal. First free the infrapharyngeal bones of the right side from their attachments with the skull. Pull the epibranchial bars and attached infrapharyngobranchials laterally and cut the posterior parts of the branchial basket free of

their attachment with the anterior end of the gut tube. Cut the attachments of the urohyal to the remaining left pectoral girdle. Finally separate the infrapharyngobranchials of the left side from their epibranchials, leaving the infrapharyngobranchials attached to the skull. Cut the branchiostegal rays and lower hyoid apparatus, except for the interhyal, free of the face bones of the left side and remove the branchial basket along with the lower hyoid bones of the left side. Further cleaning of the skull, removal of the brain through available foramina, cleaning of the branchial basket, and axial skeleton without disturbing any further joints are possible and will leave a nearly complete skeleton for examination. Almost all joints and at least the external aspects of the skull bones are now available.

It is now possible to remove further some of the skull bones of the right side such as the sphenotic, parts of the prootic, pterotic, parietal, frontal, and pterosphenoid. This will leave these bones intact on the opposite side while facilitating removal of the brain and examination of the internal aspects of the cranium.

The analysis of relationships used here follows, in a general way, the phylogenetic approach suggested by Hennig (1966) and Brundin (1966). In brief, attempts were made to determine sister-group relationships, i.e., relationships based on descent from a common ancestor. Characters found in a given group were analyzed on the basis of being primitive (plesiomorphic) or advanced (apomorphic) for that particular group. If this could not be done the characters were not used. When an apparently advanced character was found in common between two groups (synapomorphic) it was taken as possible evidence that the two groups had a common ancestor. If this character was complicated and unlikely to have evolved more than once it was accepted as evidence that the two groups had a common ancestor. Also, if a large number of synapomorphic characters was found common to two groups it was accepted as evidence that the two groups had a common ancestor even if none or only a few of these characters were so complicated that an independent development appeared unlikely. Shared plesiomorphic (symplesiomorphic) characters were not accepted as evidence of a hypothetical common ancestor because such characters are not limited to the two groups in question. Autapo-

morphic (limited to one group) characters of course cannot be used to determine relationships but are certainly useful in distinguishing a lineage.

The terms plesiomorphic, etc., are not used in the text and references to primitive versus advanced states are invariably made in regard to the group or groups being discussed so that plesiomorphy, apomorphy, synapomorphy, or symplesiomorphy can be readily determined.

MATERIALS

An alphabetical list of the genera and species of the stomiatoids prepared and examined specifically for this report follows. When specimens from other stomiatoid or salmoniform and myctophoid families are discussed, reference to the material used can be found in Weitzman (1967a or 1967b). Measurements in millimeters are of cleared and stained specimens only, even when these form part of a larger series with unstained specimens (* denotes not cleared and stained). All other measurements are of the smallest and largest specimens in a given lot.

The following abbreviations are used in the materials lists and in the text.

DANA, Carlsberg Foundation, Dana Collections, Denmark

FMNH, Field Museum of Natural History, Chicago

SIO, Scripps Institution of Oceanography, University of California at San Diego

SL, standard length, in millimeters

SU, formerly in Division of Systematic Biology, Stanford University, now in California Academy of Sciences, San Francisco

USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Definitions for abbreviations of photophore rows such as AC, PV, and IP may be found in Grey (1964), Schultz (1964), and Morrow (1964b).

Araiophos eastropas Ahlstrom and Moser. USNM 203285, three, SL 30.0, 31.0, and 35.0, 12°48′S, 118°53.5′W; *USNM 203239, one (paratype), SL 31.5, 12°48′S, 118°53.5′W.

Araiophos gracilis Grey. FMNH 73902, one (paratype), SL 25.7, Hawaii, off Mauna Loa lava flow.

Argyripnus atlanticus Maul. USNM 201351, one, SL 57.0, 18°12′N, 67°42′W; *FMNH 65693, one, SL 67.0, 18°12′N, 67°42′W.

Argyripnus sp. *USNM 135402, one, SL 81.2, Philippine Islands, near Mindinao.

Argyripnus sp. *USNM 126079, two, SL 72.0 and 79.5, Hawaii.

Argyripnus sp. *USNM 204739, 20, SL 53.4–85.7, 21°10′N, 157°25′W.

Argyropelecus aculeatus Valenciennes. USNM 179056, two, SL 49.1 and 49.5, 29°48′N, 79°57′W; USNM 199853, two, SL 40.0 and 41.2, 29°25′N, 79°51′W; USNM 199854, four, SL 24.3–44.1, 29°00′N, 88°02′W; *USNM 196700, 63, SL 16.5–62.0, 27°40′N, 90°50′W; *USNM 192808, five, SL 27.5–58.2, 29°08′N, 88°05′W; *USNM 177846, three, SL 42.5–50.5, 39°42′N, 70°08′W.

Argyropelecus affinis Garman. USNM 203258, two (of 12), SL 42.5 and 52.8, 26°12′N, 114°14.5′W; *USNM 203388, 11, SL 39.1–60.1, 32°05′N, 120°41.5′W; *USNM 203389, 35, SL 21.5–62.1, 31°00′N, 119°32′W.

Argyropelecus gigas Norman. USNM 203259, two, SL 51.5 and 52.5, 34°00′S, 80°36′W; *USNM 203343, one, SL 76.5, 03°01′S, 159°18′W.

Argyropelecus hemigymnus Cocco. USNM 164296, one (of three), SL 31.0, "South of Iceland"; USNM 203347, two (of four), SL 26.9 and 28.2, 49°10′S, 120°15′W.

Bonapartia pedaliota Goode and Bean. USNM 187083, two, SL 66.3 and 73.3, 29°10′N, 87°55′W; *FMNH 49991, one, SL 64.3, 32°08.6′N, 64°50.7′W; *USNM 203294, one, SL 52.1, 32°09.5′N, 64°23′W; *USNM 44337, one (holotype), SL 58.3, 25°20′30″N, 79°58′00″W; *USNM 69911, three (syntypes of *Zaphotias nudum* Borodin), SL 38.3–50.1, 33°N, 64°W, Bermuda; *USNM 203365, one, SL 30.0, 24°00′N, 85°27′W; *USNM 203364, three, SL 25.5–35.5, 24°04.1′N, 85°31.2′W; *USNM 203367, one, SL 23.0, 25°04′N, 89°13.5′W.

Cyclothone acclinidens Garman. USNM 260174–F15, four (of 36), SL 38.6–44.0, 33°33′S, 72°45′W; USNM 260174–F9, two (of 50), SL 32.8 and 39.6, 07°47.5′S, 81°23′W.

Cyclothone alba Brauer. USNM 203349, three (of 64), SL 32.3–36.2, 38°32′S, 95°39′W.

Cyclothone microdon Günther. USNM 203348, two (of 25), SL 46.4 and 47.3, 38°32′S, 95°39′W.

Cyclothone pseudopallida Mukhacheva. USNM 260174–F26, two (of five), SL 34.5 and 35.3, 33°33′S, 72°45′W.

Cyclothone signata Garman. USNM 260174–F5, two (of 10), SL 28.2 and 29.1, 23°33′S, 72°35′W.

Danaphos oculatus (Garman). USNM 203261, one (of seven), SL 34.5, 33°00′S, 89°28′W; USNM 203266, one, SL 23.4, 39°54′S, 107°30′W; USNM 203257, one (of two), SL 28.7, 30°28.8′N, 124°06.6′W; *USNM 203265, two, SL 27.8 and 31.4, 33°04′S, 82°14′W; *USNM 203269, two, SL 22.7 and 36.9, 33°00′S, 83°57′W; *USNM 201100, 17, SL 24.5–36.7, 33°32′S, 78°38′W.

Diplophos maderensis (Johnson). USNM 186364, two, SL 104.1 and 111.5, 07°38′N, 54°43′W.

Diplophos sp. USNM 203292, two (of 16), SL 86.0 and 118.5, ?03°37′S, 55°22′E?

Gonostoma bathyphilum (Vaillant). USNM 201135, two, SL 138.1 and 152.9, 31°32.4′N, 68°34.8′W.

Gonostoma elongatus Günther. USNM 199509, three (of 300), SL 135.0–227.0, 29°06′N, 88°02′W.

Gonostoma gracile Günther. USNM 150102, one (of two), SL 107.8, 30°22′N, 129°08′30″E; USNM 163308, two (of 36), SL 63.1 and 63.5, 45 mi. "E/N" of Ohakozaki, Japan.

Ichthyococcus irregularis Rechnitzer and Böhlke. USNM 203291, two, SL 25.0 and 37.0, 32°55′N, 118°57′W; SIO 66–42–10, two, SL 44.5 and 59.3, 31°05.4–24.0′N, 117°19.1–41.6′W; USNM 203293, one, SL 44.5, 31°05.4′N, 117°19.1′W; USNM 201384, one, SL 18.6, 32°31.8′N, 117°33.3′W; USNM 201385, one, SL 39.5, 32°45′N, 118°20′W; *USNM 203289, one, SL 65.0, 29°34′N, 118°28′W; *USNM 169735, one (holotype), SL 76.0, 35°44″N, 114°52′W.

Ichthyococcus ovatus (Cocco). USNM 203344, one, SL 32.8, 35°18′S, 70°30′E; USNM 203287, one, SL 29.0, 27°40′N, 90°50′W; USNM 40078, two (of six), SL 33.8 and 44.0, Messina, Italy.

Ichthyococcus polli? Blache. *USNM 203268, one, SL 20.7, 33°04′S, 82°14′W.

Margrethia obtusirostra Jespersen and Tåning. USNM 203284, one, SL 42.6, 32°00′N, 64°51.7′W; USNM 186287, one, SL 43.0, 26°30′N, 90°42′W; *USNM 203295, one, SL 31.3, 32°09.5′N, 64°23′W; *USNM 203342, one, SL 47.9, 04°15′S, 41°00′E.

Maurolicus muelleri (Gmelin). USNM 40070, two (of eight), SL 35.8 and 48.4, Messina, Italy; USNM 201138, one (of two), SL 45.5, 26°24′N, 79°50′W; *USNM 203270, one, SL 12.3, 33°36′S, 80°57′W; *USNM 203269, six, SL 22.1–28.1, 33°04′S, 82°14′W; *USNM 203271, three, SL 23.5–27.5, 34°00′S, 80°36′W; *USNM 203288, one, SL 16.5, 25°04′N, 89°13.5′W; USNM 203823, two (of 52), SL 14.7 and 17.4, 27°54′00″N, 34°25′30″E.

Photichthys argenteus Hutton. USNM 203407, one, SL 93.1, 48°51′S, 162°00′E; *USNM 203387, one, SL 55.7, 29°26′S, 49°10′E; *USNM 203341, one, SL 13.4, 33°36′S, 80°57′W.

Pollichthys mauli (Poll). USNM 187072, one (of three), SL 43.8, 27°30′N, 78°52′W; USNM 108276, one (of four), SL 34.2, 18°37′N, 66°24′W; USNM 201278, two (of three), SL 32.5 and 35.0, 38°33.1′N, 75°55′W; USNM 100333, one (of five), SL 29.0, 32°33′N, 72°14′W; USNM 203408, 10, SL 27.0–47.8, 31°50′N, 64°21′W.

Polyipnus asteroides Schultz. USNM 197542, six (of 84), SL 42.2–57.2, 09°03′N, 81°22′W; *USNM 190472, 10, SL 37.0–50.0, 18°12′N, 67°42′W.

Polyipnus laternatus Garman. USNM 179052, two (of 20), SL 37.6 and 38.0, 12°23′N, 89°29′W (specimen drawn in fig. 9 is not stained, SL 36.0).

Polyipnus sp. USNM 203345, two (one cleared and stained), SL 33.5 and 35.0, 29°08′S, 175°28′E.

Polyipnus tridentifer McCulloch. USNM 135535, two (of 38), SL 45.0 and 52.0, near Sombrero Island, Philippine Islands; USNM 135530, two (of 18), SL 54.5 and 57.0, Negros-Siquijor, Philippine Islands; *USNM 135536, six, SL 45.5–60.6, Negros-Siquijor, Philippine Islands; *USNM 135537, six, SL 51.1–59.1, off Kayoa, Philippine Islands.

Polymetme corythaeola (Alcock). USNM 158797, one (of two), SL 117.8, 29°10′N, 88°07′W; USNM 188236, one (of three), SL 61.0, 28°32.5′N, 88°08′W; USNM 199507, four (of 18), SL 77.7–174.0, 09°03′N, 81°22′W; *USNM 203281, 11, SL 126.5–163.7, 12°26′N, 82°24′W; *USNM 203282, one, SL 172.0, 11°46′N, 69°17′W.

Sonoda megalophthalma Grey. USNM 201350, one (paratype), SL 53.5, 14°08′N, 81°49′W; *FMNH 65982, two (paratypes), SL 50.3 and 53.5, 13°25′N, 82°01′W.

Sonoda paucilampa Grey. *USNM 196967, one (holotype), SL 67.0, 18°37.5′N, 64°57′W.

Sternoptyx diaphana Hermann. USNM 192843, four, SL 27.1–44.0, 25°30′N, 92°15′W; USNM 203263, one (of seven), SL 36.0, 25°34.7′N, 124°07′W; USNM 179061, two (of four), SL 34.3 and 45.1, 29°54′N, 80°10′W; USNM 194501, one (of five), SL 44.1, 24°33′N, 09°12′W; *USNM 203390, three, SL 29.9–37.5, 26°56.8′N, 121°32.4′W; *USNM 203391, two, SL 22.5 and 34.8, 32°45.0′N, 118°48.6′W; *USNM 203386, 10, SL 18.5–33.0, 27°36′N, 94°40′W; *USNM 158168, eight, SL 17.0–37.8, 23°26′N, 80°28′W.

Sternoptyx sp. USNM 203262, one, SL 39.0, 25°34.7′N, 124°07.0′W. (The identity of this specimen to species is uncertain. The specimen compares well with the lectotype of *S. obscura* Garman but the recent review of the genus *Sternoptyx* in Baird [1971] leaves several questions unanswered about the validity of the species recognized by him.)

Thorophos euryops Bruun. DANA 3736-VI, two (of eight paratypes), SL 35.0 and 44.7, 09°17′N, 123°58′E (one of two specimens, SL 44.7, cleared and stained).

Thorophos nexilis (Myers). USNM 151400, one (of six), SL 61.0, Point Tagolo, Philippine Islands; *SU 24798, one (holotype), SL 60.1, probably Point Tagolo, Philippine Islands; *USNM 122276, three, two measurable specimens SL 59.0 and 61.0, Point Tagolo, Philippine Islands.

Triplophos hemingi (McArdle). USNM 203283, one (of three), SL 163.0, 11°54′N, 69°23′W; USNM 199832, one, SL 175.0, 16°58′N, 87°53′W; *USNM 203296, five, SL 137.8–186.5, 09°02.4′N, 76°31.5′W; *USNM 203384, 17, SL 77.5–162.5, 12°36′N, 72°08′W; *USNM 203385, one, SL 134.0, 11°24′N, 64°25′W; *USNM 203383, two, SL 157.5 and 159.5, 11°54′N, 69°23′W.

Valenciennellus tripunctulatus (Esmark). USNM 203260, one (of two), SL 21.2, 33°11′S, 85°49′W; USNM 203267, one, SL 21.5, 33°04′S, 82°14′W; USNM 203260, one (of two), SL 21.5, 33°11′S, 85°49′W; USNM 10839, one (of three), SL 22.0, 18°44′N, 65°16′15″W; *USNM 201141, one, SL 25.4, 32°37′N, 65°03′W; *USNM 201140, two, SL 11.9 and 30.2, 28°33.1′N, 75°55′W.

Vinciguerria attenuata (Cocco). USNM 201142, one (of four), SL 44.5, 32°44′N, 65°00′W; *USNM 203399, one, SL 35.1, 33°04′S, 82°14′W; *USNM 203396, two, SL 20.5 and 21.0, 40°00′S, 119°36′W; *USNM 203398, two, SL 21.8 and 41.7, 37°12′S, 94°24′W; *USNM 203382, one, SL 24.0, 25°04′N, 89°13.5′W; *USNM 203397, one, SL 20.0, 33°36′S, 80°57′W.

Vinciguerria lucetia (Garman). USNM 201315, 12 (of 383), SL 17.7–47.6, 24°35′N, 112°42.5′W; USNM 260174–47, one (of four), SL 35.5, 07°47.5′S, 81°23′W; *USNM 203394, three, SL 36.1–39.9, 37°12′S, 94°24′W; USNM 203824, two (of 71), SL 17.6 and 18.7, 27°54′00″N, 34°25′30″E.

Vinciguerria nimbaria (Jordan and Williams). USNM 203346, one, SL 17.8, 25°07.3′N, 89°04.3′W; *USNM 203381, one, SL 29.5, 26°17.2′N, 85°03.9′W; *USNM 203373, one, SL 16.0, 31°32′N, 75°20′W; *USNM 203374, one, SL 17.0, 23°54′N, 85°28′W; *USNM 203375, one, SL 17.0, 35°05′N, 74°43′W; *USNM 203376, one, SL 17.2, 31°24.5′N, 75°25′W; *USNM 203377, one, SL 18.0, 25°47.7′N, 87°04.1′W.

Vinciguerria poweriae (Cocco). USNM 203371, one (of three), SL 32.5, 25°06′N, 89°08.8′W; USNM 203369, two (of seven), SL 27.1 and 32.0, 26°17.2′N, 85°03.9′W; *USNM 203370, three, SL 13.5–14.5, 31°24.5′N, 75°25′W; *USNM 203372, three, SL 27.5–32.0, 26°18.8′N, 85°05.8′W; *USNM 203395, one, SL 31.1, 33°00′S, 89°28′W.

Woodsia nonsuchae (Beebe). *USNM 170938, one (holotype), SL 84.6, Bermuda, SSW of Nonsuch Island; *SIO 67–67–10, one, SL 114.5, near east coast of Guadalupe Island, Mexico (face and pectoral girdle of right side cleared and stained).

Woodsia sp. USNM 203290, one, SL 22.5, 47°18′08″S, 167°36′37″W.

Yarella blackfordi Goode and Bean. USNM 186283, three (of eight), SL 133.8–180.0, 07°44′N, 54°40′W; *USNM 203340, two, SL 213.0 and 215.5, 25°05′N, 96°27′W.

ACKNOWLEDGMENTS

OSTEOLOGY AND SOFT ANATOMY

ETHMOID REGION

THE ETHMOID REGION in stomiatoid fishes has been discussed by Weitzman (1967a) and appears to primitively consist of a central ethmoid cartilage surrounded by six kinds of bones. These are two dorsolateral, dermal proethmoids (1) placed superficial and lateral to a dorsomedian, perichondral supraethmoid (2). Two lateral perichondral bones, the capsular ethmoids (3), are placed one on each side. Each capsular ethmoid lies ventral to the lateral edge of the supraethmoid to which they are usually fused. A median perichondral ventral ethmoid bone (4) is situated just dorsal to the joint between the vomer and parasphenoid. A conical median perichondral myodome bone (5) lines a conical excavation in the posterior wall of the ethmoid cartilage and serves as a surface of origin for the anterior oblique eye muscles. Two perichondral lateral ethmoids (6), one on each side, cover the lateral surface of the lamina orbitonasalis. In the stomiatoids described below, many of these bones are modified or absent and no species exhibits all of them.

The ethmoid regions of *Thorophos euryops* (figs. 17, 18) and *T. nexilis* are very similar, each
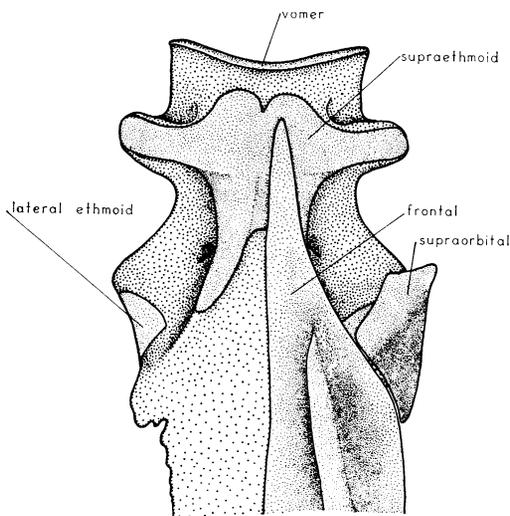
FIG. 17. Snout region of *Thorophos euryops*, SL 44.7 mm., DANA 3736-VI. Maxillary, premaxillary, and palatine bones removed. Dorsal view.

possessing a large supraethmoid bone without endochondral portions. The prenasal lateral processes of the supraethmoid are well developed and show no external evidence of being derived from, or in association with, proethmoids as in *Polymetme* (see Weitzman, 1967a, p. 519). The ethmoid cartilage is rather massive and supported mostly by the parasphenoid, vomer, and frontal bones, all other ethmoid bones being absent except for a thin, relatively small ethmoid covering part of the lateral border of the lamina orbitonasalis (preorbital or postnasal cartilages). The cartilaginous trabeculum communis, which lies on the dorsal surface of the parasphenoid and the orbital cartilages (which are fused with the tectum crani), are all well developed and fused anteriorly with the ethmoid cartilage. These help support the ethmoid region against the remainder of the cranium. At each side of the ethmoid cartilage just posterior to the prenasal lateral ethmoids is a large excavation which forms a recess for the nasal organ. The posteromedian walls of this recess are pierced by the foramen olfactorium advehens, which provides passage for the olfactory nerve to the nasal organ. The vomer of *T. nexilis* is a broad, median thin plate bearing two or three teeth on each side ventral to the basal portion of the cartilaginous ethmoid wings or processes. *Thorophos nexilis* also bears two teeth in a median longitudinal series near the point of contact between the vomer and parasphenoid. *Thorophos euryops* has four or five teeth on each side in a row more or less perpendicular to the longitudinal axis of the body. Because of damage the presence or absence of a median longitudinal row of vomerine teeth could not be determined in *T. euryops*. A myodome bone, capsular ethmoids, and a ventral ethmoid were absent in all stained specimens.

The ethmoid region of *Araiophos gracilis* is very similar to that of *Thorophos*, as comparison of figures 17-20 shows. Both genera have a similar supraethmoid bone with comparable prenasal lateral processes. Both have the anterior region of the ethmoid cartilage (here called the anterior ethmoid plate) broadly terminated with prominent anterolateral cartilaginous cornu on each side, easily seen in dorsoventral profile (com-

347

epiotic

pterotic

supraoccipital

posttemporal

parietal

frontal

supracleithrum

lateral ethmoid

supraethmoid

intercalar

premaxillary

exoccipital

sphenotic

basisphenoid

basioccipital

vomer

prootic

maxillary

opercle

palatine

hyomandibular

parasphenoid

preopercle

dentary

metapterygoid

mesopterygoid

ectopterygoid

subopercle

anterior supramaxillary

posterior supramaxillary

interhyal

angular (articular)

symplectic

coronomeckelian

interopercle

retroarticular

quadrate

FIG. 18. Cranium and face bones of *Thorophos euryops*, SL 44.7 mm., DANA 3736-VI. Lateral view right side of cranium, medial view of left side of face bones.

pare figs. 17, 19). The ethmoid cartilage is very massive and is fused with the tectal cartilage, which strongly supports the anterior dorsal surface of the head. A trabeculum communis and the lateral ethmoid bones are absent. The nasal excavations are large and the olfactory foramina are prominent. The vomer bears three or four teeth on each lateral lobe. The anterior border of the vomer is not applied to the anterodorsal edge of the cartilaginous anterior ethmoid plate as in *Thorophos. Araiophos eastropas* bears four or five teeth on each lateral vomerine lobe arranged in a row almost perpendicular to the long axis of the body. There is no midlongitudinal row of vomerine teeth in *A. gracilis* or *A. eastropas*. Other than a different tooth arrangement, *A. gracilis* and *A. eastropas* have very similar ethmoid regions. There is no myodome bone, capsular ethmoid, or ventral ethmoid in any specimen of *Araiophos* examined.

The ethmoid cartilage (figs. 21, 22) of

Maurolicus muelleri is a slender structure but is essentially similar to the ethmoid cartilage of *Thorophos* and *Araiophos* in having prominent anterolateral cornu on the ethmoid plate and a well-developed prenasal lateral cartilaginous process. The large excavations in the ethmoid cartilage for the nasal capsules do not have a cartilaginous floor as in *Araiophos* and *Thorophos*. The supraethmoid is long and relatively slender with a prominent lateral supraethmoid process on each side. A capsular ethmoid is present (fig. 22) and instead of consisting of two bones, one on each side, as in the osmerid *Spirinchus thaleichthys* (Ayres) (see Weitzman, 1967a, p. 509), it is a single perichondral bone supporting part of the median wall of the nasal capsule and continuous dorsally over (and closely applied to) the ethmoid cartilage. The supraethmoid can easily be lifted dorsally exposing the dorsal, connecting portion of the capsular ethmoid. The tectal and orbital cartilages are of moderate
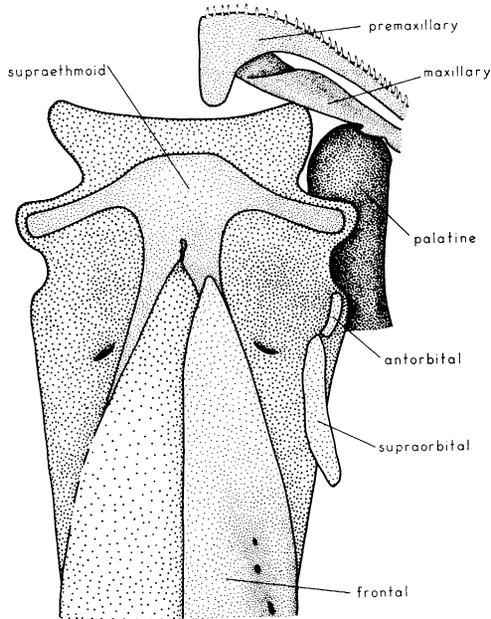
FIG. 19. Snout region of *Araiophos gracilis*, SL 25.7 mm., FMNH 73902. Dorsal view.

size and support the posterodorsal part of the ethmoid cartilage. The trabeculum communis is relatively short above the parasphenoid, extending posteriorly along the anterior half of the bone. The trabeculum communis forms the ventral attachment for the fibrous sheet of the interorbital septum. A ventral ethmoid and myodome bone are absent. The lateral pre-orbital cartilages are extensive and a lateral ethmoid covers the dorsal, lateral, anterior, and posterior faces of each preorbital cartilage. The vomer has a posterior shaft articulating with the ventral surface of the anterior process of the parasphenoid and the vomer is applied to the anteroventral, anterior, and anterodorsal surfaces of the ethmoid cartilage. Anteriorly the vomer curves dorsally to contact the anterior median portion of the supraethmoid. Three to five teeth occur in a single linear row along the posterior edge of each anterolateral vomerine process. There are no median vomerine teeth.

*Danaphos oculatus* (figs. 23, 24) lacks cartilaginous ethmoid cornu. Instead the anterior
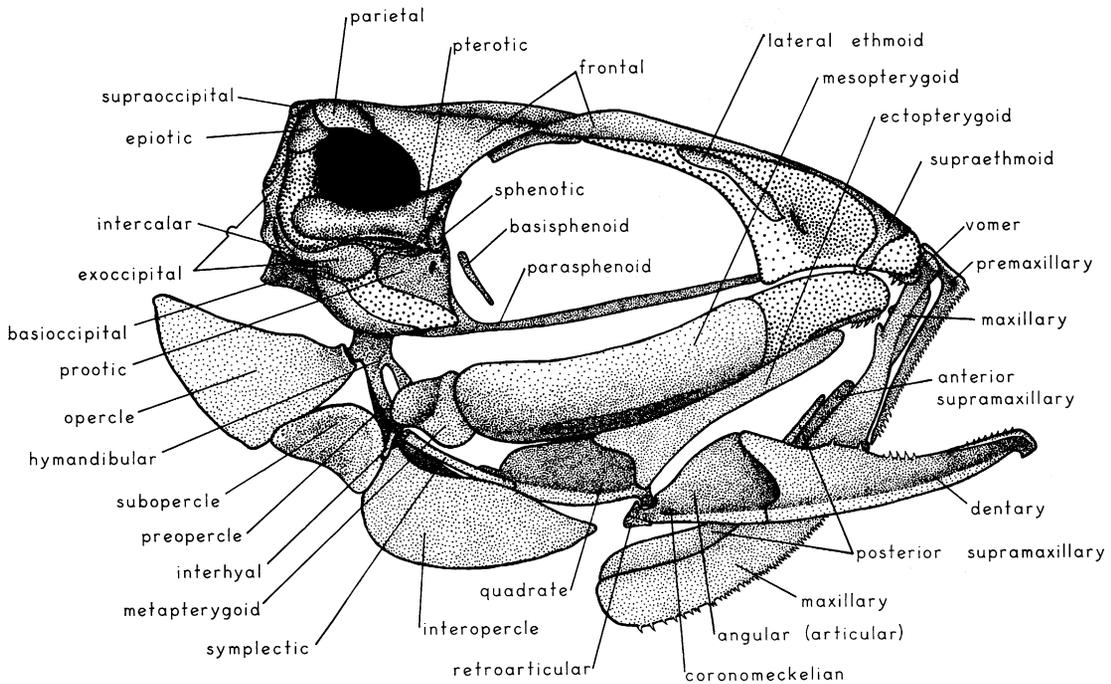
FIG. 20. Cranium and face bones of *Araiophos gracilis*, SL 25.7 mm., FMNH 73902. Lateral view of right side of cranium, medial view of left side of face bones.
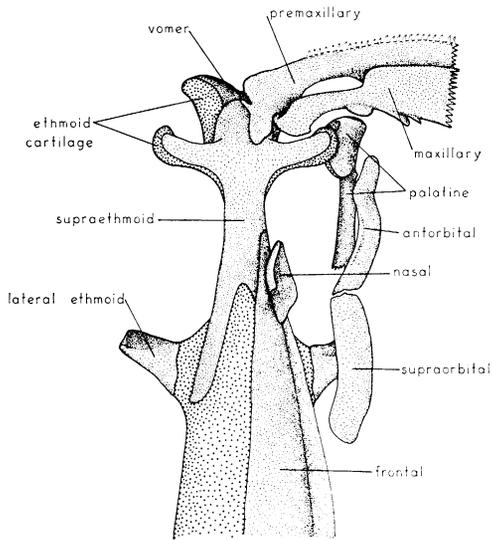
FIG. 21. Snout region of *Maurolicus muelleri*, SL 45.5 mm., USNM 201138. Dorsal view.

ethmoid plate has a slightly convex (slightly concave in one specimen) profile as seen in dorsal view. The ethmoid plate is continuous posteriorly with the anterior borders of the cartilaginous lateral ethmoid process. The supraethmoid is small, has a very reduced lateral process, and does not bear two posterior diverging processes that pass ventral to their respective frontals as in most stomiatoids. Instead it bears a single rectangular posterior process that is applied to the dorsal surface of the anterior end of the fused frontal bones. Capsular ethmoid bones are absent. The tectal cartilage is narrow and confined below the united frontals. The cartilaginous trabeculum communis is present above the parasphenoid for about one-half of the anterior length of the bone. A membranous interorbital septum attaches to the length of the trabeculum communis and extends dorsally to the frontal bones above the orbit. A ventral ethmoid and myodome bone are present. The
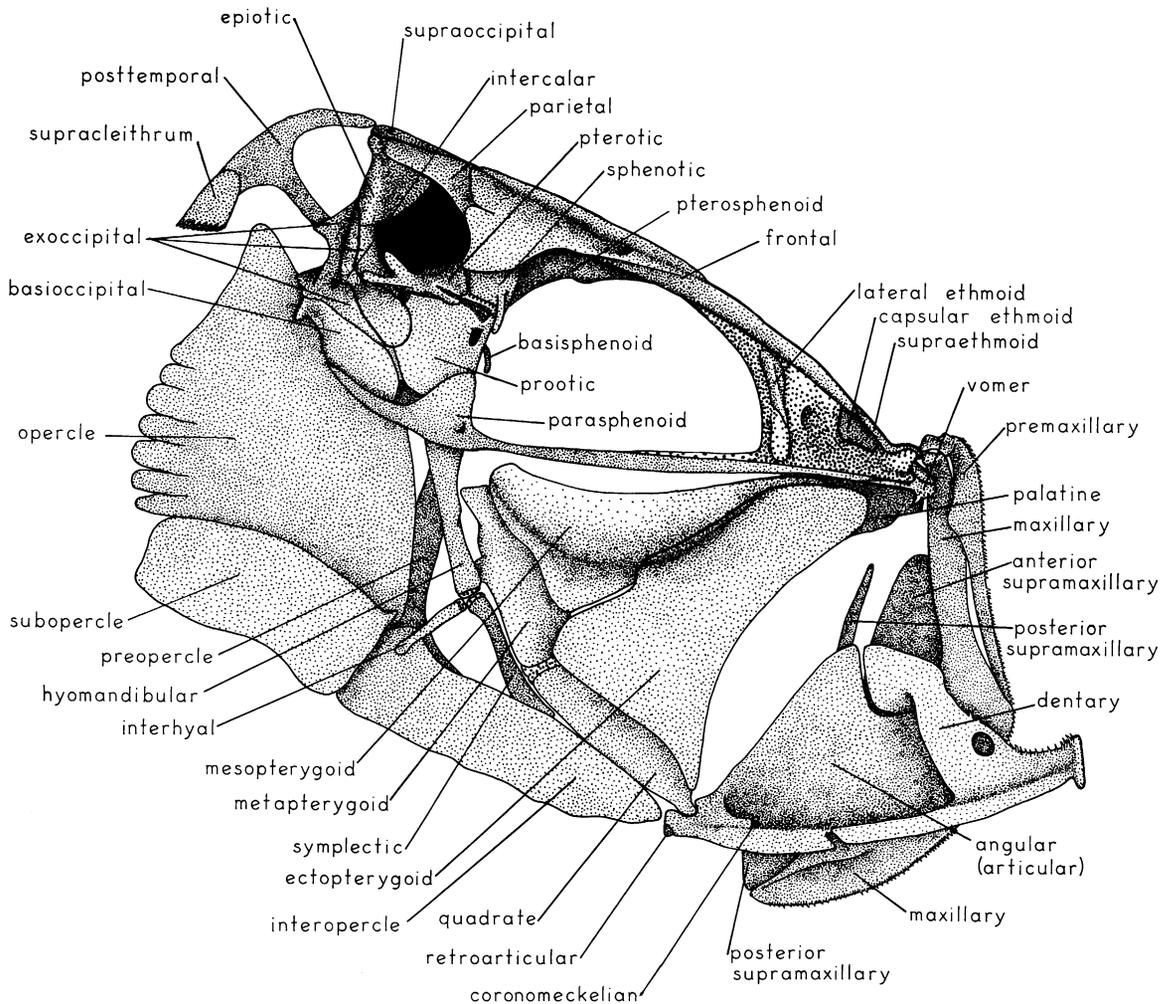
FIG. 22. Cranium and face bones of *Maurolicus muelleri*, SL 45.5 mm., USNM 201138. Lateral view of right side of cranium, medial view of left side of face bones.
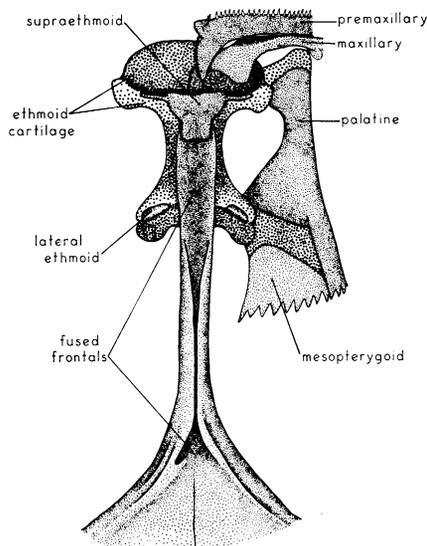
FIG. 23. Snout region of *Danaphos oculatus*, SL 34.5 mm., USNM 203261. Dorsal view.

lateral preorbital cartilages are relatively narrow and each is pierced by its respective olfactory foramen. The lateral ethmoid bone is small and appears as a perichondral cap along the dorsolateral border of each preorbital cartilage. The toothless vomer has a posterior shaft articulating with the anteroventral surface of the parasphenoid.

Valenciennellus tripunctulatus (fig. 25) is very similar to *Danaphos oculatus* and both have a reduced supraethmoid with its posterior process applied to the dorsal surface of the fused frontals. The lateral processes (fused proethmoids) are reduced to slender lateral spines. The interorbital space in *Valenciennellus* is not so narrow as that in *Danaphos*, and the anterior portions of the frontals, although partially fused over the orbits, diverge anteriorly as two lobes representing the original frontal bones of each side. *Valenciennellus*, like *Danaphos*, lacks other ethmoid bones including the lateral ethmoids, which are
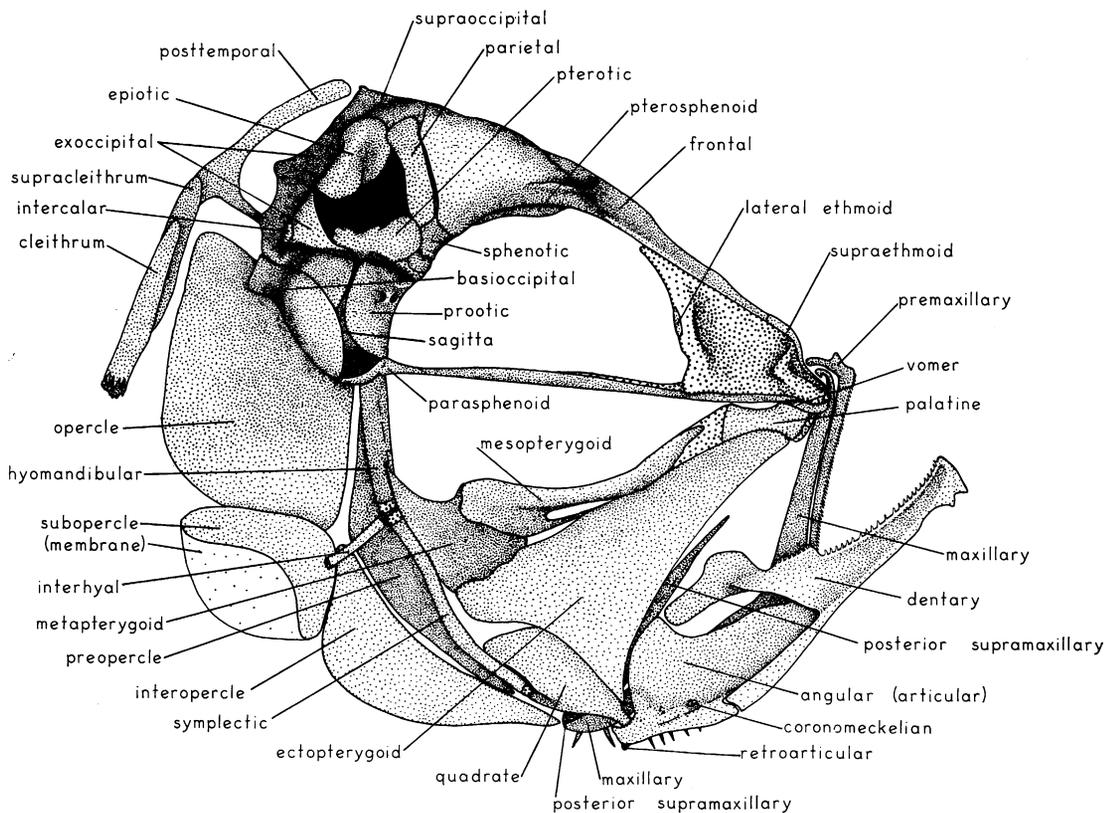
FIG. 24. Cranium and face bones of *Danaphos oculatus*, SL 34.5 mm., USNM 203261. Lateral view of right side of cranium, medial view of left side of face bones.
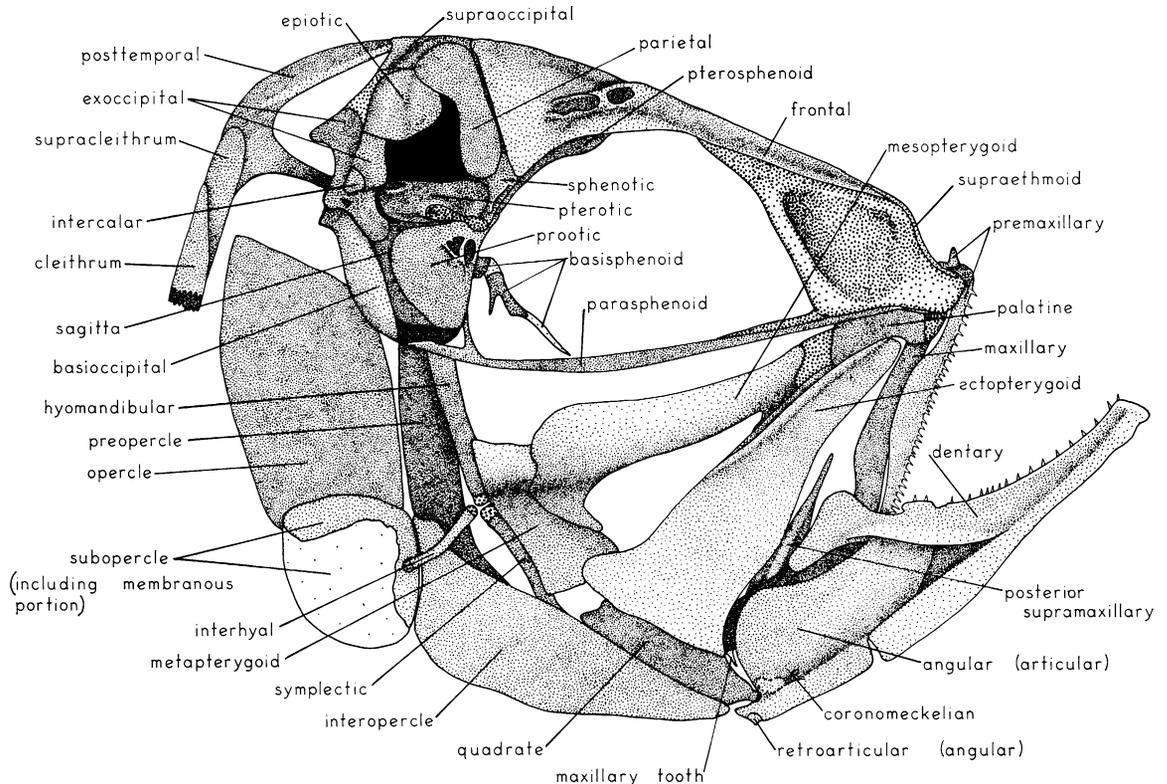
Fig. 25. Cranium and face bones of *Valenciennellus tripunctulatus*, SL 21.5 mm., USNM 203267. Lateral view of right side of cranium, medial view of left side of face bones.

present in *Danaphos*. All other features of the ethmoid region of *Valenciennellus* including the toothless vomer are so similar to those in *Danaphos* that they do not need further description.

Argyripnus atlanticus (figs. 26, 27) in dorsal aspect has a broad ethmoid plate that is somewhat concave in the anterior part of its dorsoventral profile. The anterior border of the ethmoid plate is covered by the dorsal anterior surface of the vomer. The cartilaginous lateral (prenasal) ethmoid processes are of moderate size and are continuous with the main body of the ethmoid cartilage behind the ethmoid plate. The supraethmoid is small (fig. 26) and almost without processes except for a slender anterior projection that rests on the cartilaginous ethmoid plate. The tips of each frontal lie dorsal to the respective short posterolateral process of the supraethmoid of each side. The tectal cartilage is broad and covers the dorsal region of the orbit

along the ventral surface of the frontal bones except at their lateral borders. A ventral ethmoid, myodome bone, and the capsular ethmoid bones are absent. The lateral preorbital cartilages are prominent and covered for a large part of their lateral surface by the lateral ethmoid. The vomer has a sharp, posterior shaft inserted along the ventroanterior surface of the parasphenoid. The vomer bears two or three teeth on each of its anterolateral processes.

Sonoda megalophthalma (fig. 28) is very similar to *Argyripnus atlanticus* but differs in having a shallow ethmoid region (compare depth of the ethmoid cartilages, figs. 27, 28) and in lacking a supraethmoid. Like *Argyripnus*, *Sonoda* lacks a ventral ethmoid bone, capsular ethmoid bones, and a myodome bone. The vomer in both genera is similar but that of *Sonoda* has three to six teeth in a transverse row on each vomerine lateral process. A cartilaginous trabeculum communis is present along the dorsal surface of

the anterior portion of the parasphenoid in both genera and forms the ventral attachment for the membranous interorbital septum.

Polyipnus asteroides (figs. 29, 30) has a very characteristic and specialized ethmoid region. The ethmoid cartilage, consisting of a deep, thick anterior ethmoid plate fused with lateral preolfactory cartilages (one on each side), is continuous posteriorly with the tectal cartilage and the cartilage of the lamina orbitonasalis. There is a thin, median longitudinal lamina of ethmoid cartilage contained within the capsular portions of the supraethmoid. The foramina (one on each side) for the olfactory nerves are extremely large in *Polyipnus* and lie between each lateral ethmoid and the supraethmoid (see fig. 29). The lateral ethmoids are extended ventro-anteriorly until they contact the lateral pre-olfactory ethmoid cartilages. The supraethmoid has a peculiar shape correlated with its function of forming a strong support, together with the lateral ethmoids, vomer, and parasphenoid, for the anterior ethmoid region. The capsular portions of the supraethmoid are large and each forms the lateral wall of a median vertical ethmoid plate. The posterior diverging processes of the supraethmoid are prominent and each extends beneath the anteromedian corner of its respective frontal bone. The vomer encloses the anterior portion of the ethmoid cartilage and extends dorsally along the mid-region to overlap the anterior end of the supraethmoid. The posteroventral portion of the vomer is enclosed by the ventral face and side of the parasphenoid at the anterior region of the orbit. Each lateral wing of the vomer bears a patch of three to four teeth. No other ethmoid ossifications exist in *Polyipnus*.

Argyropelecus aculeatus (figs. 31, 32) has a deep ethmoid cartilage and the supraethmoid bone is well ossified, of moderate size, and unlike other fishes in this study, not strictly perichondral. In view of the structure of the supraethmoid and capsular ethmoid bones of *Maurolicus* described above, the composition of the "supraethmoid" of *Argyropelecus* is in some doubt. (*Argyropelecus gigas* and *A. affinis* have the same type of ethmoid structure as in *A. aculeatus* described here.) The supraethmoid extends ventrally over the medial surface of the large excavations in the ethmoid cartilage for the nasal capsule. These extensions may represent capsular ethmoid bones and the whole supraethmoid may actually consist of

fused capsular ethmoid bones rather than a true supraethmoid. Although the capsular portion of the supraethmoid is perichondral, the dorsal portion dips ventrally into the ethmoid cartilage. In *A. gigas* and *A. affinis* a narrow median sulcus extends the length of the bone and is filled with ethmoid cartilage, obscuring much of the median anterodorsal portion of the supra-ethmoid from view. All other ethmoid ossifications are absent except the lateral ethmoids, which are rather well ossified and cover the dorsal portions of the lamina orbitonasalis. The vomer covers the anterior border of the ethmoid cartilage and is toothless in all species examined. The trabeculum communis is poorly developed although an interorbital septum is present and attaches to the anterior portion of the dorsal border of the parasphenoid. The tectal cartilage is thick and somewhat narrower than the combined width of the frontals. The foramen for the olfactory nerves pierces the lamina orbitonasalis along the medial border of the lateral ethmoid and part of that bone forms the lateral wall of the foramen.

Sternoptyx diaphana (figs. 33, 34), like *Argyropelecus*, has a very deep ethmoid cartilage but is peculiar in lacking all ethmoid ossifications including the lateral ethmoids and vomer. The lamina orbitonasalis is of moderate thickness but is long in its dorsal to ventral dimensions. The excavations for the nasal capsules are shallow and each is pierced by the olfactory foramen in its ventroposterior area. The tectal cartilage is continuous with the dorsal region of the ethmoid cartilage but is confined to a narrow strip below the joint line of the two rather broad frontal bones. The trabeculum communis is thick and covers the anterior half of the parasphenoid. The anterior broad border of the parasphenoid supports the ethmoid cartilage in the absence of the vomer.

FRONTAL AND PARIETAL BONES

The frontals are strong (insofar as this adjective applies to small, delicate fishes), functionally important bones in all genera examined here. The frontals plus the tectal cartilage form the main dorsal support for the ethmoid cartilage which serves to support the upper jaws. Frontal modifications in the fishes under consideration are primarily associated with the development of large eyes and a concomitant narrowing of the interorbital region. These fishes maintain the
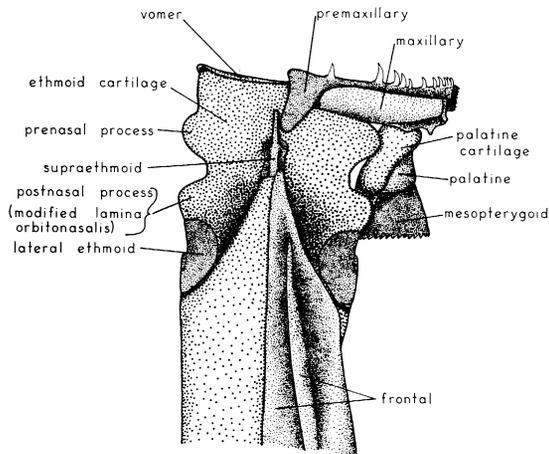
FIG. 26. Snout region of *Argyripnus atlanticus*, SL 57.0 mm., USNM 201351. Dorsal view.

supraorbital canal and the strength of this region in a variety of ways even when the interorbital area is greatly narrowed. All genera have a reasonably well-developed parietal, functioning as a protective cover and integral structural support for the dorsoposterior region of the cranium.

The frontal bones of both species of *Thorophos* (figs. 17, 18) are of smooth dermal bone. Each frontal has its anterior portion in the form of a deep longitudinal fossa for the reception of the supraorbital laterosensory canal, which is only partially covered by a crest of bone. The anterior elongate fossa in this bone helps to prevent the frontal from buckling under pressure applied dorsoposteriorly to the ethmoid region by the lower jaw or food objects in the mouth. The parietal in *Thorophos* is a smooth,
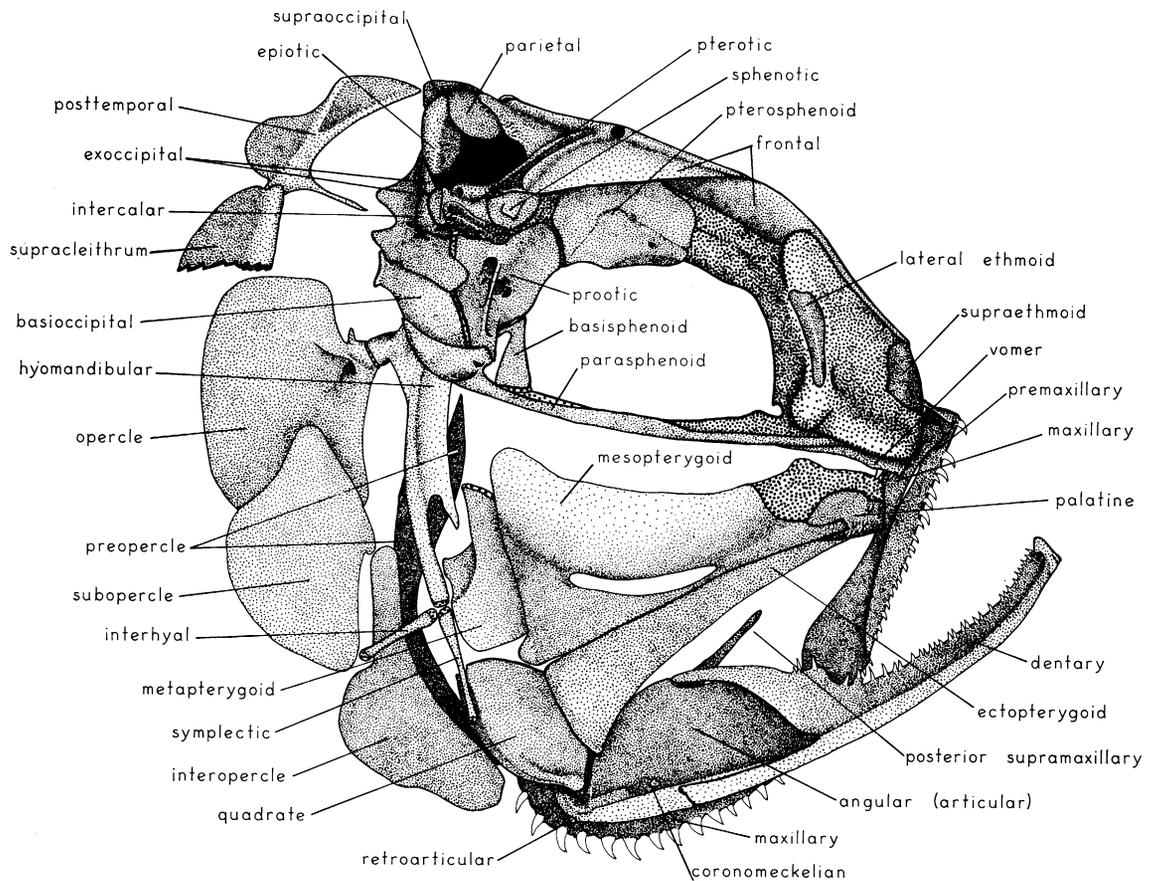
FIG. 27. Cranium and face bones of *Argyripnus atlanticus*, SL 57.0 mm., USNM 201351. Lateral view of right side of cranium, medial view of left side of face bones. Note: Dorsal end of preopercle is probably shown too far anteriorly in the drawing.
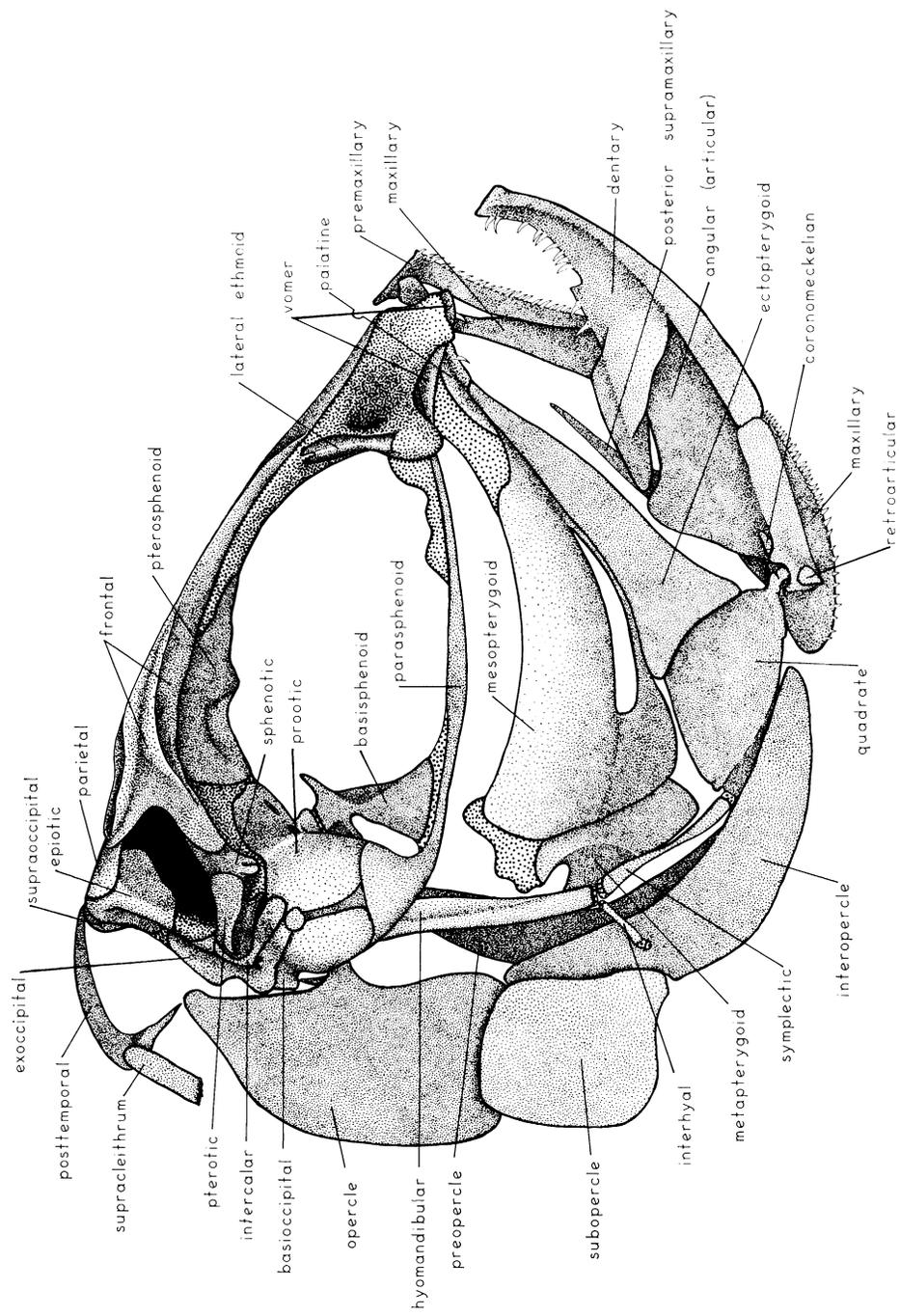
Fig. 28. Cranium and face bones of *Sonoda megalophthalma*, SL 53.5 mm., USNM 201350. Lateral view of right side of cranium, medial view of left side of face bones.
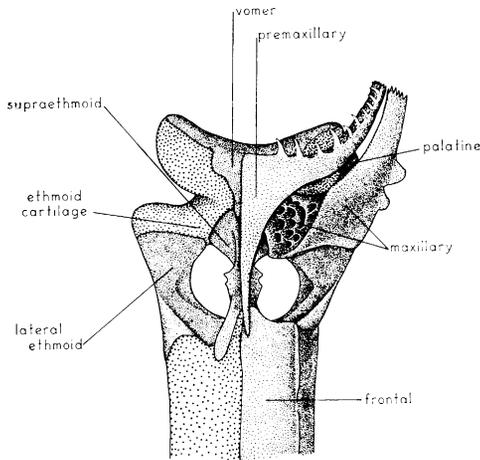
FIG. 29. Snout region of *Polyipnus asteroides*, SL 58.0 mm., USNM 197542. Anterodorsal view.

thin bone that has its anterior border ventral to the posterior border of the frontal. The antero-lateral border of the parietal contacts the anterior end of the pterotic internal to the postero-ventral end of the frontal. The parietal does not contact the sphenotic. Medially the parietals are separated from each other by the supraoccipital. The parietal contains no sensory canals. The frontal and parietal bones of *T. nexilis* do not differ significantly from the respective two bones in *T. euryops*.

Both species of *Araiophos* (figs. 19, 20) have frontals very much like those of *Thorophos*. The anterior longitudinal fossa is not so deep and the supraorbital canal is not enclosed in bone. The parietal of *Araiophos* is not so elongate laterally as in *Thorophos* and does not reach the anterior of the pterotic or the sphenotic. The parietals are
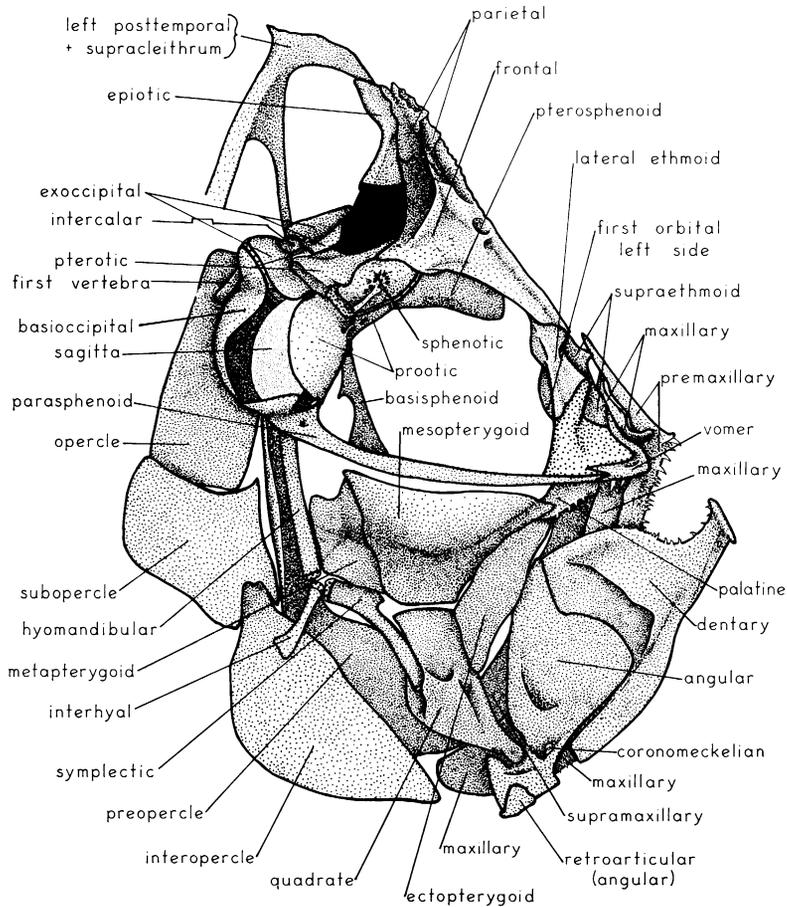
FIG. 30. Cranium and face bones of *Polyipnus asteroides*, SL 58.0 mm., USNM 197542. Lateral view of right side of cranium, medial view of left side of face bones.
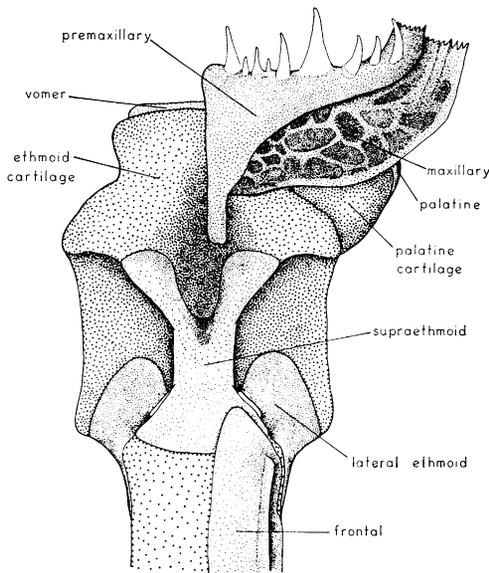
FIG. 31. Snout region of *Argyropelecus aculeatus*, SL 49.5 mm., USNM 179056. Anterodorsal view.

thin, simple bones without sensory canals and are separated by the supraoccipital.

In *Maurolicus muelleri* (figs. 21, 22) the anterior portion of each frontal over the orbit is in the shape of a deep, longitudinal fossa. The bone of the lateral border of this fossa extends over the mid-portion of the supraorbital canal and continues as an elongate bladelike ridge through the central region of the posterior portion of the frontal to the posterior termination of the frontal bone. This ridge considerably strengthens the frontal, but does not enclose the laterosensory canal completely. The parietal bone is smooth, without a laterosensory canal in its substance, and almost meets with its fellow of the opposite side over the anterior end of the supraoccipital. The parietal does not contact the pterotic but does contact the dorsoposterior region of the sphenotic beneath the posterior lateral wing of the frontal.

Danaphos oculatus (figs. 23, 24) has a very narrow interorbit, and the supraorbital region of the frontal bones of each side are fused to a single median tongue of bone that has its lateral edges rolled dorsally and inwardly to form an incompletely closed tube containing the supraorbital sensory canals. Posterior to the orbit the frontals of each side are not fused in the midline and the bone is smooth, abutting posteriorly on

the supraoccipital, parietal, and sphenotic. The parietal is elongate, extending in a lateral direction from the supraoccipital to the sphenotic and the anterodorsal border of the pterotic. The parietal and frontal bones abut one another, the frontal not being external or dorsal to the parietal as in most other stomiatoids. The parietals of each side are separated from each other by the supraoccipital.

The frontals of *Valenciennellus tripunctulatus* (fig. 25) are not confined by as narrow an interorbital space as those of *Danaphos*. Nevertheless the interorbital space is narrow and the frontals are modified by partial fusion in the area dorsal to the orbital region. Like *Danaphos*, the anteriormost region of the frontals of *Valenciennellus* is flat, the longitudinal frontal fossa of each side being well developed only over the posterior region of the orbit. The parietal of *Valenciennellus* has approximately the same relationship to its surrounding bones as that in *Danaphos* (compare figs. 24, 25).

Argyripnus atlanticus (figs. 26, 27) has a deep longitudinal furrow along the center of the orbital portion of each frontal. The supraorbital canal lies in this elongate fossa and is partially covered by a thin longitudinal blade of bone. The supraorbital canal extends dorsoposteriorly and in part posteriorly over the posterolateral part of the frontal that lies external to the sphenotic and continues in a long canal in the frontal to the posterior part of the frontal that lies dorsal to the parietal. The parietal is relatively small, separated from its fellow of the opposite side by the supraoccipital, and relatively short, not extending laterally to contact the sphenotic or anterior portion of the pterotic.

Sonoda megalophthalma (fig. 28) has frontals and parietals very similar to those in *Argyripnus*, but there is no ventrolateral branch of the posterior part of the supraorbital canal within the frontal extending to the sphenotic region, and the parietal bone extends laterally a shorter distance than that of *Argyripnus* (compare figs. 27, 28). Although it cannot be seen in figure 28, the two parietals of *Sonoda* are separated by the supraoccipital.

Polyipnus asteroides (figs. 29, 30) has a relatively broad interorbital space and each frontal has a longitudinal ridge that is continuous with, but not fused to, a similar ridge on the parietal. The parietal ridge has a lateral component similar
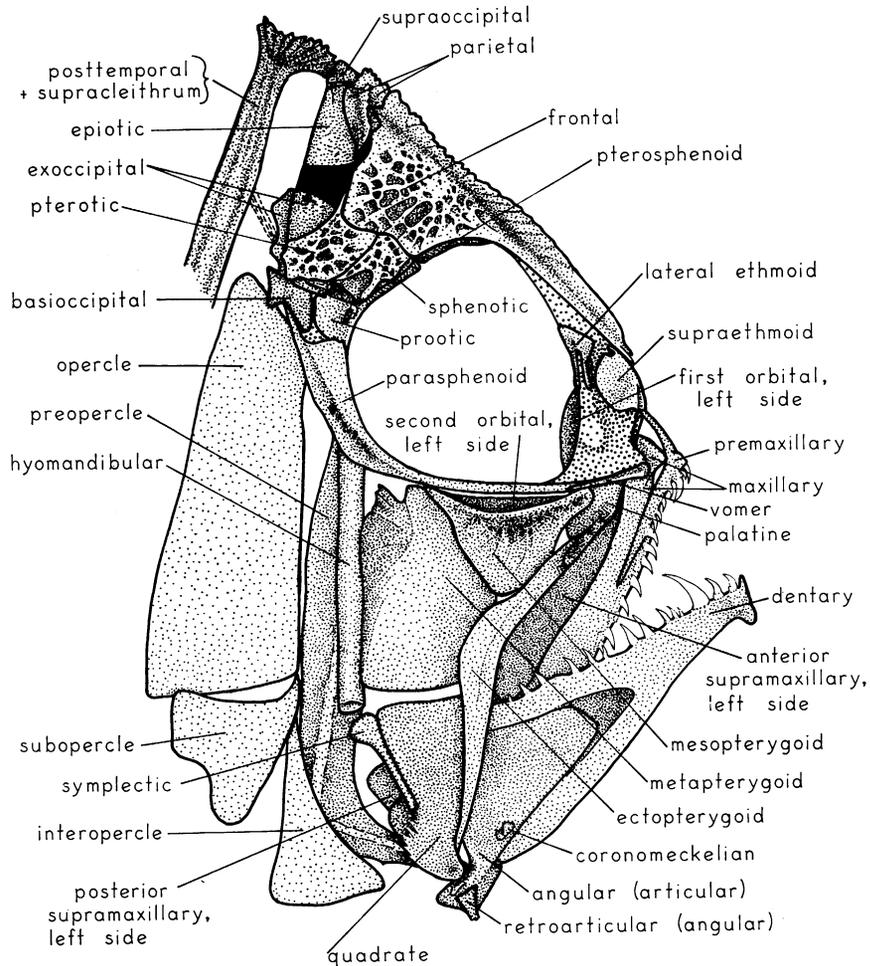
FIG. 32. Cranium and face bones of *Argyropelecus aculeatus*, SL 49.5 mm., USNM 179056. Lateral view of right side of cranium, medial view of left side of face bones.

to that in *Argyropelecus*. The frontal ridge of each side does not have a process that approaches its fellow of the opposite side as in *Argyropelecus*. The frontals and parietals are without the pits and small radial ridges found in *Sternoptyx* and *Argyropelecus*. The parietal of *Polyipnus* does not reach laterally to the sphenotic or the pterotic, and a large segment of the posterior border of the frontal inserts between these bones. The parietals are separated by the supraoccipital.

All species of *Argyropelecus* (figs. 31, 32, 35) have very large eyes and a very narrow inter-orbital space. Correlated with this, the frontals are greatly modified and a vertically oriented, median longitudinal ridge on each frontal is strongly developed, often forming a stronger support between the ethmoid region and the posterior part of the skull than the ventral, horizontally oriented part of the frontal. Together both frontals form a tube that is rather angular in cross section. The frontals are never fused as in *Danaphos* and *Valenciennellus*. Dorsal to the orbit, the longitudinal ridge of each frontal approaches but does not meet the other. In all the species examined the frontal ridges are braced against each other dorsal to the posterior part of the orbit by median projections that meet but do not fuse at the midline. The frontal ridges are continuous with and articulated with similar ridges on the parietal. The
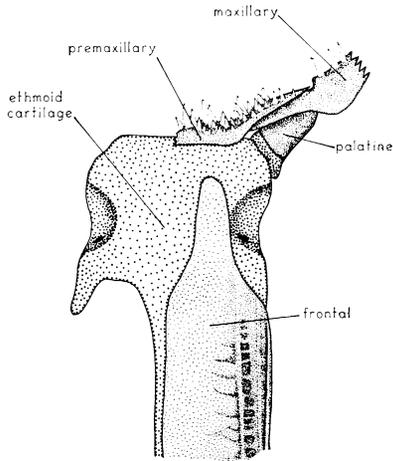
FIG. 33. Snout region of *Sternoptyx diaphana*, SL 44.0 mm., USNM 192843. Anterodorsal view.

broad posterior portion of each frontal is strengthened by radial ridges and pockets of bone. The parietals have a lateral ridge that is continuous with the posterior portion of the longitudinal parietal ridge. In *A. aculeatus* the lateral border of the parietal does not contact the sphenotic but contacts or closely approaches the anterodorsal process of the pterotic. In *A. gigas* and *A. affinis* the lateral anterior portion of the parietal closely approaches or contacts both the sphenotic and pterotic. The supraoccipital separates the parietals.

Sternoptyx diaphana (figs. 33, 34) has a frontal bone with a longitudinal ridge very similar to that of *Argyropelecus*, however, the interorbital region is not so narrow even though the eyes are very large. The longitudinal ridge of each frontal is not close to its fellow from the opposite
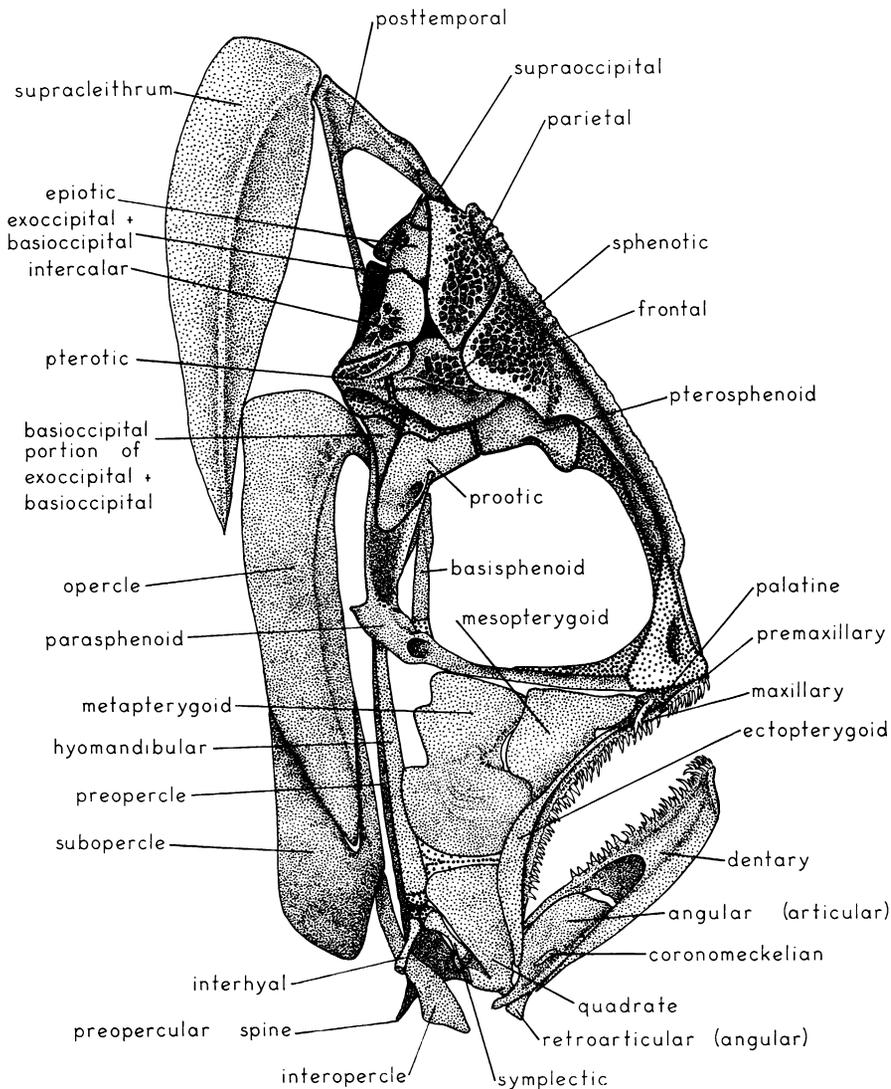
FIG. 34. Cranium and face bones of *Sternoptyx diaphana*, SL 44.0 mm., USNM 192843.
Lateral view of right side of cranium, medial view of left side of face bones.
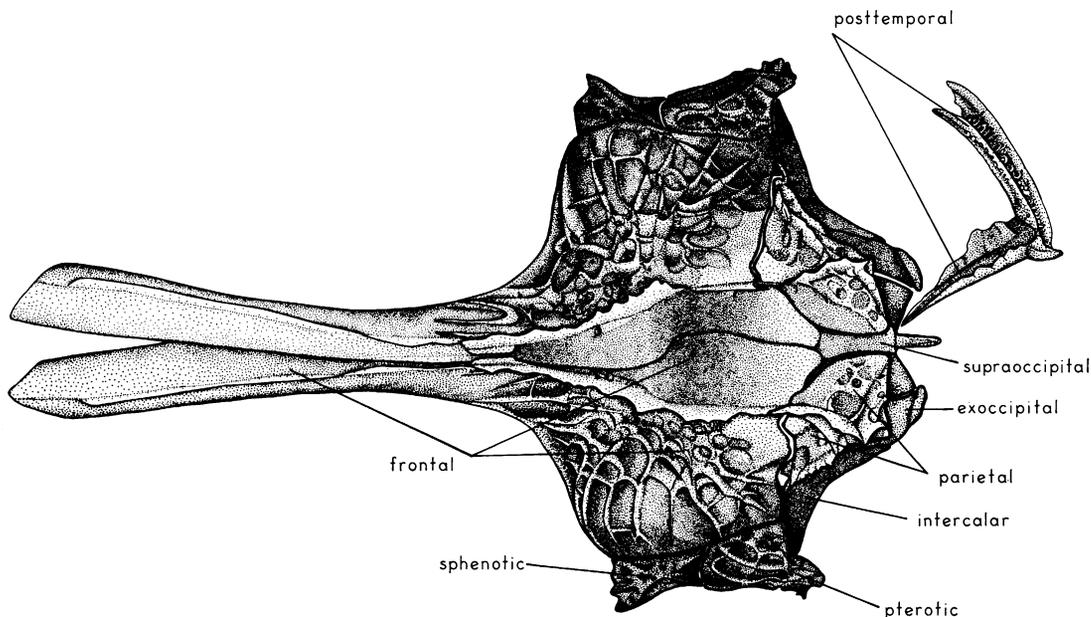
FIG. 35. Cranium of *Argyropelecus aculeatus*, SL 49.5 mm., USNM 179056. Dorsal view, snout not illustrated.

side and there are no connecting processes between the ridges. The parietal has a well-developed mid-longitudinal ridge but the lateral ridge is poorly developed and consists of a slightly better developed radial ridge between the pits and cavities that cover the surface of the parietal (as well as that portion of the frontal over the brain cavity). The lateral portion of the parietal extends to and slightly overlaps the sphenotic. The parietals do not contact the pterotic. The parietals are in contact with each other anterior to the supraoccipital.

POSTTEMPORAL FOSSA, OTIC, AND OCCIPITAL REGIONS

Weitzman (1967a) noted several osteological similarities and differences between osmerids and stomiatoids but did not discuss an important exoccipital-basioccipital relationship. In osmerids only the basioccipital forms a centrum-like facet for articulation of the first vertebra with the skull. In most, if not all, stomiatoids the exoccipitals take part in this joint by articulating with the tubular ligament between the first vertebra and the basioccipital. In paracanthopterygians and acanthopterygians exoccipital facets are present also. This may indicate that stomiatoids are related to para-

canthopterygians or scopelomorphs rather than to salmoniforms. In osmerids a pedicel-like process of each exoccipital abuts on the dorsolateral surface of the centrum-like portion of the basioccipital but does not form a posterior facet for articulation with the anterior vertebra. These pedicels lie lateral to the foramen magnum and expand into plates of bone that meet above the foramen magnum. In stomiatoids these exoccipital pedicels often meet at the midline over the basioccipital and form a bridge or shelf completely excluding the basioccipital from the foramen magnum. In addition, all gonostomatids, photichthyids, and sternoptychids have the posterior base and facets of the exoccipital pedicels enlarged at the expense of the basioccipital articular facet. Of the gonostomatid and photichthyid genera examined, *Polymetme* has exoccipitals most like those of the osmerids, the pedicels being only somewhat enlarged. In all gonostomatids, photichthyids, and sternoptychids the articular facets of the basioccipital and first vertebra retain the ligamentous connections found in most other teleosts in that there is a tubular ligament connecting the rims of one facet to the rims of the other. In stomiatoids, especially the Gonostomatidae, Photichthyidae, and Sternoptychidae, the exoccipital pedicels

contact the dorsolateral surfaces of the tubular ligament and are bound to the first vertebra by more extensive connective tissue than binds the usual teleost exoccipital pedicel to the first vertebra. Many stomiatoids have a considerable gap between the bony surface of the first vertebra and the exoccipital plus the basioccipital, thus improving the ability to move the head with respect to the vertebral column. The specialized stomiatoid relationship of the exoccipitals to this joint appears to be part of this mechanism for increased mobility of the head and is especially well developed in some of the Photichthya belonging to the superfamily Stomiatoidea.

The posterior region of the skull of both species of *Thorophos* (fig. 18) is not greatly different from that of *Vinciguerria* and *Polymetme* (see Weitzman, 1967a, figs. 8, 13). The large, open, laterally placed posttemporal fossa is bordered anteriorly for a short segment by the frontal, anterodorsally by the parietal, dorsoposteriorly by the epiotic, and ventrally by the pterotic. The bony cranial hiatus is filled with a sheet of cartilage (black in all figures showing the fossa). The exoccipital and sphenotic are excluded from the borders of the fossa and the exoccipital does not extend laterally and anteriorly far enough around the lower portion of the lateral vertical part of the cartilage enclosing the posterior vertical semicircular canal to reach the posterolateral border of the fossa. The exoccipital pedicels are quite large, covering about one-half of the centrum-like part of the basioccipital. The intercalar, somewhat difficult to observe, appears relatively small and not covering so large an area of the exoccipital or pterotic as in many teleosts, for example osmerids and many stomiatoids (compare figs. 5 and 6 in Weitzman, 1967a; figs. 2, 8, and 13 in Weitzman, 1967b; and figs. 18, 20, 22, 24, 25, 27, 28, 30, 32, and 34 of the present work). The intercalar process for attachment of the posttemporal ligament is near the pterotic. The otic bulla (saccular capsule) is large as is typical for relatively primitive stomiatoids and many salmoniform and myctophoid fishes (see Weitzman, 1967b, p. 528). Cartilage does not form a large part of the capsular wall as it does in some stomiatoids.

The prootic contains foramina for the fifth and seventh complex of cranial nerves, whereas the exoccipital contains a large foramen for the

ninth and tenth cranial nerves. This foramen is just medial to the intercalar bone.

Both species of *Araiophos* (fig. 20) have a posttemporal fossa very similar in size and position to that of *Thorophos*. However, the comparatively small size of the parietal allows the frontal to form a major portion of the anterodorsal border of the fossa and the small size of the epiotic and exoccipital allows cartilage to form most of the posterior border of the fossa. The pterotic is very elongate, extending anteriorly to contact the frontal in a broad joint. The sphenotic is extremely small and rests on cartilage of the chondrocranium. The exoccipital is moderately extensive and not unlike that of other relatively primitive stomiatoids. It forms a large part of the dorsoposterior face of the cranium and extends ventrally below those portions of the cartilage and pterotic bone covering the horizontal semicircular canal. The exoccipital maintains its contact with the prootic as it does in most fishes even though many of the endochondral skull bones in *Araiophos* are poorly developed. The exoccipital pedicels are well developed, articulate with the cranial-vertebral ligament, and meet in the middle below the foramen magnum. The intercalar is quite small and rests completely on the exoccipital. The posttemporal ligament to the intercalar attaches near the foramen for the tenth nerve. The otic capsule is large and part of its lateral wall is formed of cartilage owing to the relatively small size of the prootic. The cranium of *Araiophos* is mostly formed of cartilage. The dermal and endochondral bones are extremely thin, and incompletely ensheath the cartilaginous skull. The small size and weak development of the bones of the sexually mature specimens of both species indicate that these fishes are neotenous.

Maurolicus (figs. 22, 36), as in the genera discussed above, has a large posttemporal fossa. The dorsoanterior rim of this fossa is bordered by both the frontal and parietal, the posterior rim by the exoccipital and epiotic, and the ventral rim by the pterotic which is relatively short compared with that of *Thorophos* and *Araiophos*. The sphenotic, on the other hand, is relatively large and bears strong joints with the adjacent frontal, pterotic, pterosphenoid, and prootic. It also contacts the parietal and has a prominent sphenotic spine. As in most other stomiatoids, the exoccipital pedicels are well developed and articulate with the tubular
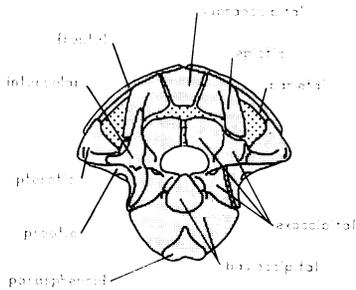
FIG. 36. Posterior cranial region of *Maurolicus muelleri*, SL 45.5 mm., USNM 201138.

ligament between the basioccipital and first vertebra. The intercalar is an extensive, thin bone covering a large part of the anterolateral portion of the exoccipital and extending anteriorly to overlie part of the prootic. The intercalar process for attachment of the post-temporal ligament lies about midway between the posterior end of the pterotic and the posterior articular facet of the basioccipital. The otic capsule is large but not excessively so and only a small portion of its wall is cartilaginous (compare fig. 18 of *Thorophos* and fig. 22 of *Maurolicus*).

Danaphos oculatus and *Valenciennellus tripunctulatus* (figs. 24, 25) have very similar post-temporal fossae. Each has the anterior border of the fossa occupied by the parietal, the dorsal border by the parietal and epiotic, the posterior border by the epiotic and exoccipital, and the ventral border by the pterotic. The sphenotic does not prominently enter into the border. The fossa is moderately deep and as in all the genera described here, not covered laterally by the parietal or by extensions of the pterotic. The exoccipital pedicels are well developed in both genera and articulate with the tubular ligament connecting the first vertebra and the basioccipital. The intercalar covers only a small portion of the exoccipital and in both genera the process for attachment of the posttemporal ligament to the intercalar is near the foramen for the tenth nerve. Both *Danaphos* and *Valenciennellus* have a large otic capsule moderately well covered by the prootic and basioccipital. In *Danaphos* the anterior portion of the exoccipital covers more of the otic capsule than it does in *Valenciennellus*.

The closely related genera *Sonoda* and *Argyripnus* (figs. 27, 28) have large, laterally placed posttemporal fossae bordered by the parietal, frontal, pterotic, exoccipital, and epiotic. In

Sonoda megalophthalma the sphenotic also forms part of the border of the posttemporal fossa. In both genera the cranial hiatus is filled with a sheet of cartilage. The intercalar is of moderate size (larger in *Sonoda*) and the process for the attachment of the ligament to the ventral process of the posttemporal is very medial, near the foramen for the tenth nerve, which is enclosed by the exoccipital. Both *Sonoda* and *Argyripnus* have the typical primitive stomiatoid arrangement of the basioccipital and exoccipital in the vicinity of the foramen magnum and first vertebra. The exoccipital pedicels of both genera are large and extend posterior to the basioccipital. They also meet in the midline above the basioccipital. The saccular otic bullae are large in both genera, especially *Sonoda*, and the basioccipital forms a large part of their posterior and lateral walls.

The otic-occipital regions of *Polyipnus asteroides* (figs. 30, 37), *Argyropelecus aculeatus* (figs. 32, 38), and *Sternoptyx diaphana* (figs. 34, 39) are characteristic, each for its own genus. In addition, all possess structural affinities, especially in the occipital region, that indicate these three sternoptychid genera are closer to one another than any one of them is to any other sternoptychid genus recognized here.
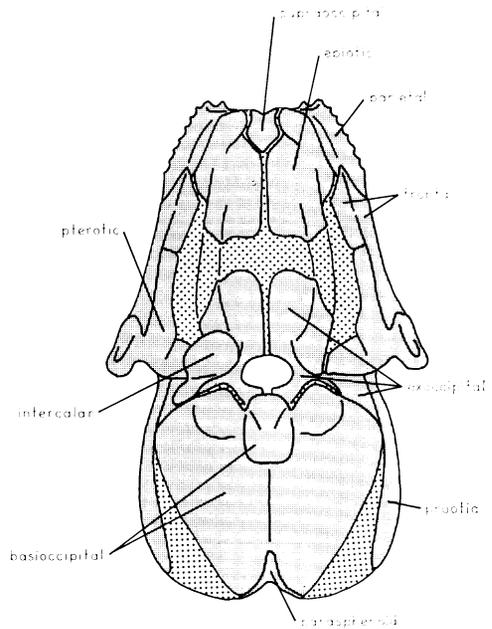
FIG. 37. Posterior cranial region of *Polyipnus asteroides*, SL 58.0 mm., USNM 197542.
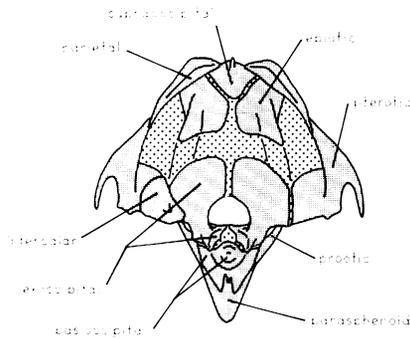
FIG. 38. Posterior cranial region of *Argyropelecus affinis*, SL 42.5 mm., USNM 203258.

Of the three genera, *Polyipnus* possesses the largest and most laterally placed posttemporal fossa (compare figs. 30, 32, 39), which has its anterior border delineated by a depression in the lateral surface of the frontal and parietal bones. The anterior edge of this depression is formed by a ventrolaterally extending, superficial frontal and parietal crest. The muscle of the posttemporal fossa takes part of its origin from this crest and from the depression. It then passes lateral to the epiotic, exoccipital, and intercalar. The intercalar bears a strong liga-
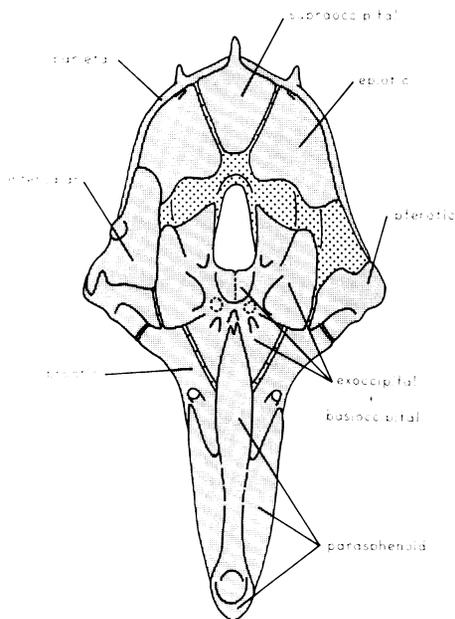
FIG. 39. Posterior cranial region of *Sternoptyx diaphana*, SL 44.0 mm., USNM 192843.

mentous attachment to the ventroanterior arm of the fused posttemporal+supracleithrum and lies over the dorsal surface of the exoccipital just lateral to the foramen and dorsal to that part of the otic bulla surrounding the asteriscus. The cartilage of the posttemporal fossa is bordered by the exoccipital, pterotic, frontal, epiotic, and to a small extent, the intercalar. The epiotic has a prominent posterodorsal process which, together with the stout but short exoccipital crest that it approaches, has a strong ligamentous attachment to the anterior tip of the dorsal process of the posttemporal and supracleithrum.

The posttemporal fossa of all species of *Argyropelecus* examined is smaller than in the species of *Polyipnus* and does not include a portion of the posterolateral surface of the frontal as in *Polyipnus*. The fossa is dorsoventrally elongate in *Argyropelecus* and includes a small segment of the posterolateral surface of the parietal. *Polyipnus* also has part of the posterolateral surface of the parietal covered by muscle of the posttemporal fossa. The fossa is bordered by the lateral ridge of the parietal and the dorsal border of the pterotic. The muscle mass of the fossa covers the epiotic, exoccipital, and intercalar. The intercalar bears a strong ligament attached to the fused posttemporal+supracleithrum at the area of the normal position of the ventral process of the posttemporal. The ventral process is not ossified in at least some species of *Argyropelecus*. The intercalar of *Argyropelecus* lies in a similar position to that of *Polyipnus* but more of it lies against the posterior surface of the exoccipital and pterotic and lateral to the area of the foramen magnum. In figure 32 of *Argyropelecus* the intercalar cannot be seen because it is medial to the posterolateral surface (see fig. 38). The epiotic does not bear a prominent posterodorsal process; however, it does have a small process (a similar process is present in most primitive stomiatoids) that is attached to the dorsoanterior process of the posttemporal by a relatively weak ligament. Most of the ligamentous attachments of the dorsal part of the posttemporal in *Argyropelecus* are from the moderately developed supraoccipital crest.

Sternoptyx diaphana and *Sternoptyx* sp. have a very modified posttemporal region and almost all evidence of the lateral portion of the posttemporal fossa is absent because of the posterior extension of the parietal and large size and position of the intercalar. The small lateral

crest of the parietal has no connection with the posttemporal fossa. Although a small part of the lateral skull wall associated with the common borders of the epiotic, parietal, sphenotic, pterotic, intercalar, and exoccipital remains cartilaginous, this area is not covered by the posttemporal muscle mass. The intercalar (figs. 34, 39) is extremely large and its lateral surface is pitted as in other exposed dermal bones. It bears a strong ligamentous attachment to the ventral arm of the posttemporal. Baird (1971, fig. 6D) labeled a bone the exoccipital. This bone is actually in the position of the intercalar in *Sternoptyx* except for a small ventral posterior segment which is more or less in the position of the exoccipital in specimens examined for this report. In *Polyipnus, Argyropelecus,* and *Sternoptyx* the intercalar is very dorsal in position. In most gonostomatids, photichthyids, and many teleosts, the intercalar lies against the exoccipital, ventromedial to the pterotic; however, a prominent dorsal extension of the intercalar covers parts of the exoccipital in many of the less advanced sternoptychids and some gonostomatids. In *Polyipnus* and *Argyropelecus* the ligamentous attachment of the intercalar lies in a more posterior and dorsal position and in *Sternoptyx* it lies dorsal to the pterotic. This shift in the functional position of the intercalar is undoubtedly correlated with the vertical lengthening of the head, body, and especially the pectoral girdle, which in *Sternoptyx* is extended dorsally more than in *Polyipnus* and *Argyropelecus.* The epiotic of *Sternoptyx* bears a very slender dorsal spinelike process (figs. 34, 39). Most of the strong ligamentous attachment of the posttemporal to the skull is through the stout supraoccipital crest but some fibers extend to the spinelike epiotic process.

The exoccipital-basioccipital relationship of the three most advanced sternoptychids, *Polyipnus, Argyropelecus,* and *Sternoptyx,* is complicated and modified from the gonostomatid condition. Each of these sternoptychid genera is modified in its own way and the area is highly dependent on, and indicative of, other specializations in the occipital-otic region such as the size of the saccular cavity, overall depth of the head, and relationships to the pectoral girdle. In this area *Argyropelecus* appears the most primitive and similar to the more primitive sternoptychid genera, like *Thorophos* and *Maurolicus.*

The exoccipital pedicels of *Polyipnus asteroides*

(fig. 37) and the other species of *Polyipnus* examined meet below the foramen magnum as a shelf just dorsal to the basioccipital. They do not fuse to each other or to the basioccipital. The shelf is modified to contact the dorsal portion of the anterior face and dorsolateral surfaces of the anteroposteriorly highly compressed first vertebra. The basioccipital articular facet is in close contact with the ventral portion of the articular facet of the first vertebra. The dorsolateral plates of each exoccipital extend dorsally, lateral to the foramen magnum. They contact each other through cartilage dorsal to the foramen. The lateralmost part of the dorsal portion of the exoccipital supports the ventral part of the posterior vertical semicircular canal and contacts the pterotic. Medially the dorsal portion of the exoccipital bears a large foramen (not visible in fig. 37) for the glossopharyngeal and vagus nerves, and just dorsal to these, supports the intercalar. Ventrally the exoccipital forms the dorsal roof of the enlarged lagenar bulla and contacts the basioccipital. The basioccipital is highly modified and primarily forms the posterior wall of the large saccular bullae. The centrum-like face of the basioccipital is very shallow, weakly ossified, and almost no more than a shallow fossa below the foramen magnum and exoccipital shelf. It lies in a posterior depression between the two saccular and two lagenar bullae.

All species of *Argyropelecus* show no external evidence of otic bullae and show less basioccipital modification than the species of *Polyipnus.* Nevertheless occipital modifications are present and, in certain respects, somewhat similar to those of *Polyipnus.* The exoccipital pedicels are modified into a shelf below the foramen magnum and the shelf itself articulates with the anterior face of the first vertebra. The dorsolateral exoccipital plates are very similar to those of *Polyipnus* and contact each other dorsal to the foramen magnum as they do in the less advanced sternoptychids (compare figs. 36, 37, 38). The intercalar lies on the posterior face of the exoccipital, and its position more nearly resembles that found in most gonostomatids and photichthyids. The basioccipital is prominent in lateral view and more nearly resembles that of most gonostomatids and photichthyids than in *Sternoptyx* or *Polyipnus.* The part of the basioccipital that articulates with the first vertebra is centrum-like in its structure.

Sternoptyx diaphana (fig. 39) and *Sternoptyx* sp. show no external evidence of otic bullae. *Sternoptyx* does have several occipital specializations carried to further extreme than the other sternoptychid genera. An exoccipital shelf is present, and the two halves of each side are fused by spicules of bone even though the dividing line between the two bones remains optically distinct. The exoccipitals are fused to the basioccipital and the centrum-like portion of the basioccipital appears very small, most of the articulation with the first vertebra taking place through the exoccipital shelf. The intercalar forms a large, lateral surface bone immediately dorsal to the pterotic and occurs in a position normally occupied by the posttemporal fossa and its muscle. The muscle masses in this region of *Sternoptyx* are confined to the posterior face of the cranium. The pterotic is comparatively small and the sphenotic is proportionally large in *Sternoptyx* when these bones are compared with those of *Polyipnus* and *Argyropelecus* (compare figs. 30, 32, 34). The sphenotic nearly contacts the intercalar in *Sternoptyx*, whereas it does not even approach this bone in any other sternoptychid.

When the three related genera *Sternoptyx*, *Argyropelecus*, and *Polyipnus* are compared, one of the most striking cranial differences is the huge otic bullae in *Polyipnus* and the apparent total lack of bullae in *Sternoptyx* and *Argyropelecus*. This is directly correlated with a size difference in otoliths discussed below.

PARASPHENOID, BASISPHENOID, AND POSTERIOR MYODOME

The parasphenoid, basisphenoid, and posterior myodome area of the sternoptychid skeleton is somewhat variable among the genera but does help to define groups.

The parasphenoid of *Thorophos euryops* (fig. 18) and *T. nexilis* has a slight S-shape, the ventral surface being concave anteriorly and convex posteriorly. A trabeculum communis is present on the entire orbital length of the parasphenoid and terminates below the anteroventral base of the basisphenoid. The posterior portion of the parasphenoid terminates on the ventral surface of the basioccipital below the otic bulla. Two dorsal wings extend to contact the prootic above. These are separated by the foramen for the carotid artery. The basisphenoid is of moderate size and dorsally extends to contact

the prootics on each side at a point where the median prootic laminae extend medially to contact each other and form a roof for the posterior myodome. The myodome is extensive and relatively deep, reaching a level from the dorsalmost part of the basisphenoid and extending ventrally to the parasphenoid directly below. Posteriorly it extends from the anterior margin of the prootic and anterior parasphenoid wing to a midline point about one-half of the length of the otic bullae and at the level of their bases.

The parasphenoid of *Araiophos gracilis* and *A. eastropas* (fig. 20) is essentially straight in profile. Only the anterior dorsal parasphenoid wing is present and it contacts the prootic. The posterior process articulates with the basioccipital at the bases of the otic bullae. The ossified portion of the basisphenoid is small and the visible portion is completely shown in figure 20. A cartilaginous and/or membranous portion of the basisphenoid contacts the parasphenoid ventrally, and the lateral base of the myodome roof of the prootic dorsally. The myodome has boundaries and a shape similar to those of *Thorophos*.

Maurolicus muelleri (fig. 22) has a relatively straight parasphenoid that posteriorly combines the anterior and posterior dorsal wings with the prootic in one single wing that encloses the carotid foramen. The posterior process of the parasphenoid terminates at the posterior end of the otic bullae on the basioccipital. The basisphenoid is small; its bony portion does not contact the parasphenoid and the membranous or cartilaginous portion extending ventrally from the basisphenoid is weak and apparently disappears before reaching the parasphenoid. Dorsally the basisphenoid is firmly attached to the prootic shelves which roof the myodome. The posterior myodome as in the genera discussed above is in part confined to a space between the anteroventral portions of the otic bullae. The myodome is relatively deep and narrow.

The shaft of the parasphenoid of *Danaphos oculatus* (fig. 24) is very straight and the parasphenoid-prootic wings are poorly developed, forming a ventral cap for the otic bullae. They are not divided into anterior and posterior wings. The carotid foramen is enclosed by the substance of the parasphenoid bone. The posterior process of the parasphenoid terminates ventral to the otic bullae on the anterior median portion of the basioccipital. An ossified basisphenoid is absent and a mem-

brane or cartilage in its place could be detected in the alizarin specimens at hand. A prootic roof over the posterior myodome is well developed and the shape and position of this space is similar to that of the preceding species.

Valenciennellus tripunctulatus (fig. 25) has a parasphenoid that is slightly convex ventrally and possesses narrow anterior prootic or dorsal wings that contact the anterior borders of the prootics. The carotid foramen apparently lies just posterior to the base of the prootic wing of the parasphenoid. The posterior parasphenoid process rests primarily on the ventral surface of the cartilaginous otic capsule. A basisphenoid is present, ossified in two portions and the cartilaginous ventral end nearly contacts the parasphenoid. The dorsal, ossified end articulates with the bases of the prootic-myodome shelves, which are well ossified. The posterior myodome is confined to a space similar to that of the preceding genera but is relatively small.

The parasphenoid of *Argyripnus atlanticus* (fig. 27) and that of *Sonoda megalophthalma* (fig. 28) are very similar but the shaft is nearly straight in *Argyripnus* and is curved ventrally in *Sonoda*. This difference is correlated with the greater depth of the ethmoid region in *Argyripnus*. In both genera the dorsal prootic processes and the posterior process are modified into a cuplike structure that caps the ventral surface of the otic bullae. The cap is more extensively developed in *Sonoda* than in *Argyripnus*. A carotid foramen is present in *Argyripnus* but could not be detected in *Sonoda*. Both genera have a relatively large, well-ossified basisphenoid that is in firm contact with the parasphenoid. Dorsally in both genera the basisphenoid contacts the prootic along the prootic shelves. In *Sonoda* the lateral bases of the prootic shelves are modified more than in *Argyripnus*, *Thorophos*, *Araiophos*, or *Maurolicus* for contact with the basisphenoid. At its ventral base, each prootic shelf sends a process ventromedially to contact its respective dorsolaterally projecting process of the basisphenoid. The myodome of both *Sonoda* and *Argyripnus* is relatively small when compared with *Thorophos* or *Maurolicus*.

The pterosphenoids of all sternoptychid genera except *Sonoda*, *Argyripnus*, *Polyipnus*, and *Sternoptyx* do not show extensively in lateral view. Both *Sonoda* and *Argyripnus* have a large pterosphenoid that projects relatively far ventrally into the interorbital space.

All species of *Polyipnus* (see fig. 30 of *P. asteroides*) have a relatively flat parasphenoid, being only slightly convex ventrally. This is undoubtedly correlated with the extremely large otic bulla posterior to it and to which it is attached. As in *Sonoda* and *Argyripnus*, *Polyipnus* has the prootic dorsal wings and posterior basal process of the parasphenoid modified into a cuplike structure covering the anterior ventral part of the otic bullae. The carotid foramen appears to lie on the shaft of the parasphenoid just slightly anterior to the cup. Although the cuplike structure of the posterior end of the parasphenoid suggests that of *Sonoda* and *Argyripnus*, in *Polyipnus* it is more of a bilobed cup with a depression between the lobes. The depression contains a median ridge continuous with the parasphenoid shaft anteriorly. The posterior myodome has boundaries similar to those of *Sonoda* and *Argyripnus* but its antero-posterior dimension is relatively small and its dorsoventral length relatively long. *Polyipnus* approaches *Sonoda* and *Argyripnus* in features that are correlated with the large size of the otic bullae. The basisphenoid of *Polyipnus* forms a firm buttress between the anterior roof of the myodome and the parasphenoid. The pterosphenoid enters into the support of the median orbital wall and is prominent in a lateral view, as in *Sonoda* and *Argyripnus*.

Argyropelecus aculeatus (fig. 32) has a strongly arched parasphenoid, its shape being dependent on the large eye, very deep head, and lack of otic bullae. The curve of the parasphenoid is a little less strong in *A. affinis* apparently because the otic bullae are large enough to influence the shape of the skull and because the head is relatively less deep. The larger relative eye size, which is correlated in some stomiatoids with a ventrally convex parasphenoid, does not seem to counterbalance the other two variables influencing the parasphenoid shape in *Argyropelecus affinis*. As the otic bullae are not obvious cranial features in any species of *Argyropelecus* the posterior end of the parasphenoid does not have a cuplike shape and consists of (1) a relatively strong single dorsal wing to the prootic and (2) a posterior process extending to and over the ventral surface of the anterior half of the basioccipital. The position of the carotid foramen is difficult to determine without dissection of fresh material but appears to lie in the parasphenoid somewhat posterior and dorsal to its

sharpest ventral angle amidst a group of pits and strengthening ridges in the bone. The posterior myodome is extremely shallow and the prootic shelves that form the roof of the myodome are almost vertical in position. The position of these shelves is not correlated with the presence of large otic bullae but appears more related to the great depth of the head and large eyes. The basisphenoid is absent and the pterosphenoid, although moderately extensive, has its flat surface at almost right angles to the long axis of the body and does not enter that part of the interorbital space between the eyes, instead forming the dorsal surface of the orbit below the posterior part of the frontal bone.

Sternoptyx diaphana (fig. 34) and *S. obscura* have an almost right-angle bend in the parasphenoid. External evidence of otic bullae is absent in *Sternoptyx* and the posterior end of the prootic contacts the cranium through the dorsal prootic wings (a single bilateral pair) and the posterior process that is applied to the postero-ventral surface of the basioccipital portion of the fused basioccipital and exoccipital. Peculiar to *Sternoptyx* is a large tube in the parasphenoid at its angle. This bony canal or tunnel contains a branch of the glossopharyngeal nerve and fibers of the autonomic nervous system of the head. These nerves enter the posterior opening of the canal and exit the anterior opening whereupon they extend to the first (anterior) gill arch. Branchial muscles are attached to the bony external surface of this canal. Also the anterior suspensory pharyngobranchial attaches to the parasphenoid near the anterior opening of the parasphenoid canal. A basisphenoid of moderate size is present and its cartilaginous ventral end contacts the parasphenoid. Its dorsal end splits into two columns of bone, each diverges laterally, and abuts the anterior edge of the prootic shelves of the myodome roof. The myodome is not so shallow or vertically oriented as it is in *Argyropelecus*. The prootic shelves of the myodome roof are nearly horizontal and the extent of the myodome dorsally into the cranium is greater than in *Argyropelecus*. The pterosphenoid is large and enters the inter-orbital space to a much greater extent than it does in *Argyropelecus*.

OTOLITHS

The usefulness of otoliths as indicators of relationships constitutes an interesting problem in the Gonostomatidae, Photichthyidae, and Sternoptychidae. The latter two families especially have species with specialized organs of hearing and balance, and part of the morphological evidence for this is expressed in the size and shape of the sagitta.

Study of stomiatoid otoliths from preserved specimens is often made difficult because apparently the preservative (either alcohol or formalin or both) alters the otolith. Frequently the otolith has the consistency of wet chalk and may be so friable as to crumble with the slightest touch of the forceps. Often the otolith is partially or even completely dissolved. In some cases, especially in *Polyipnus*, the otolith appears to have extraneous deposits of chalky material over its surface, giving the otolith a lumpy, abnormal appearance. For these reasons only otoliths collected from fresh, unpreserved specimens were used when available. Sometimes otoliths of preserved specimens were in excellent condition even though the fish and its otolith were small (for example *Danaphos* and *Valenciennellus*).

In some cases when a chalky otolith has not degenerated too far it can be saved. In the case of *Argyripnus* sp., USNM 135402 and *Thorophos nexilis*, USNM 151400, the relatively chalky otoliths appeared to retain their original shape. These were removed from the fish while still in alcohol. Each otolith was allowed to dry then sprayed with acrylic resin. After the resin hardened the otolith appeared to still retain its original shape and gained considerable structural strength, enough so that it could be easily manipulated and stored dry in a vial.

In the course of investigating partially dissolved otoliths, a membrane was discovered surrounding the chalklike remains of otoliths in *Polyipnus*, *Argyropelecus*, *Sternoptyx*, and *Argyripnus* (figs. 43B; 47A, B). So far as I am aware a membrane having the shape of the otolith and completely surrounding it is unreported in fishes. Such a structure should be expected because it probably is concerned with the deposition of otolith substance as a fish grows. The structure is called the otolith deposition membrane in the present paper and should not be confused with the otolithic membrane described for higher vertebrates or the membranous wall of the sacculus.

In order properly to understand and describe the sagitta of advanced sternoptychids it is
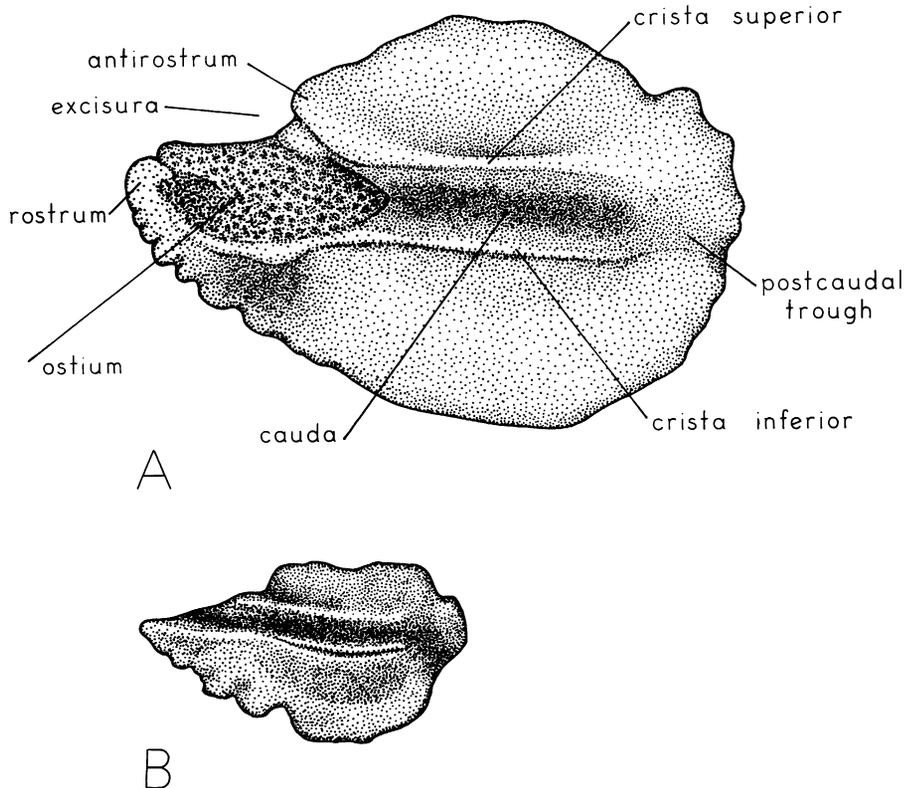
FIG. 40. Sagitta of: A. *Spirinchus thaleichthys*, SL 97.0 mm., USNM 104690. B. *Vinciguerria lucetia*, SL unknown. From an adult, collection of John Fitch.

necessary to describe the otoliths of relatively primitive photichthyids such as *Vinciguerria* and *Polymetme*. In addition, the sagitta of the osmerid genus *Spirinchus* is described because the osmerid otolith is of a relatively primitive teleost type. The otoliths of primitive gonostomatids such as *Diplophos* are similar to those of *Polymetme* and to those in the Osmeridae. They are relatively primitive teleost types.

The terminology for the parts of the sagitta follows Frizzell and Dante (1965). All otoliths are drawn to the same scale except that of *Ichthyococcus irregularis*, which is reduced compared with the others by about 25 percent. For comparative purposes measurements of otoliths are given for those specimens in which the standard length of the fish is known. Size comparisons are particularly important in the Sternoptychidae, especially in *Polyipnus*, *Argyropelecus*, and *Sternoptyx*.

A specimen of *Spirinchus thaleichthys* with a standard length of 97 mm. has a sagitta (fig. 40A) 3.3 mm. long and 2.1 mm. deep. The otolith is laterally compressed, the sulcus is straight and obviously divided into an ostium and cauda which are separated by a visible collum. Granular collicular substance lines the surface of the ostium. The cauda is smooth and bordered above and below by well-defined cristae. A shallow postcaudal trough is present that is deflected ventrally only a slight amount. The rostrum is very prominent, the antirostrum much less so. The ventral furrow is extremely shallow, whereas the dorsal furrow (dorsal to the cauda) is quite conspicuous.

Vinciguerria lucetia has a sagitta (fig. 40B) quite similar in lateral profile to that of *Spirinchus*. The otolith is laterally compressed but not so much as in *Spirinchus* and *Polymetme* (see below). The sulcus is nearly straight although the cauda is slightly bowed ventrally. The ostium and cauda are distinct and separated by a neck that con-
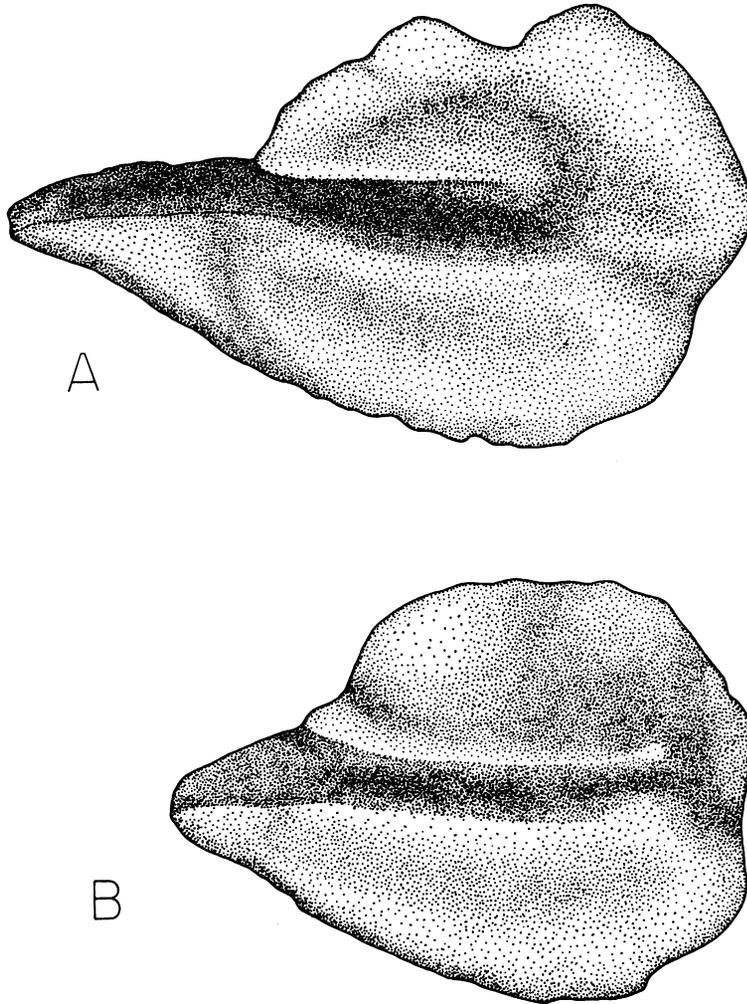
FIG. 41. Sagitta of: A. *Polymetme corythaeola*, SL 164.0 mm., USNM 203281. B. *P. corythaeola*, SL 170.0 mm., USNM 203281.

stricts the prominent cristae along their dorsal and ventral borders. The rostrum is very prominent and the antirostrum, although quite variable, is somewhat receding. A distinct, broad ventral furrow occurs below the cauda. A dorsal furrow is absent or extremely shallow.

One specimen of *Polymetme corythaeola* 164 mm. in standard length has a sagitta 3.7 mm. long and 2.4 mm. deep. Another specimen 170 mm. long has a sagitta 2.9 mm. long and 2.1 mm. deep. Figure 41 shows both of the above sagittae and these are reproduced here to give some concept of otolith variation in a single species. Dif-

ferences in the dorsal profile, distinctness of the cauda and ostium of the sulcus, position of the postcaudal trough, and length of the rostrum are obvious. Despite these differences, otoliths of *Polymetme* are characteristic of the genus when compared with the other genera described here. The otolith is laterally very compressed. The sulcus is straight or nearly straight. A well-defined crista superior is present but the crista inferior is present only as a low, rounded ridge. A shallow postcaudal trough is present and is deflected ventrally toward the posteroventral margin. Dorsal and ventral furrows are weakly
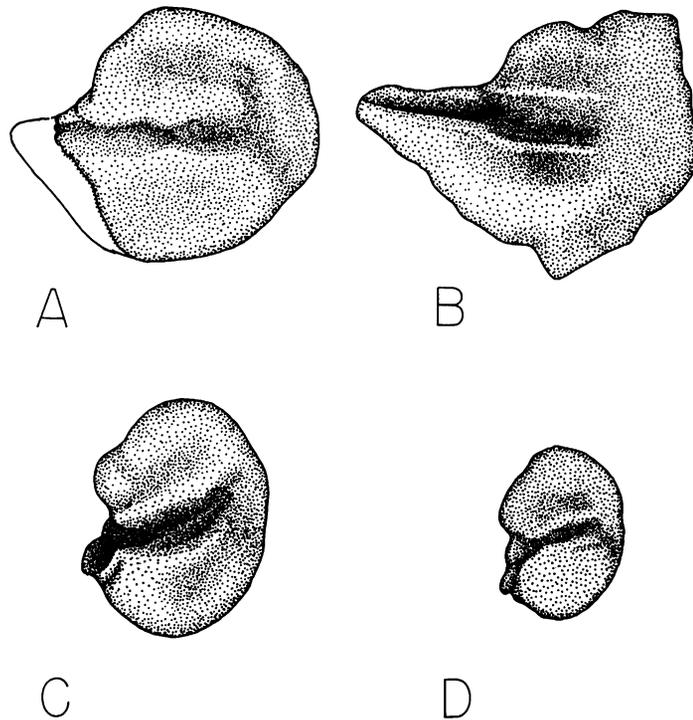
FIG. 42. Sagitta of: A. *Thorophos nexilis*, SL 67.0 mm., USNM
151400. B. *Maurolicus muelleri*, SL 45.5 mm., USNM 201138.
C. *Danaphos oculatus*, SL 34.5 mm., USNM 203261. D. *Valenciennellus
tripunctulatus*, SL 21.5 mm., USNM 203260.

developed. The rostrum is prominent, the anti-
rostrum inconspicuous.

The sagitta of *Thorophos nexilis* (fig. 42A) is
relatively discoid in profile and in a specimen
67 mm. in standard length measured 1.5 mm.
long by a little less than 1.3 mm. deep. The
otolith illustrated here was recovered from a
specimen preserved in alcohol for almost 59
years. It was dissected free, dried, and treated
with acrylic resin. The otolith appears in good
condition except for some erosion along the
margin ventral to the anterior tip of the rostrum.
The shape of the sagitta of another specimen
examined *in situ* was compared with the rela-
tively short rostrum illustrated in figure 42A.
The sulcus is essentially straight and there is a
slight constriction between the cauda and ostium,
which is smooth. Cristae appear to be absent. A
long, shallow postcaudal trough is present. The
anterior half of this trough is parallel with the
sulcus, the posterior half bends ventrally

toward the posteroventral margin. A dorsal
furrow is fairly obvious and appears continuous
with the postcaudal trough. A ventral furrow
appears little if at all developed. The rostrum or
what is left of it is short but stout and prominent
and the antirostrum not at all prominent on the
specimen illustrated, but is a sharply angled
eminence on the specimen examined *in situ*.

The sagitta of *Araiophos* was unavailable for
study, being dissolved in all specimens examined.

Maurolicus muelleri (fig. 42B) has a sagitta
shaped in profile very much like that of *Poly-
metme* and *Vinciguerria*. A specimen 45.5 mm. in
standard length has a sagitta 1.7 mm. long and
1.35 mm. deep. The otolith is laterally compres-
sed. The sulcus is almost straight and the ostium
and cauda are quite distinct and separated by a
small collum that is more like that of *Spirinchus*
than almost any other sternoptychid genus exam-
ined. The ostium is a deeper groove than the cauda
and its ventral floor cannot be seen in lateral
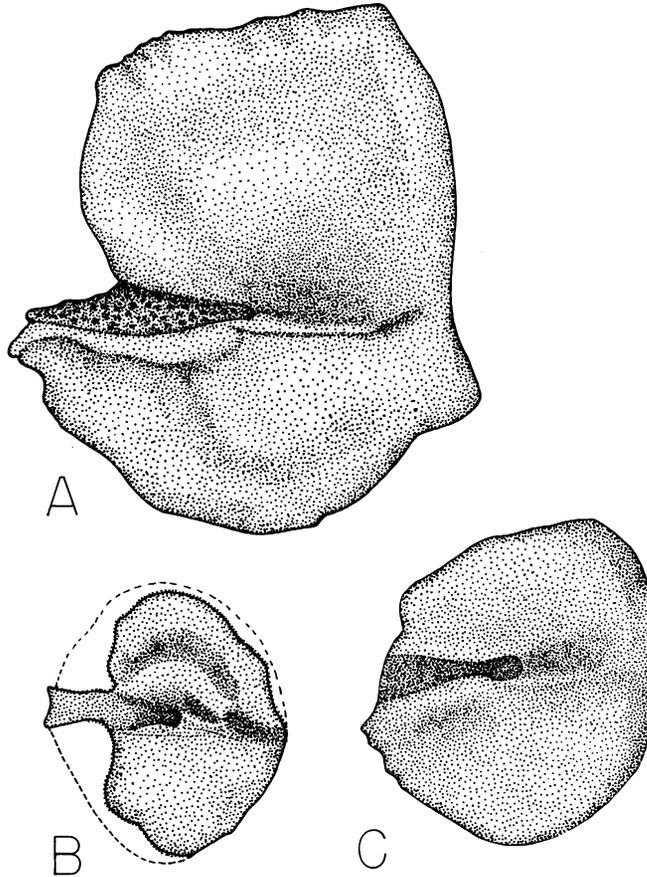
FIG. 43. Sagitta of: A. *Argyripnus* sp., SL 81.5 mm., USNM 135402. B. *A. atlanticus*, SL 57.0 mm., USNM 201351. C. *Sonoda megalophthalma*, SL 53.5 mm., USNM 201350.

view, being obscured by the ventral border of the ostium. Well-developed cristae occur along the dorsal and ventral borders of the cauda. A postcaudal trough appears absent, the region posterior to the cauda being almost flat. The rostrum is prominent; the antirostrum is receding. A ventral and dorsal furrow are present, each furrow quite shallow.

Danaphos oculatus (fig. 42C) has a deeper than long sagitta, a specimen 34.5 mm. in standard length having an otolith 0.8 mm. long and 1.1 mm. deep. The otolith is moderately compressed with its medial face rather flat, but its lateral face quite convex. The sulcus is somewhat curved and clearly divided into an ostium and cauda, which are separated by a collum. Cristae are present dorsal and ventral to the cauda but are not sharply defined. A very

shallow postcaudal trough is present and extends from the posteroventral region of the cauda toward the posteroventral margin of the otolith. The rostrum is prominent but does not extend anteriorly so far as in *Maurolicus*. The antirostrum is large and lies dorsal to the posterior region of the ostium. Dorsal and ventral furrows are present but quite shallow.

Valenciennellus tripunctulatus (fig. 42D) has a sagitta very similar in profile to that of *Danaphos*. A specimen 21.5 mm. in standard length has a sagitta 0.8 mm. deep and 0.5 mm. long. The otolith is relatively compressed and although its medial face is almost flat and sculptured, its lateral face is quite convex and very smooth. The sulcus is nearly straight and obviously divided into an ostium and cauda. The cauda has a deep anterior portion and a shallow

posterior portion. Cristae dorsal and ventral to the cauda are low and the furrows dorsal and ventral to the crista are quite shallow. A post-caudal trough is present and very shallow. The rostrum is relatively short and ventrally directed, the antirostrum is relatively prominent.

Fresh otoliths of *Argyripnus atlanticus* were not available, the only available specimens being partially dissolved (fig. 43B). In figure 43B the otolith deposition membrane is shown by the dotted line. Two specimens with partially dissolved otoliths were examined and both, although having an elongate rostrum as shown in figure 43B, were different from each other in their erosion. A specimen of *Argyripnus* sp. (fig. 43A) from off the Philippine Islands yielded an otolith that was not eroded. This otolith is a little deeper (2.5 mm.) than long (2.4 mm.) and came from a fish 81.5 mm. in standard length. The sagitta is laterally very compressed. The sulcus is straight and the ostium and cauda quite distinct. Granular collicular substance lines the surface of the ostium and there is a distinct collum separating the ostium and cauda. The cauda is bordered only by a ventral crista, the dorsal crista being absent. The deep surface of the cauda gradually merges with the medial face of the otolith dorsally. A small postcaudal trough is present. The rostrum is not very long but is prominent, whereas the antirostrum appears as a low prominence on the anterior dorsal margin. Ventral and dorsal furrows appear to be present but are very shallow.

The sagitta of *Sonoda megalophthalma* (fig. 43C) is laterally compressed and its major surfaces quite flat. A specimen 53.5 mm. in standard length has a sagitta 1.5 mm. deep and 1.3 mm. long. The otolith illustrated is not a fresh specimen but its surface appears not to be dissolved in any way even though the otolith was accidentally fractured by a light touch of forceps after the drawing was made. The sulcus is nearly straight. The ostium is constricted near its posterior end and then expands somewhat before terminating at a prominent collum. The cauda is very shallow, and a dorsal crista above it is absent, whereas the ventral crista is weakly developed. The rostrum is poorly developed, whereas the antirostrum is of moderate size. Dorsal and ventral furrows and the postcaudal trough are apparently absent or so shallow as to be almost unnoticeable.

The sagitta in *Polyipnus* (fig. 44A, B) is large (see also fig. 45C) and quite specialized in having an elongate, rather peculiar rostrum and a very deep body. There appear to be two similar types of otoliths in *Polyipnus*. *Polyipnus asteroides* (fig. 44A) exemplifies one type and may be described as follows: The sagitta is large, especially in its vertical dimension, this being greater than its anterior-posterior dimension. A specimen 56 mm. in standard length has an otolith 3.7 mm. in depth and 2.8 mm. in length. The otolith has a fairly flat medial face and a very convex lateral face so that when the structure is seen in dorsal view it appears hemispherical. The sulcus is well developed but relatively shallow and broad. It is not clearly divided into an ostium and a cauda. A crista is present ventral to the sulcus on the body of the otolith but not on the rostrum. This area of the sulcus on the body of the otolith probably is equivalent to the cauda. In *Spirinchus* and *Polymetme* for example, the ventral crista continues onto the rostrum, often to its tip. In *Polyipnus* the ventral crista ends at the dorsal base of the rostrum about where the dorsal crista ends in *Polymetme* and *Spirinchus*. Gross dissection reveals that the cristae define the border of the macula of the sagitta in *Spirinchus* and *Polymetme* (see fig. 45A). In these fishes the saccular ramus of the stato-acoustic nerve approaches the medial face of the sagitta, flattens and expands in an anterior and posterior direction, and the neurons terminate in the elongate macula that lies against the sulcus from the anterior tip of the ostium on the rostrum to the posterior end of the cauda. A portion of the nerve but not the macula covers the medial face of the antirostrum. In *Polyipnus asteroides* the saccular ramus of the nerve (fig. 45C) divides into two main trunks, one going to the rostrum, the other to the area of the sulcus on the body of the otolith. The macula is spread in a straight line from the anterior tip of the rostrum, along the rostrum posteriorly along the sulcus where the macula is enlarged as a flat disc occupying an area internal to and defined by the ventral crista which posteriorly arches upward and forward to end dorsal to the deepest portion of the sulcus. Obvious dorsal and ventral furrows and a postcaudal trough appear absent in the sagitta of *Polyipnus asteroides*. The rostrum is represented by a small projection anterior and
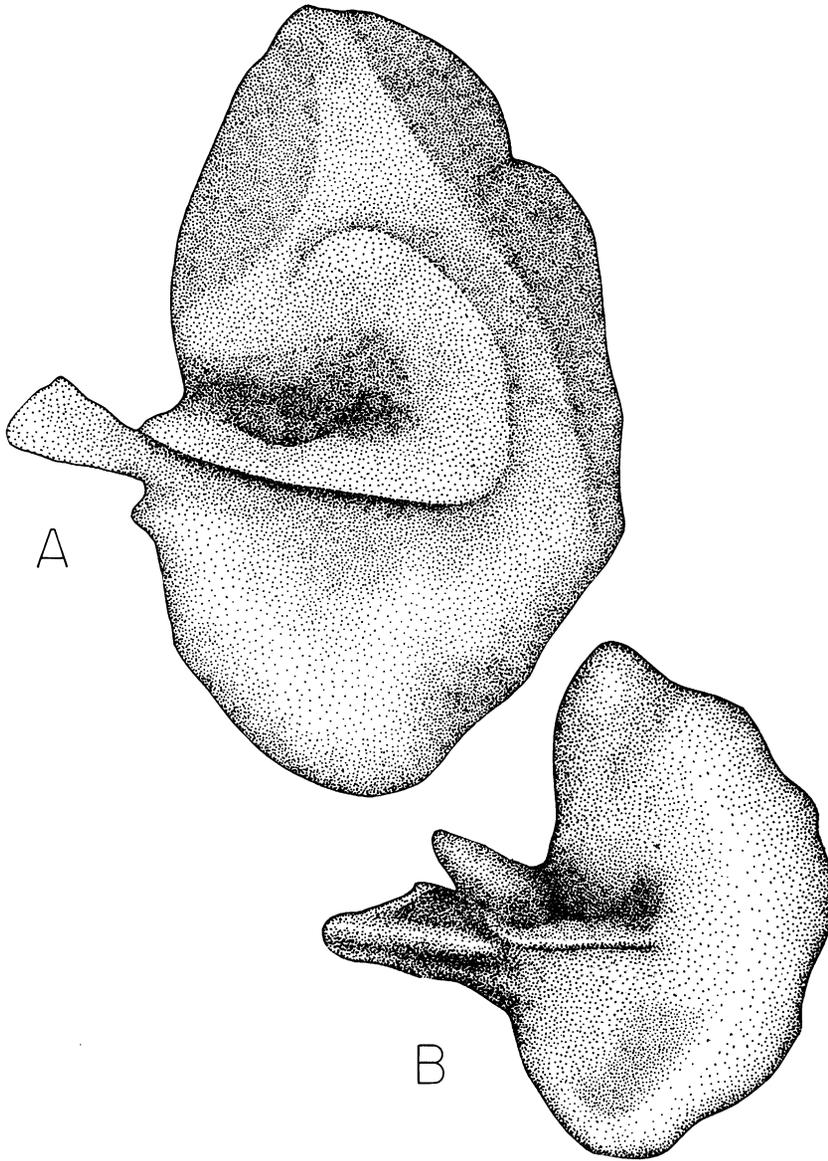
FIG. 44. Sagitta of: A. *Polyipnus asteroides*, SL 56.0 mm., USNM 297542. B. *P. aquavitis*, SL 35.0 mm., USNM 203345.

ventral to the excisura or anterior "opening" of the sulcus. No evidence of an ostium is present along the rostrum even though the macula of the anterior branch of the stato-acoustic nerve occurs along the rostrum. However, all specimens available had the rostrum somewhat eroded and presumably evidence of the ostium was lost. The antirostrum is represented by the

gentle curve of the anterior border of the otolith dorsal to the rostrum and excisura.

The other type of otolith is represented by *Polyipnus aquavitis* (fig. 44B). In this species a specimen 35.0 mm. in standard length has a large otolith 2.5 mm. deep by 2.5 mm. long. The otolith has a relatively flat medial face and a very convex lateral face. The sulcus is present,
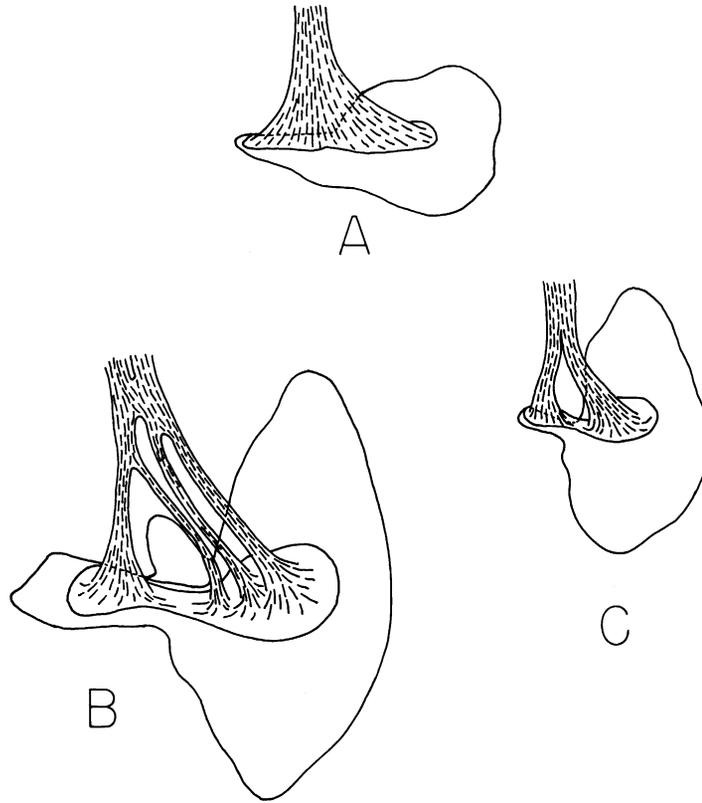
FIG. 45. Distribution of stato-acoustic nerve to sagitta in: A. *Polymetme corythaeola*, SL 160.0 mm., USNM 203281. B. *Ichthyococcus irregularis*, SL 65.0 mm., USNM 203289. C. *Polyipnus asteroides*, SL 62.0 mm., USNM 190472.

relatively straight and not clearly separated into an ostium and a cauda. There is a ventral crista present ventral to the sulcar area that is probably equivalent to the cauda. Anteriorly the crista bends dorsoanteriorly across the base of the rostrum and merges with a large conical process that is apparently part of the rostrum. This process is probably the same as the low eminence at the dorsal base of the rostrum in the sagitta of *P. asteroides*. This eminence is continuous with the ventral crista in *P. asteroides*. A deep groove occurs at the base of the conical process of the rostrum in *Polyipnus unispinus* and the posterior branch of the stato-acoustic nerve passes medially in this groove to expand over the macular area that fits into that area of the sulcus on the body of the otolith. The ventral process of the rostrum extends anterior to the

dorsal, conical process and has a groove that probably represents the ostium of the sulcus. The anterior branch of the stato-acoustic nerve supplies the macula in this area. The possibility that the large conical process of the rostrum represents the antirostrum seems remote considering the position of the stato-acoustic nerve and the ventral crista. The excisura, then, occurs just dorsal to the base of the dorsal, conical process of the rostrum. The antirostrum is represented by the gentle curve of the border of the otolith above the excisura. A shallow ventral furrow is present but a dorsal furrow and a postcaudal trough appear to be absent.

Ichthyococcus irregularis (figs. 45B, 46) has a very large sagitta very much like that of *Polyipnus* sp. A specimen 65.0 mm. in standard length has a sagitta 5.0 mm. deep and 4.5 mm.
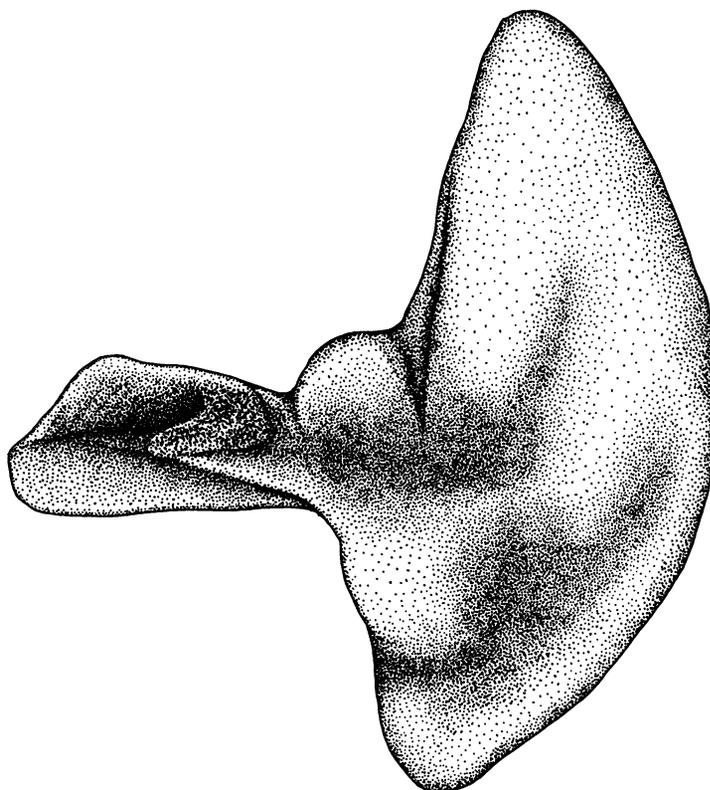
FIG. 46. Sagitta of *Ichthyococcus irregularis*, SL 65.0 mm., USNM 203289. This drawing is not at the same scale relative to the other otolith drawings in this paper, being reduced 25 percent.

long. The otolith body has a relatively flat medial face and a convex lateral face. The sulcus is curved in that the posterior portion extends dorsally along the central region of the body of the otolith. The sulcus is divided into an ostium and cauda in a somewhat more obvious fashion than in *Polyipnus*. The ostium is confined to the rostrum and has a roughened surface at the point where the nerve and its macula contact it. The medial face of the rostrum is concave and the midportion of this face is in contact with the macula. The cauda is a shallow furrow not bordered by cristae. The collum between the ostium and cauda occurs at the anterior base of the low, rounded, dorsal rostral process. This process is shown as a rounded eminence in figure 46; however, in some specimens it has the conical shape found in *Polyipnus* sp. and is shown this way in figure 45B. The posterior branch of the stato-acoustic nerve passes posterior to the

dorsal rostral process and medial to the low or almost absent antirostrum. Essentially it passes medially to the excisura. A ventral furrow is present and a postcaudal trough is absent.

Fresh otoliths of *Argyropelecus aculeatus* were not available and the otoliths were completely dissolved in all preserved specimens examined. Figure 47A is an outline drawing of the deposition membrane found within the saccular cavity of this species. The sagitta in this species is quite small and a specimen 54 mm. in standard length has an otolith deposition membrane about 0.6 mm. in its vertical dimension. Good specimens of the sagitta of *A. affinis* were available (fig. 47C) and may be described as follows: Sagitta of small size, about 1.6 mm. deep and 0.9 mm. long. Body compressed, lateral face somewhat convex, medial face relatively flat. A preserved specimen with a deposition membrane of this dimension was 66.0 mm. in standard
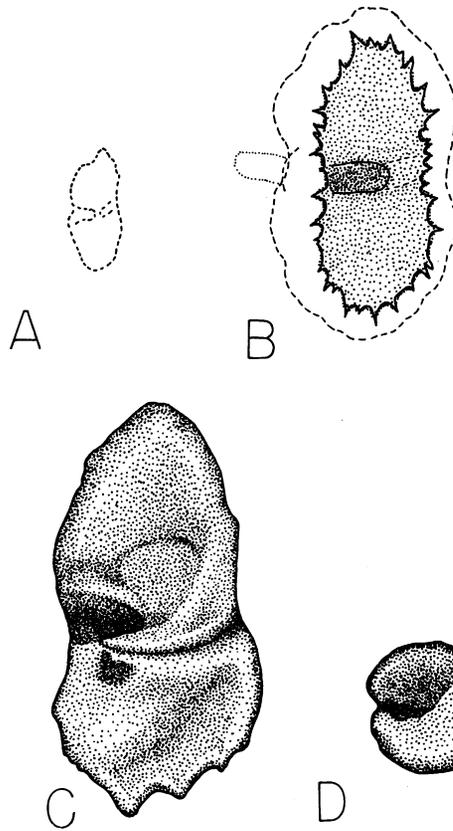
FIG. 47. A. Deposition membrane (dashed line) of sagitta of *Argyropelecus aculeatus*, SL 54.0 mm., USNM 192808. B. Deposition membrane and partially dissolved sagitta of *A. affinis*, SL 66.0 mm., USNM 203398. C. Sagitta of *A. affinis*, SL unknown, collection of John Fitch. D. Sagitta of *Sternoptyx diaphana*, SL 36.0 mm., USNM 203263.

length. A sulcus is present and in part is very deep in its lateral dimension, so deep that its lateral wall is very thin. This deep area represents the ostium, the cauda being represented by a shallow depression dorsoposterior to the ostium. The ventral edge of the cauda is bordered by a rather sharply defined, thick crista that extends to the posterior edge of the otolith. The anterior one-fourth of the crista occurs along the ventral border of the posterior half of the ostium. A postcaudal trough is not apparent. A rostrum is virtually absent and the antirostrum is represented by a low eminence of the anterior border of the otolith dorsal to the ostium. A ventral furrow is present but a dorsal one is apparently absent. Figure 47B represents a partially dissolved sagitta of *A. affinis* with its deposition membrane. The sagittae of *A. gigas*, *A. hawaiensis*, *A. lychnus*, *A. olfersi*, and *A. intermedius* are all essentially similar; however, there is some variation in the presence or absence of a ventral furrow and in the depth of the ostium. The pit may be absent in some specimens of *A. affinis* and is absent in the otoliths of the other species mentioned above.

Sternoptyx diaphana (fig. 47D) has a very characteristic, simple, small sagitta. A specimen 36.0 mm. in standard length has a sagitta approximately 0.7 mm. in depth and 0.65 mm. in greatest length. The rim or border is usually
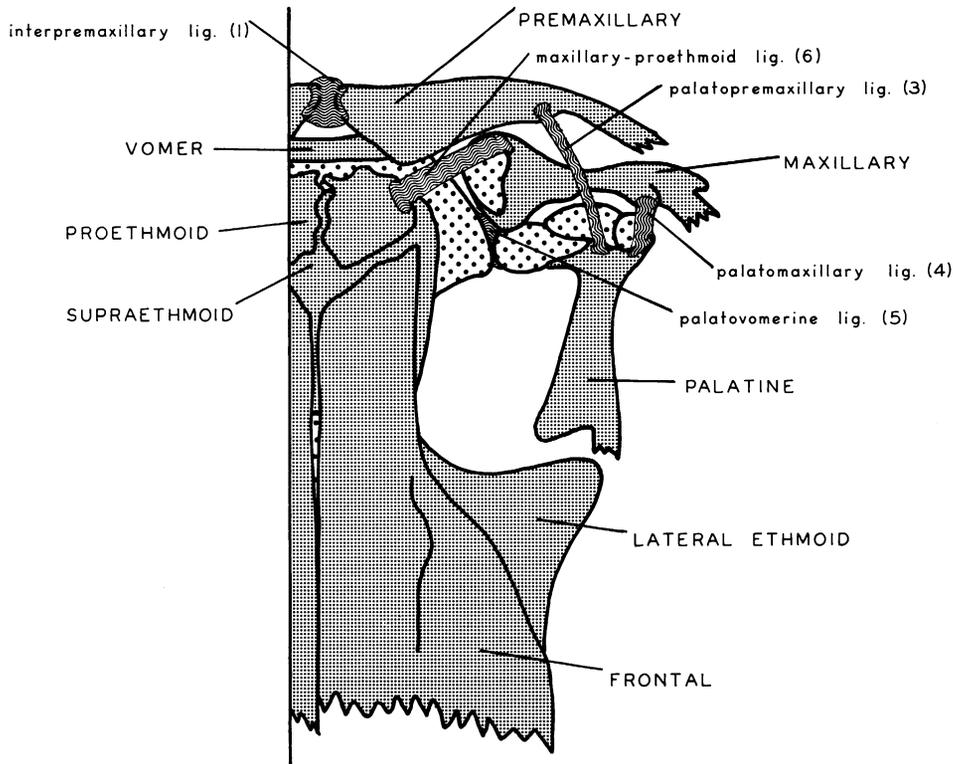
FIG. 48. Diagrammatic view of the dorsal surface of the snout region of *Spirinchus thaleichthys*, SL 108.5 mm., USNM 104689. Cartilage is shown by heavy dots and bone by small dots. Ligaments are shown by wavy lines.

circular in outline, and in one specimen the posterior vertical border was relatively straight. The medial face is relatively flat and the lateral face convex. The sulcus is suggestive of that of *Argyropelecus* with a very deep ostium, a shallow cauda, and an ill-defined border. Cristae, a postcaudal trough, and dorsal and ventral furrows are apparently absent. The rostrum and antirostrum are small, and the rostrum does not appear to have any part of the ostium on its surface.

UPPER JAW

The upper jaws of many of the genera under discussion have undergone a considerable degree of specialization and may be used to define, distinguish, and relate genera. In order to gain a proper perspective of the evolution in the jaws of maurolicids and sternoptychids it is necessary to review the structure of the jaws and their ligamentous attachments to the snout region in osmerids and some gonostomatids and photichthyids.

Osmerids and stomiatoids have a basic complement of about six to eight cordlike ligaments joining the palatine, premaxillary, maxillary, and ethmoid bones and cartilages. These ligaments and their associated articulations, bones, and cartilages vary considerably among the genera investigated here and provide useful information about relationships. In addition to the basic ligaments a fair amount of fibrous connective tissue is present joining the various bones and cartilages together. In specialized genera it seems probable that sometimes new cordlike ligaments have been formed from this fibrous connective tissue and at other times it appears more likely that new ligaments were formed by division and/or realignment of old ligaments.

The following basic, major ligaments and
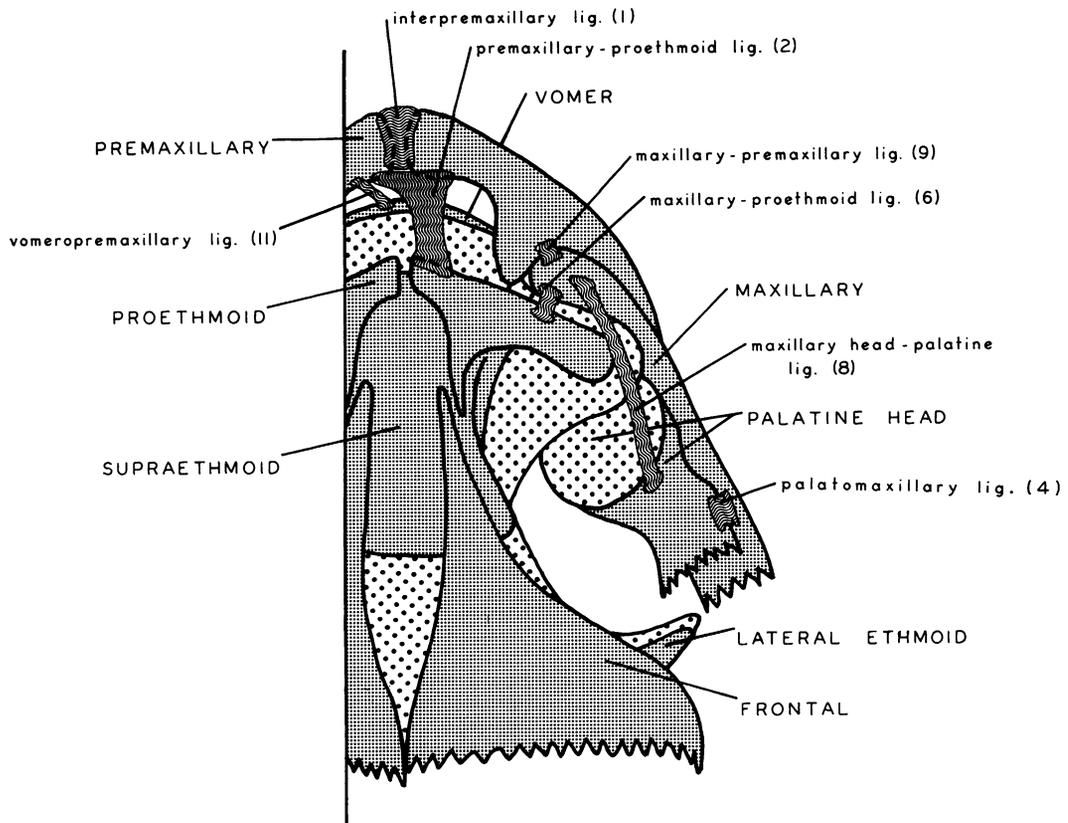
FIG. 49. Dorsal view of the ligaments of the snout region of *Polymetme corythaeola*, SL 61.0 mm., USNM 188236.

tendons were found in the fishes examined here: (1) The interpremaxillary ligament (fig. 48) binds the anterior premaxillary ends of each side together and is usually strongest between the anterior median tips of these bones. (2) The premaxillary-proethmoid ligament (fig. 49) attaches to the proethmoid or the proethmoid area of the supraethmoid. It or its modifications were only found in the Gonostomatidae, Photichthyidae, and Sternoptychidae. (3) The palatopremaxillary ligament (fig. 48) or some modifications of it was found in all osmerid genera examined and in many stomiatoid genera. It extends usually from somewhere on the dorsoanterior portion of the premaxillary, often over the lateral wing of the ethmoid, and then ventrally to attach to the dorsal area of the anterior head of the palatine. (4) The palato-maxillary (fig. 48) is usually a short ligament

extending from a prominence on the dorsal border of the anterior end of the maxillary to any of several points on the anterior portion of the palatine. (5) The palatovomerine (visible in figs. 48, 61 of *Polyipnus* where it is highly modified) is one of the strongest ligaments in the snout region and it or its equivalent is constantly present in all the fishes examined, even in the one genus (*Sternoptyx*) without a vomer bone. The ligament ordinarily extends from the ventromedial edge of the palatine head to the lateralmost portion of the vomer. (6) A maxillary-proethmoid ligament (figs. 48, 49) is present only in osmerids and the photichthyid genus *Polymetme* and extends from the anterior or lateral border of the proethmoid or proethmoid process of the supraethmoid to the medial anterior head of the maxillary. (7) The maxillary tendon (figs. 55, 57) is present in all genera
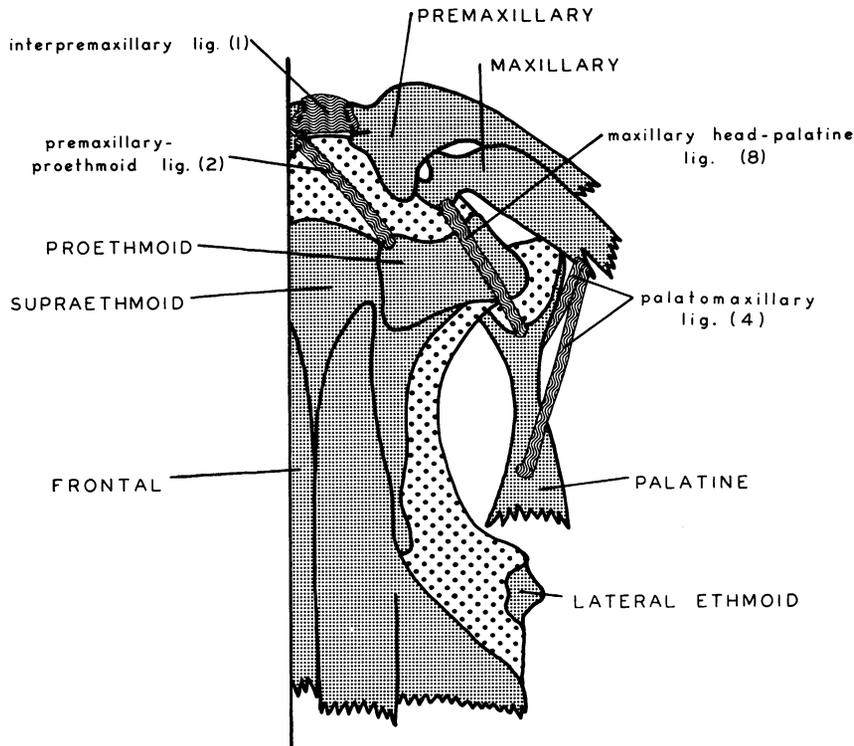
FIG. 50. Dorsal view of the ligaments of the snout region of *Vinciguerria lucetia*, SL 49.0 mm., USNM 201315.

examined and extends from the anterior dorsal border of the maxilla, usually from a process a short distance distal to the attachment of the palatomaxillary ligament. (8) A maxillary head-palatine ligament (figs. 49, 50) from the anteromedial maxillary head to the antero-dorsal part of the head of the palatine and (9) a maxillary-premaxillary ligament (fig. 49) from the anterodorsal portion of the premaxillary near the base of the ascending process to the dorsal surface of the head of the maxillary appear to be modifications of the palatopre-maxillary ligament. (10) The suspensory palatine ligament (fig.57) extends from the lateral ethmoid to the anterior portion of the palatine and may attach to the palatine in several places. (11) In one genus, *Polymetme*, a short cordlike ligament, the vomeropremaxillary ligament (fig. 49) extends from the antero-posterior border of the premaxillary in a ventro-median direction and attaches to the vomer. This ligament is apparently formed from loose

fibrous connective tissue extending between the vomer and premaxillary.

The basic ligament pattern and method of upper jaw attachment to the skull in stomiatoids is probably based on the type found in osmerid fishes. This was briefly described but not illus-trated by Weitzman (1967a, pp. 510–511). In order to point out the lines of specialization in jaw attachment in the Sternoptychidae, Photich-thyidae, and Gonostomatidae a more complete account and illustration is presented here. Compare figure 48 with figures 1 and 2 of Weitzman, 1967a, pp. 509 and 510. Of the 12 ligaments described above, *Spirinchus thaleichthys* (fig. 48) has seven. One of these, the maxillary-proethmoid (6) is characteristic of osmerids and some relatively primitive gonostomatids such as *Polymetme* (fig. 49). A strong interpremaxillary ligament binds the anterior ends of the pre-maxillaries together. The only other cordlike connective tissue binding the premaxillary to other skull bones is the palatopremaxillary (3),

a ligament well-developed in *Spirinchus* but extremely reduced or absent in some other osmerid genera (*Osmerus* and *Mallotus*). A ligament that plays a prominent role in attaching the premaxillary to the skull in gonostomatids, photichthyids, and sternoptychids, the premaxillary-proethmoid (2), is absent in all osmerids examined. However, there are moderately strong connective tissue fibers connecting the premaxillary to the proethmoid, supraethmoid, and vomer in osmerids. These probably form the "raw material" for development of the premaxillary-proethmoid ligament (number 2 or its various modifications) and the vomeropremaxillary ligament (11). The interpremaxillary may also contribute to the formation of these ligaments.

The maxillary-proethmoid ligament of *Spirinchus* (6), is very strong and binds the median head of the maxillary bone to the ethmoid region. The ligament is present in all osmerids examined but goes to a single median proethmoid in *Mallotus*. A strong, short palatomaxillary ligament (4) binds the anterior portion of the maxillary bone to the lateral part of the anterior head of the palatine in all osmerids examined. The palatovomerine ligament (5) firmly binds the anterodorsomedian head of the palatine to the lateral wing of the vomer in all osmerids examined. A maxillary tendon (7) is present as well as a suspensory palatine ligament (10). Both attach to their respective bones as described in the introductory list of ligaments and tendons above. Further description of this region can be found in Weitzman (1967a, pp. 510–511).

A relatively primitive photichthyid, *Polymetme corythaeola* (fig. 49), as an arrangement of upper jaw ligaments similar to those of *Spirinchus*. Although inspection of figures 48 and 49 shows that the ethmoid, premaxillary, maxillary, and palatine bones are somewhat altered (see Weitzman 1967a, p. 521, for a discussion), two characteristic osmerid ligament relationships remain. One is a short palatomaxillary (4) and the other is the presence of a maxillary-proethmoid ligament (6). The primary gonostomatid and photichthyid feature that has appeared is a premaxillary-proethmoid ligament (2). In *Polymetme* this ligament is broad, takes one of its attachments from the proethmoid, and extends primarily to the premaxillary of the same side but in part crosses its fellow of the opposite side

to attach to the contralateral premaxillary. This ligament varies greatly in the Gonostomatidae, Photichthyidae, and Sternoptychidae and some of its variations are described below. Another important innovation in *Polymetme* is the apparent alteration of the palatopremaxillary ligament (3) into two ligaments, a relatively long maxillary head-palatine ligament (8) and a short maxillary-premaxillary ligament (9). This pattern of ligaments 8 and 9 appears again in part in *Vinciguerria* (fig. 50) and in full in *Polyipnus* (fig. 61) and *Argyropelecus* (fig. 63). Another new ligament occurs ventral to number 2 in *Polymetme*. This is the vomeropremaxillary ligament (11). In addition to those ligaments just described, ligaments and tendons 1, 5, 7, and 10 are present. The last two are not visible in figure 49.

Another relatively primitive photichthyid *Vinciguerria lucetia* (fig. 50; Weitzman, 1967a) appears to have the upper jaw ligaments somewhat more modified than *Polymetme*. *Vinciguerria* has lost the osmeroid maxillary-proethmoid ligament (6) shown in figures 48 and 49 present in *Polymetme* and has greatly increased the length of the palatomaxillary ligament (4), a ligament that is very short in the osmerids and *Polymetme*. A strong interpremaxillary ligament (1) is present and the premaxillary-proethmoid ligament (2) consists of fibers crossing from the premaxillary of one side to the anteromedian border of the proethmoid of the opposite side. Thus the ligament of one side would cross that of the other if both ligaments were shown in figure 50. There may be a few ligamentous fibers joining the premaxillary and proethmoid of the same side but they do not form a strong ligamentous attachment. The palatopremaxillary ligament (3) is apparently modified to a maxillary head-palatine ligament (8). The palatomaxillary ligament (4) is long and consists of two parts, one extending to the dorsal surface of the shaft of the palatine and a second, shorter part to the ventral surface of the posterior part of the head of the palatine. Ligaments 5, 7, and 10 are well developed in *Vinciguerria* but are either not visible or not shown in figure 50.

The primitive sternoptychid ligamentous attachment of the maxillary, premaxillary, and palatine bones is well exemplified by *Thorophos euryops* (fig. 51) and *T. nexilis*, which have an unmodified palatopremaxillary ligament (3)
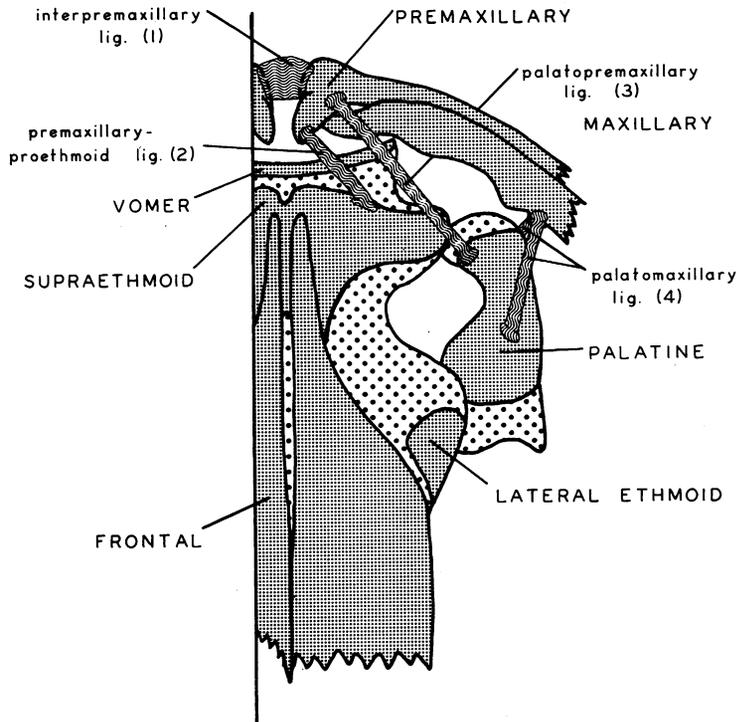
FIG. 51. Dorsal view of the ligaments of the snout region of *Thorophos euryops*, SL 44.7 mm., DANA 3736-VI.

and a long palatomaxillary ligament (4) similar to that described for *Vinciguerria lucetia*. The interpremaxillary ligament (1) is strongly developed and a maxillary-proethmoid ligament (6) is absent as it is in all sternopty-chids. The premaxillary-proethmoid ligament (2) is variable in sternoptychids but appears to be in its most primitive form in both species of *Thorophos* in which it extends from the medial ascending process of the premaxillary to the anterior border of the proethmoid process of the supraethmoid of the same side. Therefore the premaxillary-proethmoid ligaments of both sides do not cross in *Thorophos*. In addition, ligaments 5, 7, and 10 are present but not illustrated in figure 51. Both species of *Thorophos* exhibit the same ligament arrangement.

The upper jaws of *Thorophos euryops* and *T. nexilis* (figs. 18, 51–53) are very similar and the description below applies to both species except where noted. Each premaxillary has a moderate-ly long ascending process similar to that shown for *Araiophos* in figure 19. The premaxillaries and

maxillaries of both species are relatively slender and the maxillary is not angulate as in *Danaphos* or angulate and expanded as in *Maurolicus* (compare figs. 51, 56, 58). Bruun (1931, p. 288) in describing *Thorophos euryops* and Myers (1932, p. 61) in describing *Neophos nexilis* reported that the jaw teeth were uniserial in both. Examination of the specimens now at hand definitely shows two rows of teeth in the premaxillaries of each species (fig. 53) and therefore the genera cannot be separated on the basis of the number of tooth rows in these bones as attempted by Grey (1964, p. 85). See Appendix for a synonymy of *Thorophos* and *Neophos*. The premaxillaries do show differences in the two species, for there are almost 50 teeth in the small tooth row in *euryops* and 25 in *nexilis*. There are approximately 40 teeth in the large tooth row in both species. Of the two species, *T. nexilis* tends to have larger teeth in the premaxillaries of equivalent-sized specimens. This is especially noticeable in the small outer secondary tooth row. The teeth of this row are
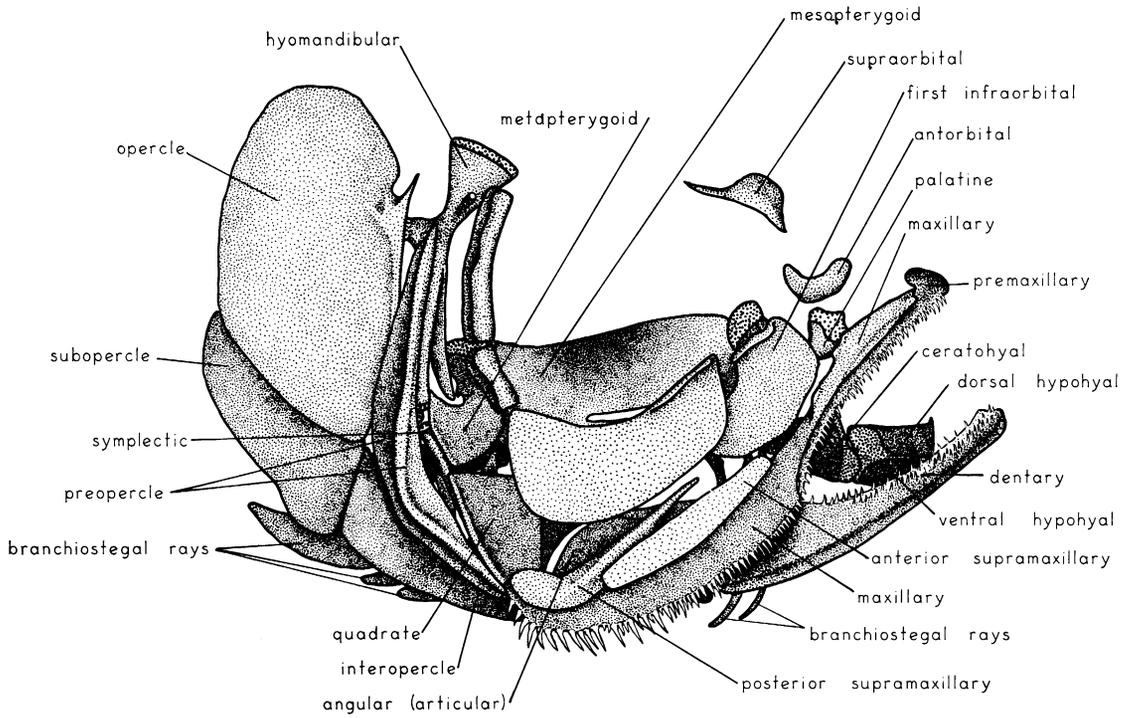
FIG. 52. Lateral view of the face bones of the right side of *Thorophos euryops*, SL 44.7 mm.,
DANA 3736-VI.
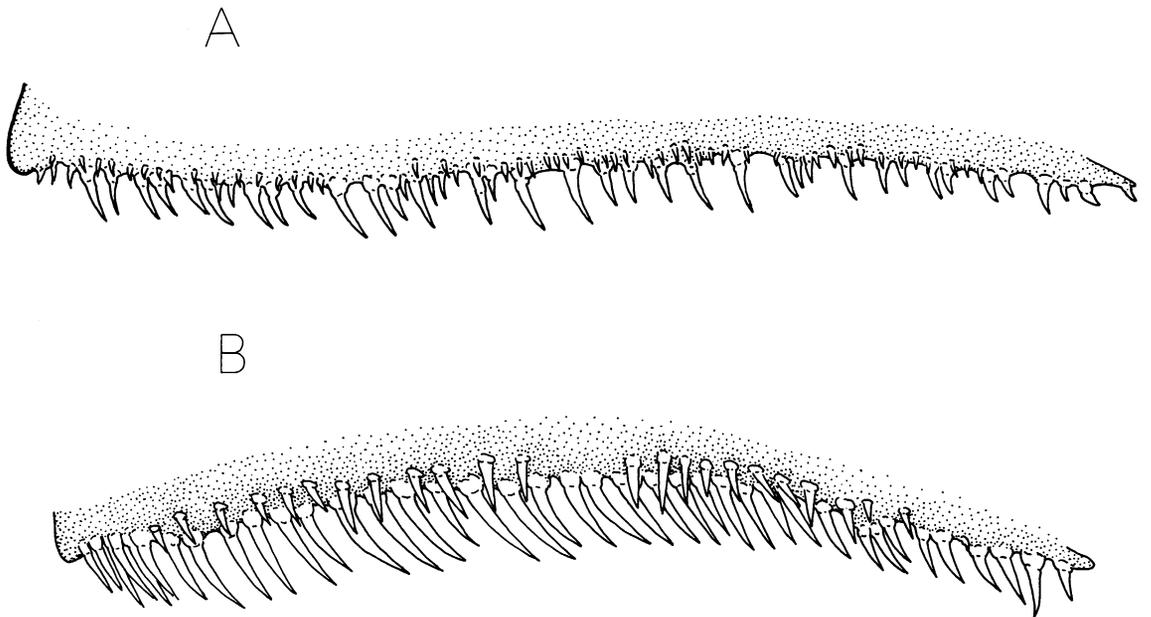
FIG. 53. A. Premaxillary teeth of left side of *Thorophos euryops*, SL 44.7 mm., DANA 3736-VI. Anterior is left.
B. Premaxillary teeth of left side of *T. nexilis*, SL 57.0 mm., USNM 151400. Anterior is left.
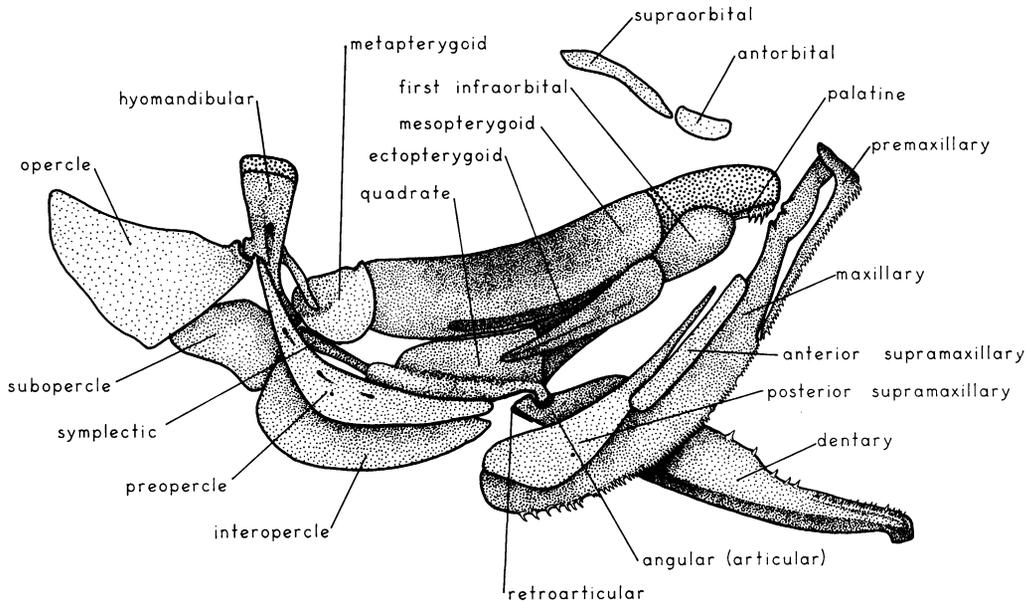
FIG. 54. Lateral view of the face bones of the right side of *Araiophos gracilis*, SL 25.7 mm., FMNH 73902.

minute in *T. euryops*. The maxillary of *euryops* bears approximately 55 teeth in a single row along its ventral border. The posterior teeth in the maxillary row of *euryops* are two to three times as long as the anterior teeth of the same series. There are approximately 65 teeth in this series in the stained specimen of *T. nexilis*. The posterior maxillary teeth of *T. nexilis* are about twice as long as the anterior teeth. Relatively elongate anterior and posterior supramaxillaries are present in both species. All upper jaw teeth are firmly ankylosed and nonmovable.

Araiophos gracilis and *A. eastropas* have essentially the same ligament pattern and jaw structure as the species of *Thorophos*. The ligament pattern will not be described here. The premaxillary bears a moderate-sized ascending process (see figs. 19, 20, 54) and the maxillary is not markedly angular at the junction of its toothed and nontoothed limbs. In *A. gracilis* the premaxillary bears about 40 teeth in a single row along its border and the maxillary of one specimen has 60 teeth in a single row. Grey (1961, p. 464) recorded for *A. gracilis* "all teeth minute, not numerous, uniserial in upper jaw." It is extremely difficult to see and count these teeth under the resolving power of an ordinary dissecting microscope and counts in the present case were made with a compound microscope. One specimen of *Araiophos eastropas* has 37 premaxillary teeth and 38 maxillary teeth. All these are in a single row. Two or three of the posteriormost maxillary teeth are much larger than the remaining anterior teeth. All the premaxillary teeth are of about equal length.

The shape of the jaws and ethmoid region of *Maurolicus muelleri* is considerably different from that of *Thorophos*. Nevertheless the ligament attachments (fig. 55) of the jaws and palatine bone to the ethmoid region are basically the same as in *Thorophos*. The interpremaxillary ligament (1) is confined in part to the anteromedial border of the premaxillaries and in part to the medial border of a posteromedial dorsal process of the interpremaxillary joint. The premaxillary-proethmoid ligament (2) extends from the posterior region of the dorsal medial process of the premaxillary just mentioned to the midlength of the anterior border of the proethmoid process of the supraethmoid of the opposite side and is therefore a crossed ligament (where the ligaments of each side cross, each forms two bands and these four ligaments alternate and interdigitate at the crossing point). In figure 55 only the premaxillary-proethmoid ligament of one side is shown. The palatopre-
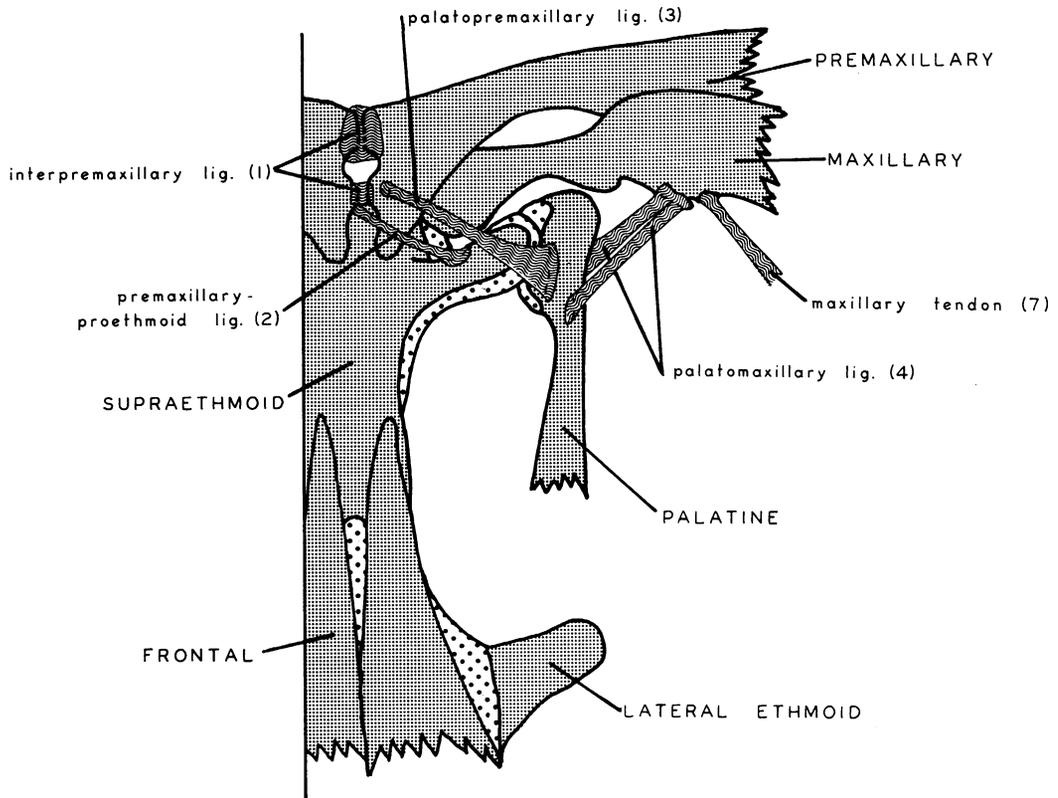
FIG. 55. Dorsal view of the ligaments of the snout region of *Maurolicus muelleri*, SL 45.5 mm., USNM 201138.

maxillary ligament (3) extends to the same areas of the palatine and premaxillary bones and crosses dorsal to the maxillary head. The long palatomaxillary ligament (4) is divided into two rami that extend to similar areas on the palatines as in *Thorophos*. Ligaments 5, 7, and 10 are present and strongly developed. One difference between *Thorophos* and *Maurolicus* is that the premaxillary-proethmoid ligament is crossed in *Maurolicus* and uncrossed in *Thorophos*.

The upper jaw of *Maurolicus muelleri* (figs. 21, 22, 56) has a markedly angular border at the point where the toothless and toothed limbs of the maxillary meet. The posterior half of the maxillary bone is considerably expanded ventrally and accounts for the especially angular structure of that bone. The premaxillary bears a single row of 65 to 70 teeth and the maxillary bears a single row of approximately 50 teeth. Both the anterior and posterior supramaxillaries

are present and cover a large area of the cheek dorsal to the maxillary.

The arrangement of the ligaments binding the upper jaws to the ethmoid region of *Danaphos oculatus* (fig. 57) is similar to that of *Maurolicus* and *Thorophos*. The shape of the palatine bone is more like that of *Thorophos* than that of *Maurolicus*; however, *Danaphos* has its own advanced ligaments. The interpremaxillary ligament (1) is like that of most shallow-bodied sternoptychids but there is no posterior band as in *Maurolicus*. *Danaphos* has the premaxillary-proethmoid ligament (2) divided into two parts. Both parts attach at the same point on the lateral-most part of the proethmoid process of the supraethmoid. One part extends as an uncrossed ligament dorsal to (over) the ascending premaxillary process of the same side to attach to the medial border of that same ascending process. The second, a crossed ligament, ex-
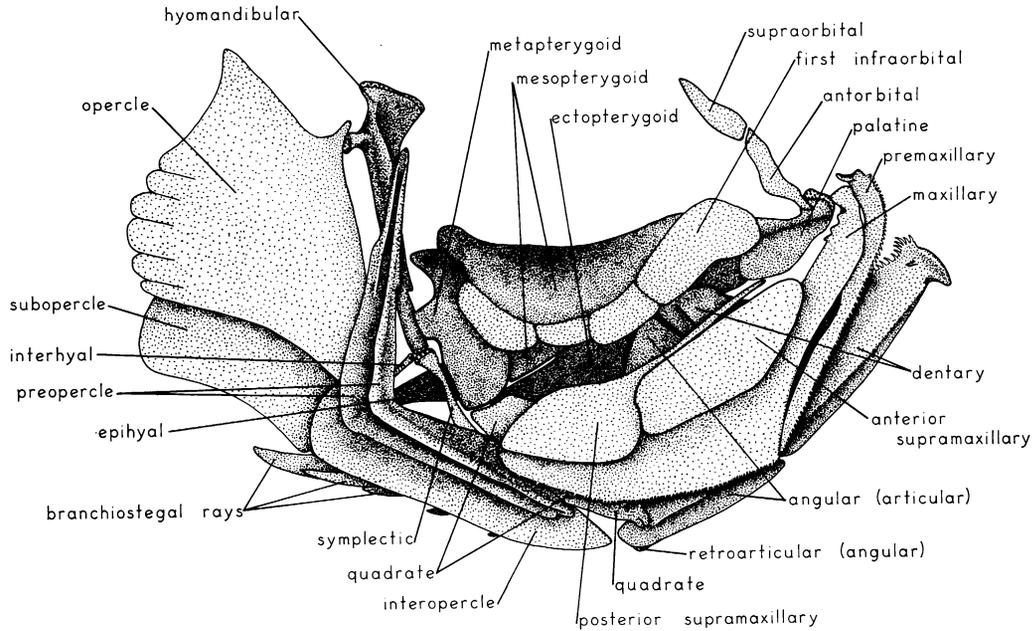
FIG. 56. Lateral view of the face bones of the right side of *Maurolicus muelleri*, SL 45.5 mm., USNM 201138.
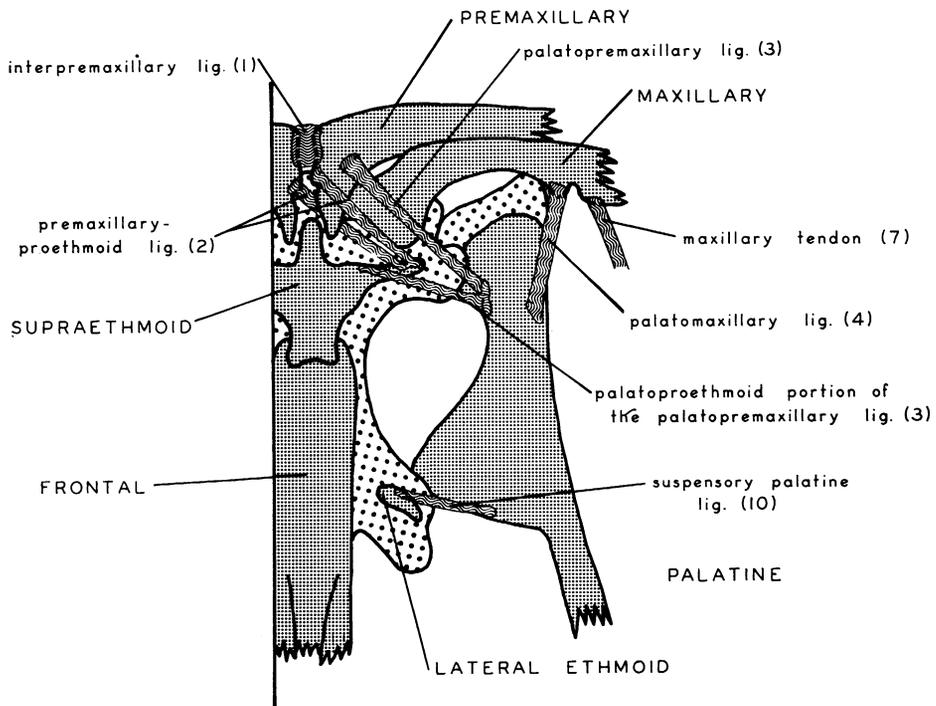
FIG. 57. Dorsal view of the ligaments of the snout region of *Danaphos oculatus*, SL 34.5 mm., USNM 203261.
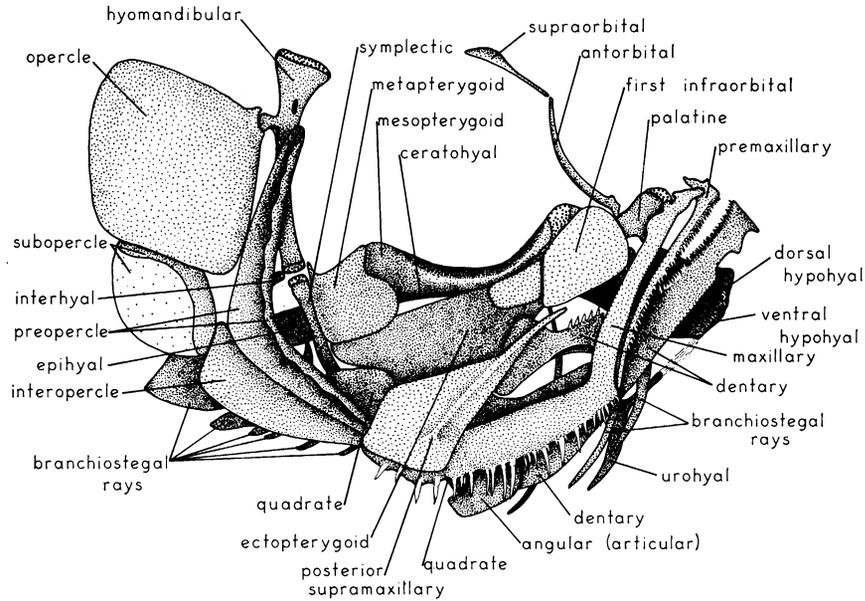
FIG. 58. Lateral view of the face bones of the right side of *Danaphos oculatus*, SL 34.5 mm., USNM 203261.

tends ventral to the ascending premaxillary process of the same side to the medial border of the ascending premaxillary process of the contralateral side. (This ligament passes dorsal to [over and across] the ascending process in *Maurolicus*.) It crosses its counterpart in the space between the two ascending premaxillary processes. The palatopremaxillary ligament (3) is peculiar in *Danaphos* in having a palatoproethmoid branch as well as the usual palatopremaxillary branch. The palatomaxillary ligament (4), as in *Thorophos*, *Maurolicus*, and *Vinciguerria* have a very short band from the maxillary to an area on the ventral surface of the palatine and relatively long segment to the dorsolateral palatine surface. In addition, ligaments 5, 7, and 10 are present and strongly developed.

The upper jaw of *Danaphos oculatus* (figs. 23, 24, 58) has a markedly angular border, the narrow toothed limb of the maxillary meeting the anterior toothless limb in an obtuse angle. The premaxillary is very slender and bears about 50 minute teeth in a single row. The maxillary bears about 25 to 30 canine teeth in a single row. The anterior 10 to 14 of these teeth are one-half to one-fourth the length of most of

the posterior teeth. A posterior supramaxillary is present, an anterior supramaxillary is absent.

The arrangement of upper jaw ligaments in *Valenciennellus tripunctulatus* is the same as that in *Danaphos* and are therefore not described here. Likewise the shape of the maxillary and premaxillary bones is almost the same in *Valenciennellus* and *Danaphos*. In a stained specimen, *Valenciennellus* has about 40 teeth in a single row along the premaxillary and 40 (right side) to 50 (left side) teeth in a row along the maxillary. All teeth are counted as if in a single row on the maxillary. Actually the teeth are more or less separated into rows, there being a row of about 20 large canine teeth, each bearing one or two smaller teeth at its base. The smaller teeth project in a more lateral direction and could be counted as a supplemental row. This situation also occurs in *Danaphos*. The posterior four or five maxillary teeth tend to move dorsally onto the lateral face of the maxillary and suggest the teeth similarly placed in *Sonoda* (see below). As in *Danaphos*, *Argyripnus*, and *Sonoda* the anterior supramaxillary is absent and the posterior supramaxillary is present in *Valenciennellus*.

The ligamentous attachment of the upper jaw and palatine bone to the snout region of

interpremaxillary lig. (I)

PREMAXILLARY

palatopremaxillary lig. (3)

VOMER

MAXILLARY

premaxillary-
proethmoid lig. (2)

SUPRAETHMOID

palatomaxillary
lig. (4)

PALATINE

FRONTAL

suspensory palatine
lig. (10)

LATERAL ETHMOID
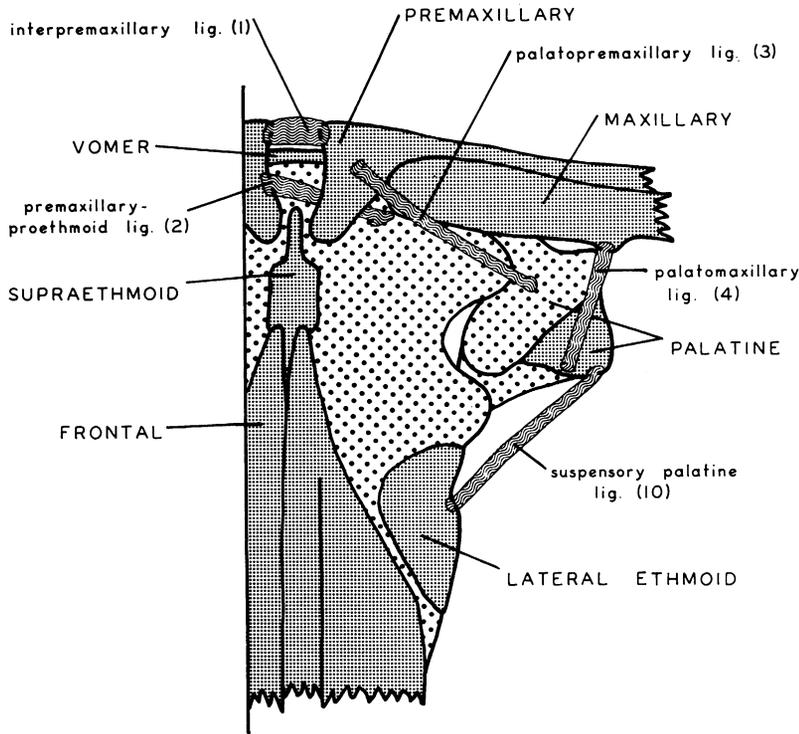
FIG. 59. Dorsal view of the ligament of the snout region of *Argyripnus atlanticus*,
SL 57.0 mm., USNM 201351.

Argyripnus atlanticus (fig. 59) is basically similar to that of *Thorophos*, *Araiophos*, and especially *Maurolicus*. There are, however, some important modifications: The interpremaxillary ligament (1) is the same, extending primarily between the anteromedian parts of the two premaxillaries but without an isolated posterior border as in *Maurolicus*. The premaxillary-proethmoid ligament (2) is modified in that its fibers extend from the medial border of the ascending process of one side, pass ventral to the ascending process (rather than dorsal to as in *Maurolicus*) of the contralateral premaxillary and attach to the anterodorsal region of the ethmoid cartilage of the opposite side. Thus the two premaxillary-proethmoid ligaments are crossed, approaching the condition in *Maurolicus* and *Vinciguerria* rather than that in *Thorophos* where the ligament is uncrossed. In *Argyripnus* the supraethmoid is reduced and appears to bear no proethmoid process. The palatopremaxillary ligament (3) is relatively unmodified in *Argyripnus*; however, its palatine end attaches to the surface of cartilage rather

than bone. The palatomaxillary ligament (4) is divided into two parts as in *Thorophos* and *Vinciguerria*, a dorsolateral ramus (illustrated in fig. 59) that extends to the posterior dorsal end of the palatine bone, and ventromedial ramus (not visible in fig. 59) that attaches to the anterior ventromedial portion of the palatine, just lateral to the palatine teeth. The palatovomerine ligament (5) (not visible in fig. 59) is strong, its best developed portion attaching to a small anterolateral bony vomerine process. Another part of the ligament attaches to the adjacent ethmoid cartilage. The articulation between the cartilaginous part of the palatine head and the anterolateral portions of the ethmoid cartilage is through two separate cartilaginous processes on each structure. The prenasal ethmoid process (see fig. 26) articulates with the anterior part of the palatine head, the postnasal head (actually a modified lamina orbitonasalis) with the posterior part of the palatine head. In almost all gonostomatid, photichthyid, sternoptychid, and all osmerid
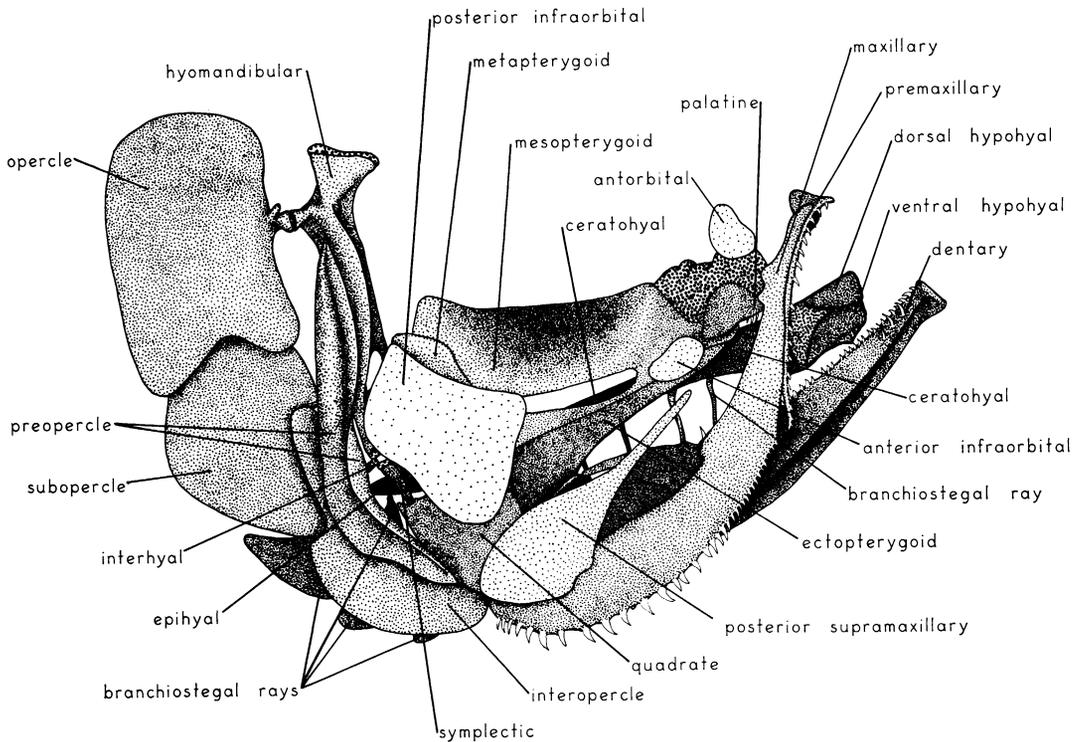
FIG. 60. Lateral view of the face bones of the right side of *Argyripnus atlanticus*, SL 57.0 mm., USNM 201351.

genera the head of the palatine articulates with the prenasal process. In *Sonoda*, *Argyripnus*, and *Polyipnus* the palatine head articulates with both prenasal and postnasal cartilaginous processes of the ethmoid. The maxillary-proethmoid ligament (6) is absent; however, both the maxillary tendon (7) and suspensory palatine ligament (10) are present.

The upper jaw of *Argyripnus atlanticus* (figs. 26, 27, 60) in lateral profile has a markedly curved dental border and there is no sharp angle at the junction of the toothed and non-toothed rami of the maxillary, as for example occurs in *Maurolicus* and *Danaphos* (figs. 56, 58). The premaxillary bears about 18 small teeth in a single row. The maxillary bears approximately 16 small teeth in a single row followed by a single row of about 20 larger teeth. There are no teeth on the lateral posterior surface of the maxillary. The anterior supramaxillary is not present but the posterior supramaxillary is very prominent.

Sonoda megalophthalma (fig. 28) does not differ

significantly in upper jaw structure and attachment from *Argyripnus*, and the ligamentous attachment of the premaxillary, maxillary, and palatine is almost identical with that of *Argyripnus*. The teeth of the upper jaws are somewhat different in having about 30 premaxillary teeth in a more or less single row and having about 70 teeth along the ventral edge of the maxillary. In addition, the posterolateral face bears about 10 to 15 minute teeth ventral to the ventral edge of the large posterior supramaxillary. The anterior supramaxillary is absent.

The attachment of the upper jaw to the snout region in *Polyipnus asteroides* (fig. 61) is the most complex of any of the genera studied in this report. Nevertheless the modifications diagrammed in figure 61 can be easily seen to be further evolutionary derivations of the ligaments in *Argyripnus*. The attachment of interpremaxillary ligament (1), as in most of the less advanced sternoptychids with a well-developed ascending process, is confined to the anteromedial area of
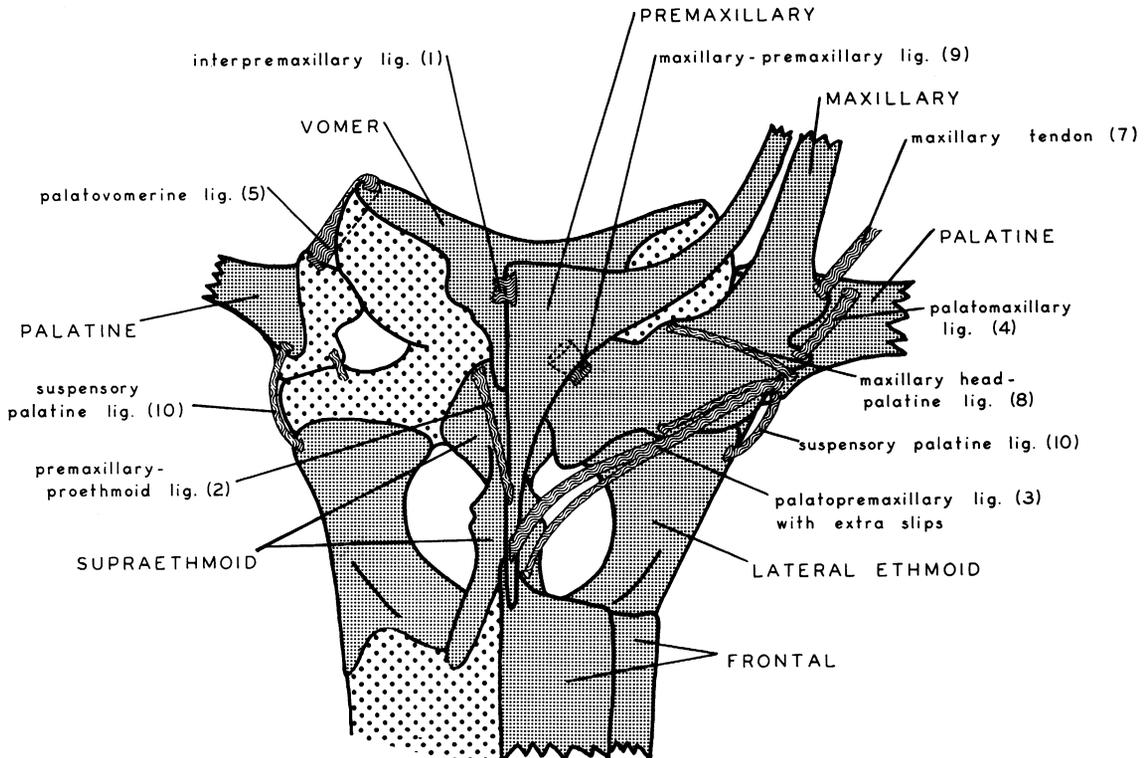
FIG. 61. Anterodorsal view of the ligaments of the snout region of *Polyipnus asteroides*, SL 58.3 mm., USNM 197542.

the premaxillary bone. The premaxillary-proethmoid ligament (2) is crossed and very similar (passing beneath the ascending process of the contralateral side) to that of *Argyripnus* except that the ascending premaxillary process is long and therefore the premaxillary attachment lies posterior to the ethmoid attachment (compare figs. 59, 61 and note that ligament [2] is shown on the left side in fig. 61 of *Polyipnus*, and on the right side in fig. 59 of *Argyripnus*). In *Polyipnus*, ligament (2) attaches to the antero-lateral border of the supraethmoid rather than to the ethmoid cartilage as in *Argyripnus*. The palatopremaxillary ligament (3) is complex in *Polyipnus* and divided into three parts, a slender palatomaxillary branch or slip, a relatively thick palatopremaxillary branch, and a very narrow palatosupraethmoid branch. All three of these slips attach to the palatine at the same point, slightly anterior to the connection of the suspensory palatine ligament (10) to the palatine. The palatopremaxillary branch joins the

premaxillary near the frontal end of the ascending premaxillary process. The palato-supraethmoid branch is joined to the palato-premaxillary branch along about half the length of the latter then parallels it for most of the rest of its length, dipping ventrally to connect to the base of the posterior supraethmoid process of the same side. In addition a maxillary head-palatine ligament (8) and a short, strong maxillary-premaxillary ligament (9) are present. Presumably these two ligaments were originally formed from the palatopremaxillary ligament even though they are now completely separate. Compared with the other genera studied here, the upper jaws of *Polyipnus* are somewhat pro-tractile, and compared with *Sternoptyx* and *Argyropelecus* the premaxillary and maxillary as a unit are relatively mobile. There is a considerable degree of motion between the maxillary and premaxillary, especially at their distal ends. This motion pivots around the maxillary-premaxillary ligaments. The upper jaw of
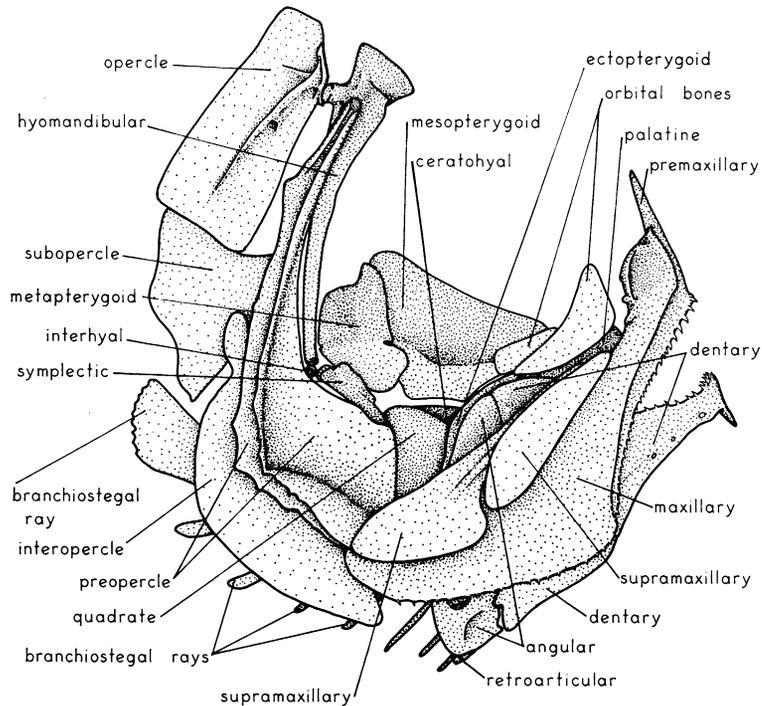
FIG. 62. Lateral view of the face bones of the right side of *Polyipnus asteroides*,
SL 58.3 mm., USNM 197542.

Polyipnus is not, however, greatly protractile, motion being limited by the palatomaxillary ligament and the palatovomerine and suspensory-palatine ligaments. The palatomaxillary ligament, although relatively long compared with that of *Polymetme*, considerably restricts the motion of the maxillary bone dorsally over the palatine. The palatine itself is more or less immobilized in an anterior-posterior direction by the palatovomerine (5) and suspensory palatine (10) ligaments and by its two articular facets with the prenasal and postnasal processes. This does not restrict motion in a lateral, swinging fashion and therefore expansion of the oral cavity is readily possible. The posterior palatine facet is connected to the postnasal ethmoid process by the suspensory palatine ligament (10). This joint appears capsular in nature but this could not be determined with certainty from a gross dissection. The small dorsomedial supplementary suspensory ligament (unlabeled in fig. 61) may be simply a strengthened part of a capsular ligament. It

connects only cartilage to cartilage. A maxillary tendon (7) is present as in all genera studied.

The upper jaw of *Polyipnus asteroides* (figs. 29, 30, 62) is strongly angulate in profile and the maxillary has its surface expanded. This is true for all species of this genus examined. The maxillary of *P. tridentifer* is less expanded and angulate and apparently more primitive than that of *P. asteroides*. According to the figures published by Baird (1971) some of the species of *Polyipnus*, for example *P. kiwiensis* Baird, appear to have almost no angle in the maxillary and the maxillary appears little expanded. The premaxillary of *asteroides* has a long, slender ascending process and a moderately strong, toothed shaft bearing 27 to 30 relatively small canine teeth in a single row. *Polyipnus tridentifer* on the other hand has five or six (anteriorly) to three (posteriorly) very irregular rows of premaxillary teeth which total 150 to 180 teeth. The maxillary of *P. asteroides* bears about 18 to 20 very small teeth in a single row, whereas that of *P. tridentifer* bears about 25 to 30 teeth similar

interpremaxillary lig. (I)

PREMAXILLARY

maxillary-premaxillary lig. (9)

maxillary tendon (7)

VOMER

premaxillary-proethmoid lig. (2)

palatomaxillary lig. (4)

PALATINE BONE

maxillary head-palatine lig. (8)

PALATINE

PALATINE CARTILAGE

suspensory palatine lig. (10)

SUPRAETHMOID

LATERAL ETHMOID

FRONTAL
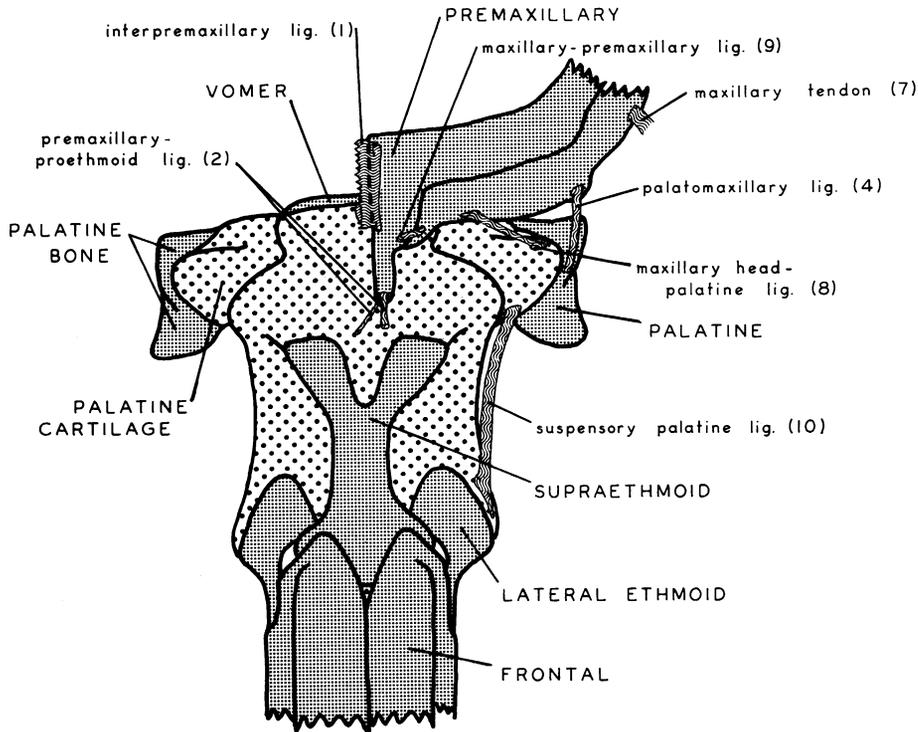
FIG. 63. Anterodorsal view of the ligaments of the snout region of *Argyropelecus aculeatus*, SL 49.5 mm., USNM 179056.

to those of *P. asteroides*. Both species have five or six rows of small eminences over the lateral surface of the maxillary. These may bear teeth in life and a few teeth are retained on some eminences in the preserved specimens at hand. Four to five tooth rows extend the length of the tooth-bearing maxillary shaft and indicate that the total number of teeth on the maxillary may approach 80 to 100. These are not indicated in figure 62. The other genera in the present study with teeth over the lateral surface of the maxillary are *Sternoptyx*, *Sonoda*, to a very minor extent *Argyripnus*, *Thorophos*, *Maurolicus*, and *Danaphos*. Both the anterior and posterior supramaxillaries are present in *Polyipnus*.

The attachment of the upper jaws to the skull in *Argyropelecus aculeatus* (fig. 63) and other species of *Argyropelecus* differs in several important respects from that of *Polyipnus*. The premaxillary has a relatively long ascending process and the interpremaxillary ligament (1), although relatively weak at any given area, is

strong in its entirety and distributed over a little more than one-half of the joint area between the two premaxillaries and their ascending processes. A very strong ligamentous cord connects each premaxillary to the cartilage ventral to the premaxillaries. This cord is relatively lax allowing considerable movement between the premaxillaries on the one hand and the ethmoid region on the other. The premaxillary-proethmoid ligament (2) is relatively small but still allows considerable premaxillary movement and extends as an uncrossed cord to the ethmoid cartilage ventral and posterior to the tip of the ascending premaxillary process. A slender, crossed portion extends from the attachment of the thicker cord to the tip of the ascending premaxillary process to an area on the dorsal surface of the ethmoid cartilage just anterior to the attachment of the thick noncrossed cord of ligament (2) of the opposite side. The only parts of the palatopremaxillary complex of ligaments similar to those present in *Polyipnus*
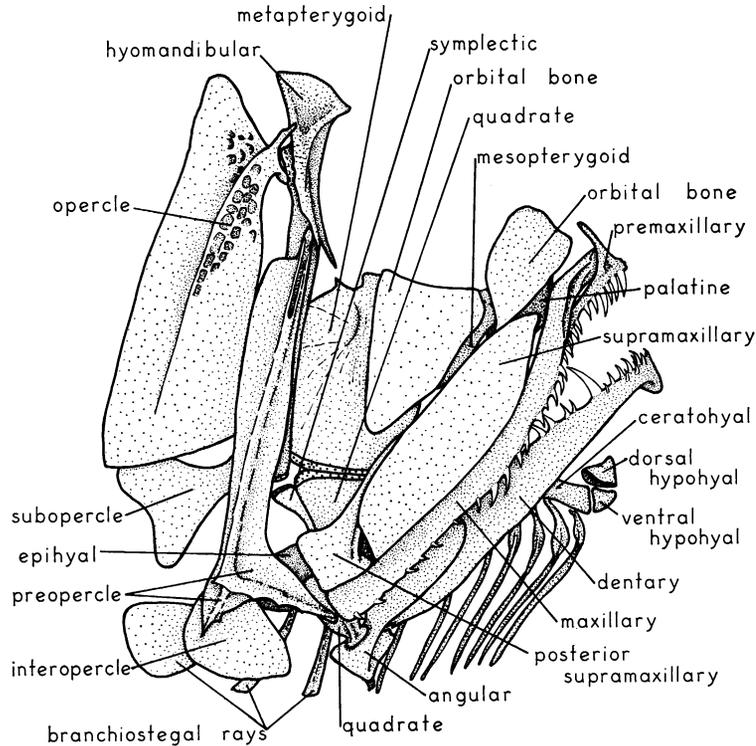
FIG. 64. Lateral view of the face bones of the right side of *Argyropelecus aculeatus*, SL 49.5 mm., USNM 179056.

are the maxillary head-palatine ligament (8) and a small maxillary-premaxillary ligament (9). Of the other ligaments, 4, 5, 10, and the maxillary tendon (7) are present and well developed. The suspensory palatine ligament (10) is relatively long, not short as in *Polyipnus*. This is correlated with the fact that the palatine head is distinct from the postnasal process in *Argyropelecus*. In fact, the palatine head articulates only with the prenasal cartilaginous process. Although the upper jaws of *Argyropelecus* retain the ability to move in an anterior-posterior direction, pivoting around their ethmoid and palatine attachments, and to swing in a lateral direction to allow expansion of the oral cavity, their protractility appears to be less than that found in *Polyipnus*.

The upper jaw profile of *Argyropelecus aculeatus* (figs. 31, 32, 64) is not angulate and the toothless limb of the maxillary is only about one-fourth of the total maxillary rather than approximately one-half as in *Polyipnus*. There are approximately

nine canine teeth along the premaxillary of *A. aculeatus*. This does not count replacement teeth behind them or small supplementary ones at the base of the larger teeth. These teeth are arranged more or less in a single row. There are 18 to 20 teeth along the border of the maxillary. About the first 12 teeth point posteroventrally, the remaining six to eight point anteriorly. The posterior and anterior supramaxillaries are present and well developed. There are no teeth over the lateral surface of the maxillary. All species of *Argyropelecus* examined have the general tooth, ligament, and bone pattern described above. Several species have more teeth in their jaws than does *A. aculeatus*.

Of all the species examined, *Sternoptyx diaphana* (figs. 34, 65) and *Sternoptyx* sp. have the most derived and in many ways the simplest of upper jaw attachment to the skull. The premaxillary is slender and the interpremaxillary ligament (1) covers the entire interpremaxillary joint. There are no supraethmoid or proethmoid
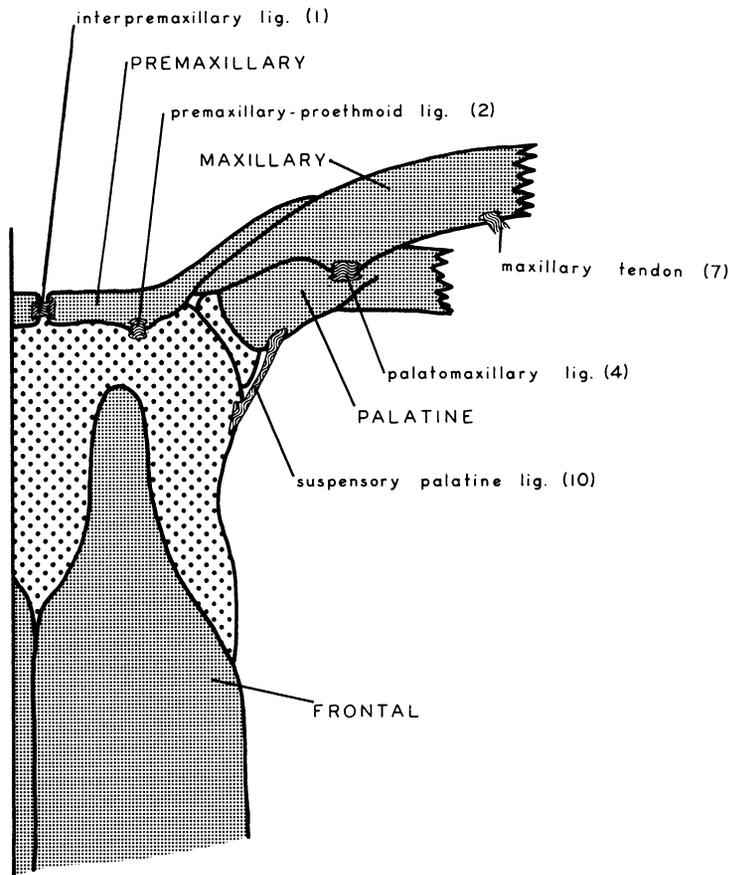
FIG. 65. Anterodorsal view of the ligaments of the snout region of
Sternoptyx diaphana, SL 44.0 mm., USNM 192843.

bones and the very short premaxillary-proeth-
moid ligament (2) closely binds the premaxillary
to the ethmoid cartilage. The maxillary is
bound closely and firmly to the palatine by a
very short palatomaxillary ligament (4). The
palatovomerine ligament (5) is altered to form
the ventral part of a capsular ligament between
the palatine cartilage and ethmoid cartilage.
The vomer bone is missing and ligament (5)
attaches to the ethmoid cartilage. Tendon (7)
and ligament (10) are also present. There is no
lateral ethmoid bone and the suspensory pala-
tine ligament (10) is attached to the prenasal
process rather than the orbitonasalis which
ordinarily underlies the lateral ethmoid. As in
Argyropelecus the palatine head articulates only
with the prenasal process of the ethmoid carti-
lage and in this respect these two genera are

extremely unlike *Polyipnus* where the attachment
is ligamentous to the postnasal ethmoid process.

The upper jaws of *Sternoptyx diaphana* (figs. 33,
34, 66) and *Sternoptyx* sp. are characterized by a
short premaxillary and a long, slender maxillary
with a very short, anterior toothless process that
equals about one-sixth the length of the entire
bone. The teeth of the premaxillary are arranged
in irregular rows (see fig. 33) and total about 30.
The maxillary has three rows of teeth anteriorly
and total about 70 to 80. This number can be
increased by counting replacement teeth. The
actual count is difficult to determine. An
anterior supramaxillary is absent, the posterior
supramaxillary is present and small. The
maxillary is not angulate but sinuous in profile.
In figure 66 the maxillary looks as though it
contains a laterosensory canal. This is not so,
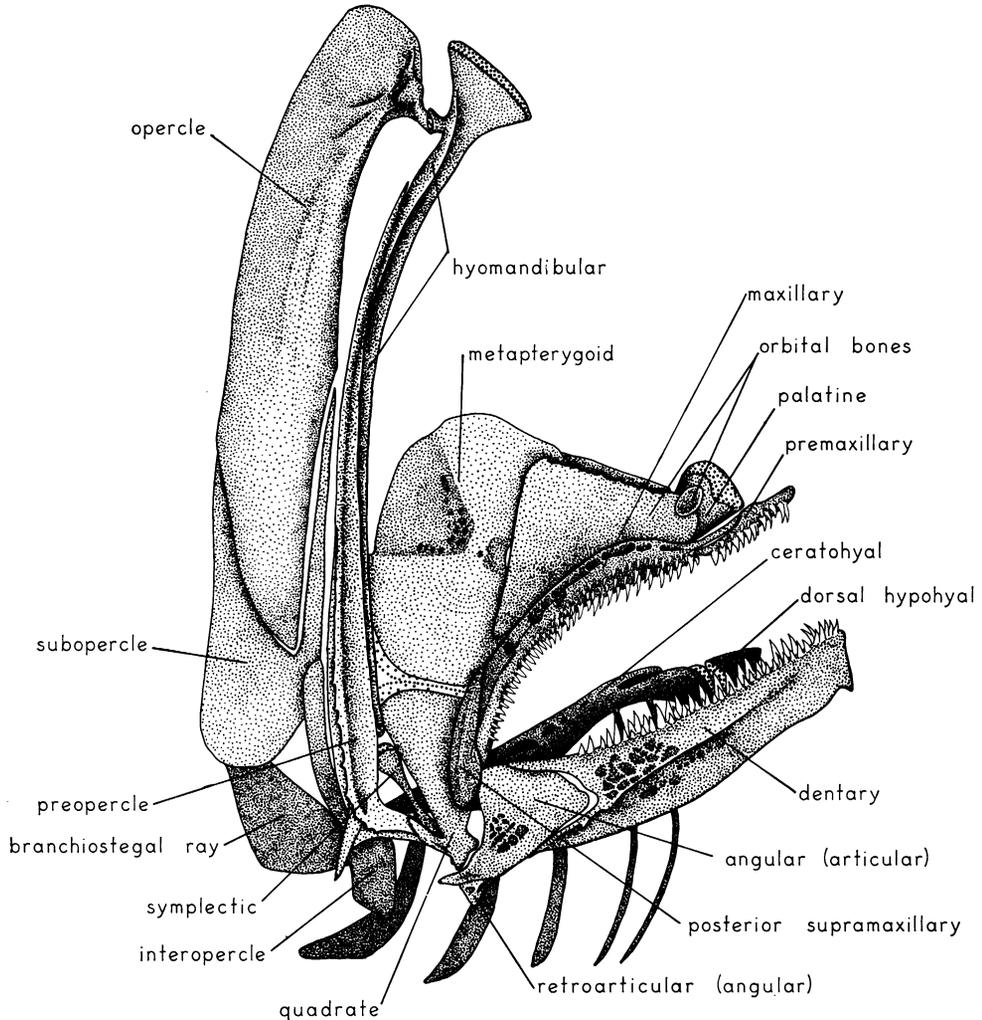
FIG. 66. Lateral view of the face bones of the right side of *Sternoptyx diaphana*, SL 44.0 mm., USNM 192843.

the thin bone simply being full of pits and strengthening ridges to lighten its weight.

LOWER JAW

The lower jaw of *Thorophos euryops* (figs. 18, 52) and *T. nexilis* are very similar to that described by Weitzman (1967a, p. 517) for *Vinciguerria lucetia* and presumably represents a relatively primitive sternoptychid jaw. Bruun (1931, p. 288) recorded a single row of teeth in the lower jaw of *T. euryops* and Grey (1964, p. 85) questioned this. I find that posteriorly the dentary has a single tooth row but anteriorly has three rows. The inner, longest row consists of about 30 teeth, the second row, about two-thirds the length of the inner row, also has about 30 teeth, and the very short third outermost row near the anterior tip of the dentary has five to six teeth. Myers (1932, p. 61) recorded a single series of teeth in the lower jaw of *T. nexilis*, whereas Grey (1964, p. 85) noted that the dentary teeth were biserial in the anterior half of the jaw. I find that *T. nexilis* has a comparatively slender, elongate jaw and also has three rows of minute teeth. The inner row contains 30 to 35 teeth, the teeth being quite dense posteriorly

and sparse anteriorly. The anterior one-third of the inner tooth row has only about six teeth. The second or outer row bears approximately 15 to 16 teeth and the third or outermost row about 12 teeth. A "platform" (see discussion below under *Araiophos*) is almost absent. The bony pocket or recess on the medial face of the dentary for the insertion of the Aw section of the adductor mandibulae muscle (see Winterbottom, In press), is large and placed posteriorly on the bone. The articular is large but not excessively deep-bodied as in a few genera described below. The coronomeckelian bone is very small and situated just dorsal to Meckel's cartilage near the midlength of the medial face of the articular. The retroarticular has a prominent spine for attachment of a ligament extending to the posterior end of the lateral furrow of the epihyal seen in figure 67. A small segment of this ligament attaches to the medial face of the midlength of the dorsal border of the interopercle.

Araiophos gracilis (figs. 20, 54) and *A. eastropas* have a slender lower jaw very similar to that of *Thorophos*. Grey (1961, p. 464) recorded an outer row of three to four dentary teeth in *A. gracilis*. There are two rows of teeth on the dentary but these are difficult to define because of the shape of the dentary and the interrupted nature of the inner or medial row. The posterior half of the medial tooth row bears about five to eight teeth. Anteriorly it bears about eight teeth, some of which cannot be seen in figure 54 because they are hidden by the dorsal border of the dentary. Another type of division occurs in the inner tooth row suggestive of a distinct division descibed below for *Danaphos*, *Valenciennellus*, *Argyripnus*, and *Sonoda*. In these four genera a distinct break in the jaw line occurs just anterior to the posterior two to eight teeth. The posterior teeth rest on a distinct "platform." In *Araiophos* the jaw profile noticeably rises just anterior to the posterior two widely spaced teeth suggesting the type of structure in the four genera just mentioned. The outer row along the anterior region of the dentary bears 15 to 20 teeth. This outer row may actually represent two rows because anteriorly it is rather irregular. Thus the general tooth pattern on the lower jaw of *Araiophos* is not greatly different from that of *Thorophos*, probably three somewhat indistinct tooth rows being present. The remaining bones of the lower jaw are so similar to those of *Thorophos* that they need no

further description. The ligament between the retroarticular and the epihyal has the same distribution as in *Thorophos*.

Maurolicus muelleri has a very deep lower jaw (figs. 22, 56). The dentary appears specialized in this respect (but see discussion above under *Thorophos*). Grey (1964, p. 228) has noted a considerable amount of tooth variation in all tooth-bearing bones in *Maurolicus*. In the specimens examined here there are 12 to 14 teeth in a single row along the anterodorsal edge of the dentary and two or three posteriorly. A single tooth in the outer dentary row is found near the symphysis. The large hole in the dentary shown in figure 22 appears constant. The articular is the largest bone in the lower jaw (rather than the dentary as in most other genera). The coronomeckelian rests at the point of attachment of the posterior end of Meckel's cartilage to the articular. The retroarticular is small but the ligament between it and the posterior end of the lateral furrow on the epihyal (fig. 68) is large. This ligament is bound to the dorsal border of the interopercle along its midlength but does not appear to give off a separate ligament to the interopercle.

The lower jaw of *Danaphos oculatus* (figs. 24, 58) is somewhat modified from the presumably relatively primitive stomiatoid condition found in *Thorophos*. The medial tooth row of the dentary is, however, clearly divided into posterodorsal and anteroventral segments. The anteroventral segment bears about 20 to 25 teeth, the posterior or "platformed" segment about five to eight. Bruun (1931, p. 286) reported a single row of teeth in the lower jaw, whereas Grey (1960a, p. 112) reported two or more rows. In the specimens examined here I find three rather irregular rows, the outermost with about 25 teeth and the short, irregular middle row with four to six teeth. These could not be clearly shown in figure 58. The dentary recess for the insertion of the Aw section of the adductor mandibulae muscle is posteriorly placed. The hiatus between the articular and dentary was found in all specimens examined and is probably associated with the small size of the fish. The coronomeckelian bone is in the usual place, near the posterior termination of Meckel's cartilage. The ligament from the retroarticular extends to the dorsal border of the interopercle to which it is attached. A separate ligament extends from the medial face of the interopercle

to the posterior border of the groove on the lateral face of the epihyal (fig. 69).

The lower jaw of *Valenciennellus tripunctulatus* is almost exactly the same as that of *Danaphos* and has the hiatus between the dentary and articular and the separation of the medial tooth row of the dentary into an anteroventral and posterodorsal set. The posterodorsal set includes two teeth, the anteroventral about 16. There are only two tooth rows and the outer, shorter row, consisting of small, relatively crowded teeth, also contains about 16 teeth. The ligament between the retroarticular and dorsal border of the interopercle is similar to that in *Danaphos* but appears to have a few fibers continuous with the ligament between the interopercle and the lateral epihyal groove.

The lower jaw of *Argyripnus atlanticus* (figs. 27, 60) is similar to that found in *Danaphos* in that the posterior teeth of the medial tooth row of the dentary are elevated and separated from the anterior teeth by a distinct gap. The hiatus between the dentary and articular is very small and the anterior ramus of the dentary is slender contrasting sharply with the posterior portion of the lower jaw which is deep, but not so deep bodied as in *Maurolicus muelleri*. The medial dentary tooth row consists of 30 to 35 teeth. The anterolateral row has three to four teeth, each about twice the size of the anterior teeth of the inner row. The coronomeckelian bone lies somewhat anterior to the posterior attachment of Meckel's cartilage to the articular. The ligament between the retroarticular and the posterior end of the groove on the lateral side of the epihyal (fig. 70) is bound along its midcourse to the dorsal border of the interopercle and sends a slender segment to attach to the posterodorsal border of the interopercle.

Sonoda megalophthalma has a lower jaw (fig. 28) very much like that of *Argyripnus atlanticus*. The posterodorsal portion of the medial tooth row has two to three teeth, the anteroventral portion has nine to 12 relatively large, canine-like teeth. The anterior outer row (not visible in fig. 28) consists of 14 to 16 smaller caniniform teeth. The articular constitutes about one-half of the length of the lower jaw and there is a small hiatus between the dorsoposterior limb of the dentary and the articular. The coronomeckelian is apparently not ossified at the attachment of the tendon of the adductor mandibulae muscle to the articular as is ordinarily the case in the other fishes examined here. Instead the bone was found just anterior to the quadrate-articular joint, posterior to the attachment of the adductor mandibulae tendon. This bone was thin and peeled off the articular. Its identification is uncertain but it is labeled coronomeckelian in figure 28. The ligament between the retroarticular and the epihyal takes the same course in *Sonoda* as it does in *Argyripnus*; however, a large percentage of the fibers from the retroarticular end on the dorsal border of the interopercle and a large percentage of the fibers from the epihyal end on the posterodorsal medial face of the interopercle. This is close to the situation found in *Danaphos* and *Valenciennellus* (see description above).

Polyipnus asteroides has a very deep lower jaw (figs. 30, 62), perhaps more suggestive of *Maurolicus* in this respect than any other fish examined. There are approximately 16 to 20 teeth in a medial row along the dorsal border of the dentary and three or four in a single outer row. The dentary pocket is placed rather far forward in all species of *Polyipnus* examined and a process of the articular does not enter it as it does in all nonhatchetfish sternoptychids. The coronomeckelian is placed near the attachment of Meckel's cartilage to the articular. The ligament from the retroarticular goes directly to the posterior part of the lateral face of the epihyal and only sends a small branch to the dorsal border of the interopercle. This is the type of arrangement found in the Osmeridae.

The lower jaw of *Argyropelecus aculeatus* (figs. 32, 64) is very different from that of *Polyipnus*. The overall profile of the jaw on one side is triangular, being deepest at the posterior end. The dentary pocket for the reception of the Aw section of the adductor mandibulae muscle is small and relatively far anterior. The dentary teeth are large, one or sometimes two of them being prominent canines. There are 12 to 16 teeth in the median row and about four teeth in a smaller, outer anterior row near the symphysis. The coronomeckelian bone lies very close to the posterior termination of Meckel's cartilage. The ligament between the retroarticular and epihyal goes directly to the posterior lateral base of the epihyal where it is associated with the posterior termination of a broad, shallow groove on the lateral face of the epihyal (fig. 73). A few fibers extend from the retroarticular to the dorsal border of the interopercle. The jaws of all species of *Argyropelecus* examined are similar to

those of *A. aculeatus* with some differences in tooth count and size and placement of the larger canine teeth.

Sternoptyx diaphana (figs. 34, 66) and *Sternoptyx* sp. have a lower jaw similar to that of *Argyropelecus* in its slender shape. The jaw is not so deep posteriorly as that of *Argyropelecus* and there is a hiatus between parts of the dentary and articular. The shape and position of the pocket in the dentary for the Aw section of the adductor mandibulae muscle is similar in both genera and different from that in *Polyipnus*. None of the dentary teeth are especially long (as they are long in *Argyropelecus*). The teeth are more or less arranged in one (posterior) to four (anterior) rows. It is difficult to assign any particular tooth to a definite row and the total number of teeth in the lower jaw may reach as many as 50. It is difficult to distinguish replacement teeth from fully functioning dentary teeth and the count of 50 may include several replacement teeth. The coronomeckelian bone is rather elongate, a little more so than the somewhat elongate bone in *Argyropelecus*. The ligament between the retroarticular and epihyal goes directly to the posterolateral face of the epihyal (fig. 74) and does not appear to send a branch to the interopercle.

ORBITAL BONES

The orbital bones of most stomiatoids appear somewhat reduced when compared with those of osmerids, and this is especially true of sternoptychids. However, in these delicate fishes it is difficult to determine the presence or absence of orbital bones because of their very thin structure and the frequent loss of superficial structures because of friction in the collecting nets. In some of the rare genera where only one or two specimens were available it was sometimes impossible to be certain that a bone is actually absent in a species and not just missing from the specimen at hand. Although the value of a comparison of orbital bones in these fishes thus is reduced, nevertheless there appears to be a trend toward a reduction of orbital bones in the more advanced genera.

Thorophos euryops (fig. 52) has a full orbital ring of four bones plus an antorbital and a supraorbital. As in many stomiatoids the first (anterior) infraorbital is associated with a photophore (often called the suborbital organ; see Morrow, 1964b, p. 276). The second infra-

orbital is large and covers most of the muscle mass of the cheek ventral to the eye. The remaining two orbitals are tube bones that extend dorsally to the frontal. In some of the primitive stomiatoids, for example *Polymetme*, and in the osmerids the posterior rim of the orbit has several shorter tube bones (see Weitzman, 1967a). Presumably the long tube bone in *T. euryops* is a slight specialization and perhaps represents a fusion of two or more bones. The orbital bones of *T. euryops* and *T. nexilis* appear to be alike.

Araiophos gracilis has a reduced orbital ring (fig. 54) presumably correlated with its small size. A supraorbital, antorbital, and first (associated with the suborbital photophore) and second infraorbital bones are present. All others are absent. *Araiophos eastropas* has the same orbital bone arrangement.

Maurolicus muelleri has a partially incomplete orbital ring (fig. 56) consisting of a supraorbital, first infraorbital (associated with a photopore), and three flat plates behind the first infraorbital. Tube bones are absent and there is a postorbital gap in the orbital series between the posterior infraorbital and the frontal.

Danaphos oculatus (fig. 58) has a supraorbital, antorbital, first infraorbital (associated with a photophore), and a single, small, flat, platelike second infraorbital. Tube bones are absent.

Valenciennellus tripunctulatus has a supraorbital, antorbital, a large, flat, first infraorbital (associated with a photophore), a very small second infraorbital and at least one relatively long postorbitally placed tube bone that dorsally almost contacts the frontal and sphenotic. Except for this one tube bone and a relatively large first infraorbital, the orbital bones of *Valenciennellus* are very similar to those of *Danaphos*.

Examination of the orbital bones of *Argyripnus* (fig. 60) was not completely satisfactory. In the stained specimen USNM 201351) of *A. atlanticus* no supraorbital could be found, and some of the infraorbitals are apparently missing. *Argyripnus* sp. from the Philippine Islands (USNM 135402) has a very large supraorbital, and a piece of a supraorbital was found in a specimen of *A. atlanticus* (FMNH 656393). The antorbital appears to be of moderate size in all specimens with the bone, including the Philippine *Argyripnus* (USNM 135402). This specimen has a large first infraorbital, several times larger than the infraorbital illustrated for *A. atlanticus* in figure

60. One or two narrow infraorbitals extend
posterior to the first infraorbital, reaching the
anterior border of the large, posterior infra-
orbital plate. Because of damage, the specimen
in figure 60 is apparently missing these narrow
infraorbitals. Specimens of *Argyripnus* sp. (USNM
126079) have a complete ring of four infra-
orbitals, two small anterior bones, a large
posterior bone with a tube in its posterior
dorsal angle, and a fourth dorsal infraorbital
posterior to the eye that, although partly
damaged, bears at least part of a tube.

All specimens of *Sonoda megalophthalma* ex-
amined were heavily damaged in the orbital
region. One specimen had an antorbital, and
first and second infraorbitals. The antorbital
was very similar in size and shape to that
illustrated for *Argyripnus atlanticus*.

Polyipnus asteroides (fig. 62) has two orbital
bones, the first or anteriormost infraorbital is
associated with the suborbital photophore. All
species of *Polyipnus* examined have the orbital
bone pattern of *P. asteroides*.

Argyropelecus aculeatus (fig. 64), as in *Polyipnus*,
has two orbital bones. The first or anterior is
associated with the suborbital photophore. The
second is expanded over the adductor mandibu-
lae muscle and is of much greater size than the
same bone in *Polyipnus*. No antorbital or supra-
orbital is present. All species of *Argyropelecus*
examined have a very similar orbital bone
arrangement.

Sternoptyx diaphana (fig. 66) and *Sternoptyx* sp.
have two orbital bones. The first is very small
and is associated with a suborbital photophore.
The second is a very large, flat plate much like
the same bone in *Argyropelecus*. An antorbital,
supraorbital, and all other circumorbitals other
than the two described are absent.

PALATINE ARCH AND DORSAL
PORTION OF THE HYOID ARCH

Of all the genera treated here, the general
shapes and proportions of the palatine and
hyoid arch bones of *Thorophos* appear most like
those of *Polymetme* and *Spirinchus* (compare figs.
17 and 51 with Weitzman, 1967a, figs. 2, 3, 13,
14). *Thorophos* is therefore assumed to be the most
primitive sternoptychid genus in this region. The
relationships of the palatine to the upper jaw
and the ethmoid region in sternoptychid fishes
has been described above in the section on the

upper jaw and therefore is treated only briefly
here.

The palatine bone of *Thorophos euryops* bears
four to five teeth in a single row (see figs. 18, 52)
and has a shape in lateral view very similar to
that in *Polymetme corythaeola* and *Spirinchus
thaleichthys*. The palatine of *Thorophos euryops*
lacks the posterior bracing process covering the
anterior end of the ectopterygoid in *Polymetme*
and *Spirinchus*. The cartilaginous lamina that
lies between the palatine and mesopterygoid
has almost exactly the same shape in *Thorophos*,
Polymetme, and *Spirinchus*. The shape of the
palatine in *Thorophos nexilis* is almost the same as
that in *T. euryops* except that a small posterior
bracing palatine process is present and extends
toward the ectopterygoid. In *T. nexilis* there is
a single row of five or six teeth on each palatine,
otherwise the palatine is essentially the same as
that of *T. euryops*.

The toothless mesopterygoid of *T. euryops* is
relatively elongate compared with the toothed
mesopterygoid in *Polymetme* and *Spirinchus* and
is much like the toothless mesopterygoid found in
Vinciguerria lucetia (compare with Weitzman,
1967a, fig. 8). The mesopterygoid of both
species of *Thorophos* has a central, ventrally
placed oval fenestra that is completely surroun-
ded with bone. The metapterygoid of *T. euryops*
and *T. nexilis* is relatively short in its anterior-
posterior dimension, being a little more than
one-third the length of the mesopterygoid. In
Polymetme and *Spirinchus* the metapterygoid
almost equals the mesopterygoid in length.
Vinciguerria has a short metapterygoid, in
proportion very similar to that in *Thorophos*. The
dorsal border of the metapterygoid bears a notch
spanned by connective tissue that binds the hyo-
mandibular spine. The toothless ectopterygoid
is elongate and contacts the palatine, meso-
pterygoid, metapterygoid, and quadrate in both
species of *Thorophos*. Its shape is much like that
of *Spirinchus* and *Vinciguerria*.

The hyomandibular of *Thorophos*, like those of
Spirinchus and *Vinciguerria*, is only moderately
elongate. Its total length in all three is about
half the length of the cranium. The hyomandib-
ular of *Polymetme* is about equal to the cranial
length. A blunt hyomandibular spine is well
developed and primitive for stomiatoids. The
symplectic is an elongate, slender bone with its
ventral end lodged against the posterior dorso-
median face of the quadrate. The dorsal

articulations of the quadrate are primarily with the ectopterygoid and mesopterygoid.

The palatine arch of *Araiophos gracilis* (figs. 20, 54) and *A. eastropas* is relatively elongate when compared with that of *Thorophos*. The arch of *Araiophos* is relatively shallow and the articulation between the quadrate and the angular (articular) is shifted anteriorly occurring at a point well anterior to a line extended ventrally from the midpoint of the mesopterygoid rather than posterior to such a line as in *Thorophos*. The toothed, bony palatine of *Araiophos* (four to five teeth in a single row in both species) is small and neither the bone nor its associated cartilage has the shape found in *Thorophos*, *Polymetme*, or *Spirinchus* (compare figs. 18, 20).

The toothless mesopterygoid is an elongate, almost quadrangular bone with a central area of thin, almost cancelous bone occupying an area similar to the fenestra in the mesopterygoid of *Thorophos*. The metapterygoid of *Araiophos* is more than a quarter the length of the mesopterygoid. Its dorsal surface does not bear a notch for the hyomandibular spine. Instead the spine attaches to the lateral face of the metapterygoid which is braced against the ventral limb of the hyomandibular and the dorsal portion of the symplectic. The ectopterygoid is a relatively strong, elongate bone having its posterior border fully confluent with the anterior border of the quadrate and its dorsal border along the ventral edge of the mesopterygoid and half of the palatine. The toothless ectopterygoid is elongate but little arched. It does not contact the metapterygoid as in *Thorophos*, *Maurolicus*, *Valenciennellus*, *Danaphos*, *Polymetme*, *Vinciguerria*, and *Spirinchus*.

The hyomandibular is short in *Araiophos*, being a little more than one-fourth the length of the cranium. The articulation for the opercle is at the midlength of the hyomandibular rather than relatively close to its dorsal border as in all the other genera examined here. Both the symplectic and quadrate are relatively elongate in an anteroposterior direction. The quadrate has a strong articulation with the ectopterygoid and also with the ventral border of the mesopterygoid. It too is distant from the metapterygoid.

The toothless palatine of *Maurolicus muelleri* is well ossified and its shape is only partially suggestive of that found in *Thorophos* (compare figs. 18, 56). The cartilaginous hiatus between the posterior end of the palatine bone and the anterior end of the mesopterygoid is absent or well ossified by palatine bone. In dorsal view the palatine of *Maurolicus* is elongate and slender, very different from that of *Thorophos* (compare figs. 51, 55).

The toothless mesopterygoid is triangular and without a central fenestra. Posteriorly it broadly articulates with the medial surface of the short, but dorsoventrally deep, metapterygoid. The anteroposterior length of the metapterygoid is a little less than a third of the length of the mesopterygoid. Along its midposterior border the metapterygoid bears a process that contacts the distal end of the hyomandibular. The toothless ectopterygoid of *Maurolicus* is exceptionally large for a stomiatoid and, in addition to contacting the palatine, mesopterygoid, and quadrate, also has a joint surface with the metapterygoid.

The hyomandibular is about one-half the length of the cranium and has the hyomandibular spine very poorly developed. The symplectic is a rather stout bone lying along the posterior border of the quadrate and ventral half of the metapterygoid. The quadrate is elongate and does not bear a posterodorsal groove or process that clasps the lateral distal surface of the symplectic. The quadrate, as in many stomiatoids, has a strong, elongate joint surface with the ectopterygoid. As in *Araiophos*, the articulation between the quadrate and the lower jaw of *Maurolicus muelleri* (see fig. 22) lies anterior to a line drawn downward from the middle distance between the anterior and posterior ends of the mesopterygoid; however, the palatoquadrate arch is deep and the relative distance between the parasphenoid and distal end of the quadrate is much greater in *Maurolicus* than in *Araiophos*.

As in other skull characteristics, the palatoquadrate arch and upper hyoid bones of *Valenciennellus tripunctulatus* and *Danaphos oculatus* (figs. 23, 24, 25, 58) are similar. Both have toothless palatines which are rather typical of primitive stomiatoids (compare with fig. 18 of *Thorophos*). The cartilaginous lamina between the mesopterygoid and palatine is well developed (see especially fig. 23 of *Danaphos*). The posterior ventral lamella of the palatine is well developed and contacts both the mesopterygoid and the ectopterygoid in both genera.

In both genera the toothless mesopterygoid

is relatively long but is excluded from contact with the quadrate by the ectopterygoid. The ventrolateral border of the mesopterygoid of *Valenciennellus* does not have a completely enclosed fenestra as is found in *Danaphos* and *Thorophos*. In both *Danaphos* and *Valenciennellus* the metapterygoid is short in its anterior-posterior dimension. The bone is especially deep or long in its dorsal-ventral dimension in *Valenciennellus*. In both genera the bone has relatively extensive joint surfaces with the ventral process of the hyomandibular and the elongate, rather slender symplectic. The toothless ectopterygoid is quite large in both genera and, as in *Maurolicus*, forms the main structural member of the palatoquadrate arch. The posterior border of the ectopterygoid is strongly braced against the anterior border of the quadrate, and the dorsoposterior angle of the ectopterygoid has an important and firm joint with the metapterygoid.

The hyomandibular is a little less than one-half the cranial length in both genera and does not bear a hyomandibular spine. The symplectic is slender and relatively long in *Danaphos* and *Valenciennellus*, about equal in length to the hyomandibular. The joint between the quadrate and the lower jaw lies fairly far anterior on the skull, being well ventral to a point on the anterior one-fourth of the mesopterygoid. The quadrate has a groove along its posterior medial border for the ventral end of the symplectic.

Sonoda megalophthalma and *Argyripnus atlanticus* have similar palatoquadrate arches; however, *Sonoda* has the quadrate-angular (articular) joint farther anterior and *Argyripnus* has a greater vertical dimension in the arch (compare figs. 27, 28).

The palatine bone of *Sonoda megalophthalma* is reduced to a thin bone enveloping the ventral surface of a massive palatine cartilage. Each palatine bears one tooth. The palatine of *Argyripnus atlanticus* is similar but has three rows of teeth, a lateral row of six, and two inner rows each with two teeth.

The metapterygoid is short but relatively deep in its vertical dimension, being about one-third the length of the mesopterygoid in *Sonoda* and *Argyripnus*. In both genera the posterior border of the metapterygoid is in contact with the ventral part of the hyomandibular and the slender symplectic. In *Sonoda* only a small portion of the metapterygoid borders the

hyomandibular and the metapterygoid adjoins the symplectic for most of the length of the latter. This is correlated with the relatively more anterior position of the quadrate in *Sonoda*. The toothless mesopterygoid in both genera is the largest single bone in the palatoquadrate arch and has a well-developed fenestra. It closely approaches the quadrate and contacts the metapterygoid and ectopterygoid in both genera. The ectopterygoid in both genera is very similar in shape, being an elongate, triangular, toothless bone.

The hyomandibular equals about one-half the skull length in *Sonoda*, whereas it is about two-thirds of the skull length in *Argyripnus*. *Sonoda* lacks a hyomandibular spine, but *Argyripnus* retains the spine. The symplectic in *Sonoda* barely touches the posterior medial groove of the quadrate, whereas in the more posteriorly placed quadrate of *Argyripnus* the symplectic accompanies the medial posterior groove for almost one-half of the length. The anterior tip of the quadrate lies below the posterior portion of the anterior third of the mesopterygoid in *Sonoda* and below the anterior portion of the posterior third of the mesopterygoid in *Argyripnus*.

The palatoquadrate arch of *Polyipnus asteroides* (figs. 24, 61, 62) as well as other species of *Polyipnus* is very deep or long in its vertical dimension and the quadrate-angular (articular) joint is very far forward, being below the anterior tip of the mesopterygoid and the anterior border of the eyes.

The palatine bears a single anterior-posterior row of seven to eight teeth in *P. asteroides*. *Polyipnus laternatus* and *Polyipnus* sp. have five to seven teeth similarly arranged. *Polyipnus tridentifer* lacks palatine teeth. All the species of *Polyipnus* examined have a large, clavate palatine cartilage with its dorsolateral and ventral surfaces clasped by a fairly large palatine bone. The palatine bone and cartilage tapers posteriorly where both articulate with the ectopterygoid and mesopterygoid. This shape is considerably modified from that found in primitive stomiatoids such as *Thorophos* (compare figs. 61 of *Polyipnus* with 51 of *Thorophos*).

The largest bone in the palatoquadrate arch in all species of *Polyipnus* examined is the toothless mesopterygoid. The dorsal lamella below the eye is especially large in this genus. The bone has extensive articular surfaces with the ecto-

pterygoid, metapterygoid, and the dorsal border of the quadrate. The last joint surface excludes the ectopterygoid from contact with the metapterygoid. As in the nonhatchetfish genera, the metapterygoid is relatively small and its posterior and ventral borders have structurally important joint surfaces with the spineless ventral end of the hyomandibular and the dorsal portion of the symplectic. The toothless ectopterygoid is a relatively small but strong bone with its long axis nearly vertical.

The spineless hyomandibular bone is moderately elongate, being about three-fourths the length of the cranium in all species. The articular process for the opercle is quite dorsal in position and occurs at the dorsal fifth of the length of the hyomandibular. The symplectic is stout with a quadrangular dorsal body in contact with the ventral border of the metapterygoid and an elongate ventral ramus articulating with the dorsal posterior part of the quadrate. The dorsal half of the anterior border of the quadrate is articulated to the ectopterygoid. In all other genera of sternoptychids three-fourths or more of the anterior border of the quadrate contacts the ectopterygoid.

The palatoquadrate arches of *Argyropelecus* and *Sternoptyx* (see figs. 32, 34, 64, 66) are very different from *Polyipnus* and show certain similarities to each other. Both have long vertical dimensions, both have the quadrate-angular (articular) joint relatively more posterior (under the midregion of the eye and posterior area of the mesopterygoid), both have a relatively slender toothless ectopterygoid, both have a large metapterygoid and a small mesopterygoid, and finally, both have an elongate hyomandibular that slightly exceeds the cranium in length. The hyomandibular is spineless in *Sternoptyx* but has a spine in *Argyropelecus*.

The palatine of *Argyropelecus* bears a single row of teeth, four to seven teeth in *A. aculeatus*, two to three in *A. gigas* and *A. hemigymnus*, and about six in *A. pacificus*. The palatine bone of all species of *Argyropelecus* (see figs. 31, 63) is highly modified (compare with fig. 51 of *Thorophos*) but possesses a posterior tooth-bearing process that articulates with the ectopterygoid. This process is similar to that found in relatively primitive stomiatoids such as *Polymetme* (see Weitzman, 1967a, p. 520, fig. 13). All species of *Argyropelecus* examined have a relatively large metapterygoid very similar to the one illustrated

for *Argyropelecus aculeatus* (fig. 32). In *A. gigas* and *A. pacificus* the mesopterygoid about equals the metapterygoid in size. In all the other species the mesopterygoid is smaller than the metapterygoid. In all species of *Argyropelecus* the mesopterygoid is excluded from contact with the quadrate by the metapterygoid, not the ectopterygoid as in *Danaphos*, *Valenciennellus*, *Maurolicus*, and *Thorophos*. In this respect *Argyropelecus* is more like *Polymetme*, *Spirinchus*, and *Vinciguerria* in which a joint between the dorsal border of the quadrate and ventral border of the metapterygoid is prominent. The ectopterygoid is long, slender, and tapers to almost a point on both ends, the dorsoposterior border binding the mesopterygoid, metapterygoid, and quadrate in a series.

The hyomandibular bone of *Argyropelecus* bears a spine associated with the metapterygoid, and the articular surface for the opercle occurs within the dorsal one-fourth of the length of the hyomandibular. The clavate shape of the symplectic in *Argyropelecus* is consistent among the species examined and, importantly, it does not have an articular surface with the metapterygoid. Of the other genera so far illustrated here or by Weitzman (1967a), only *Sternoptyx*, *Polymetme*, and *Vinciguerria* do not have a joint surface between the metapterygoid and symplectic. The quadrate is triangular and elongate as in the other hatchetfishes. Its greatest length is vertically oriented rather than at a posterior sloping angle. Its dorsal border contacts the ventral border of the metapterygoid rather than the mesopterygoid as in *Polyipnus*.

Sternoptyx diaphana (figs. 34, 66) and *Sternoptyx* sp. have almost identical palatoquadrate arches whose essential organization is close to that found in *Argyropelecus*.

The palatine of *Sternoptyx* is roughly conical to cuboidal with an apex of the bone and cartilage extending posteriorly. A slender bony process (see fig. 34) bearing one to three teeth extends posteromedially from the ventral border of the palatine for one-half to three-fourths the length of the palatine bone. This palatine dental process is characteristic of *Sternoptyx*.

The mesopterygoid is small and contacts only about the dorsal one-third of the ectopterygoid and half the anterior border of the metapterygoid. The latter bone does not contact the short symplectic and has a structurally important joint with the dorsal border of the quadrate.

The ventral half of the posterior border of the metapterygoid is firmly bound to the ventral process of the hyomandibular.

The articular surface on the hyomandibular for the reception of the opercle occurs within the dorsal one-eighth of the length of the hyomandibular. The hyomandibular is exceedingly elongate, spineless, and contacts a very short clavate symplectic. The quadrate is triangular, moderately elongate in its vertical dimensions, and has its entire dorsal border in contact with the metapterygoid.

VENTRAL PORTION OF THE HYOID APPARATUS

McAllister (1968, pp. 48–51) reported the branchiostegal ray number of many stomiatoids and recorded seven to 10 for "maurolicids" and five to 11 in "sternoptychids." His records are almost all taken from the literature and are based on various authors (mostly Grey, 1964, and Schultz, 1964) who did not utilize cleared and stained material. Unfortunately many of these counts are in error and experience has led me to consider no counts valid unless taken on
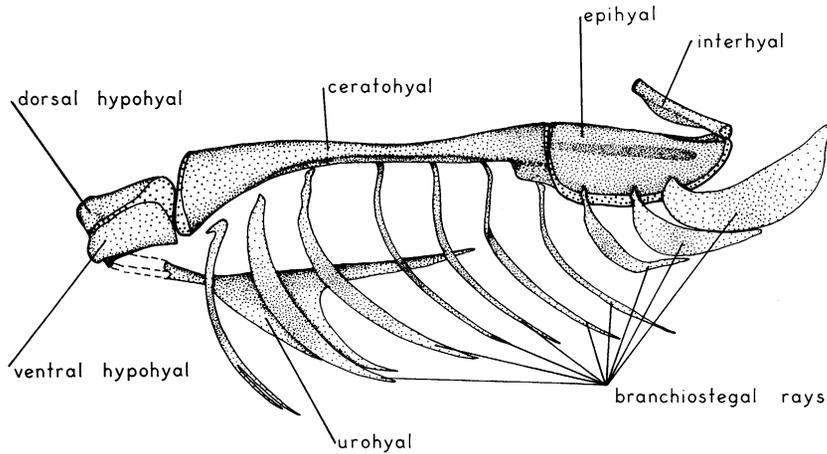
FIG. 67. Lateral view of the left side of part of the hyoid apparatus of *Thorophos euryops*, SL 44.7 mm., DANA 3736-VI.
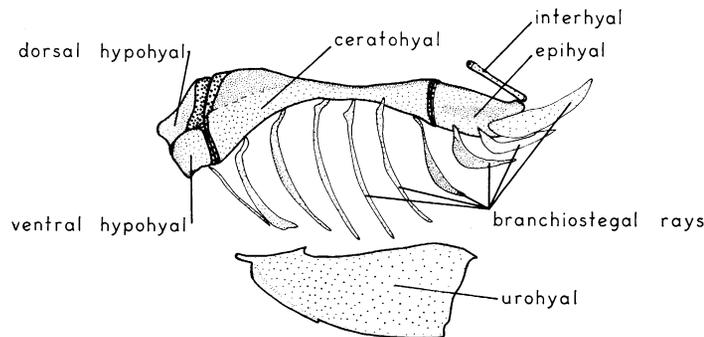
FIG. 68. Lateral view of the left side of part of the hyoid apparatus of *Maurolicus muelleri*, SL 45.5 mm., USNM 201138.
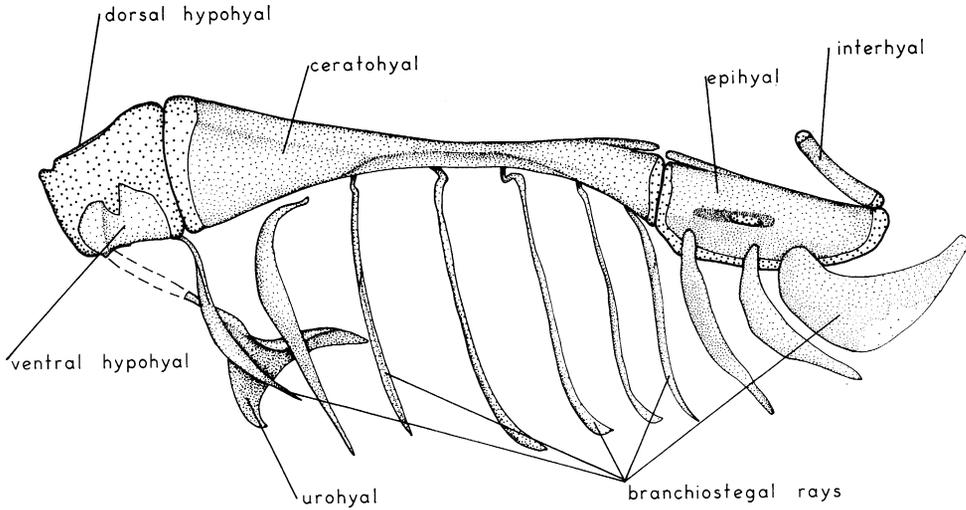
FIG. 69. Lateral view of the left side of part of the hyoid apparatus of *Danaphos oculatus*, SL 34.5 mm., USNM 203261.
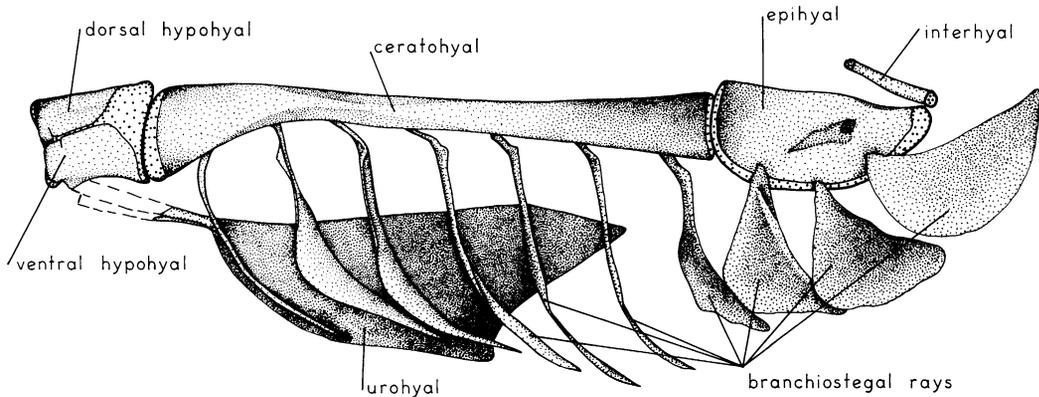
FIG. 70. Lateral view of the left side of part of the hyoid apparatus of *Argyripnus atlanticus*, SL 57.0 mm., USNM 201351.

specimens stained with alizarin. Epihyal rays are easily overlooked, especially as they are not associated with photophores as are the rays along the ceratohyal. All sternoptychid species examined here have a total of 10 branchiostegal rays except members of the genus *Sternoptyx* which have a total of six (see figs. 67–74). Counts of nonstained specimens at hand confirm a count of 10 branchiostegal rays for all sternoptychids. This count and my counts of alizarin specimens include some specimens counted as eight by Grey (1960a, 1960b, 1961,

1964). Presumably an occasional specimen may have one less or one more than the counts recorded here, but I have been unable to find a variant number of rays. All sternoptychid genera had three rays attached to the ventro-lateral face of the epihyal. The remaining rays were attached to the ventral or ventromedian face of the ceratohyal except the anterior ray in *Maurolicus*, *Valenciennellus*, and *Danaphos*. In these genera it was attached to the ventral hypohyal or at the joint between the ventral hypohyal and the ceratohyal in which case most of
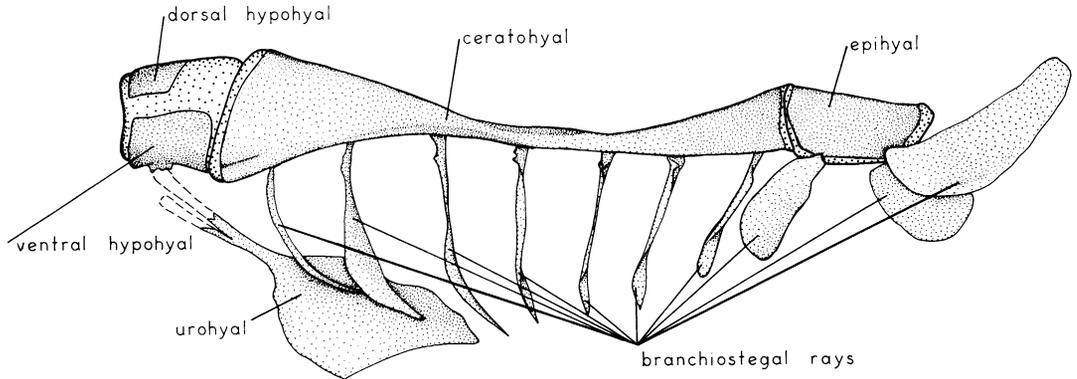
FIG. 71. Lateral view of the left side of part of the hyoid apparatus of *Sonoda megalophthalma*, SL 53.5 mm., USNM 201350.
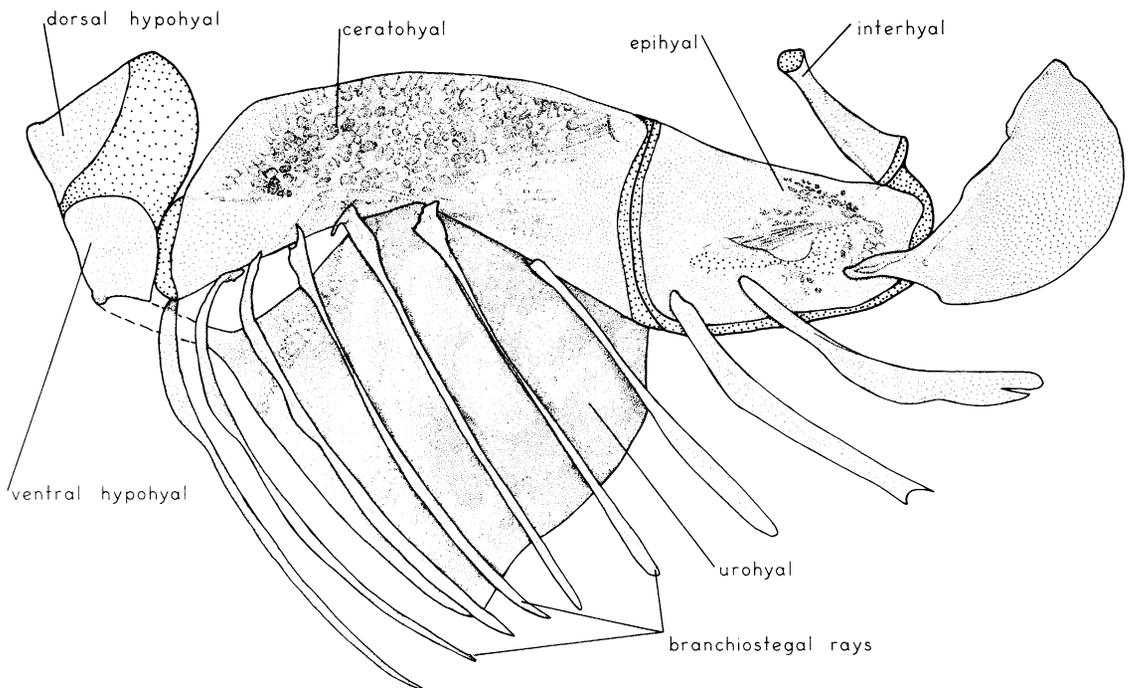
FIG. 72. Lateral view of the left side of part of the hyoid apparatus of *Polyipnus asteroides*, SL 58.5 mm., USNM 197542.

the connecting ligament extends onto the ventral hypohyal.

Polyipnus and *Argyropelecus* have seven ceratohyal branchiostegal rays, whereas *Sternoptyx* has three for a total count of six. McAllister (1968) reported 10 to 21 branchiostegal rays in the gonostomatids (including photichthyids). Counts on all the specimens listed here in the materials section produced a range of 12 to 16 in the gonostomatids and 11 to 22 in the photichthyids. All gonostomatid genera have either four, five, or six branchiostegal rays on the
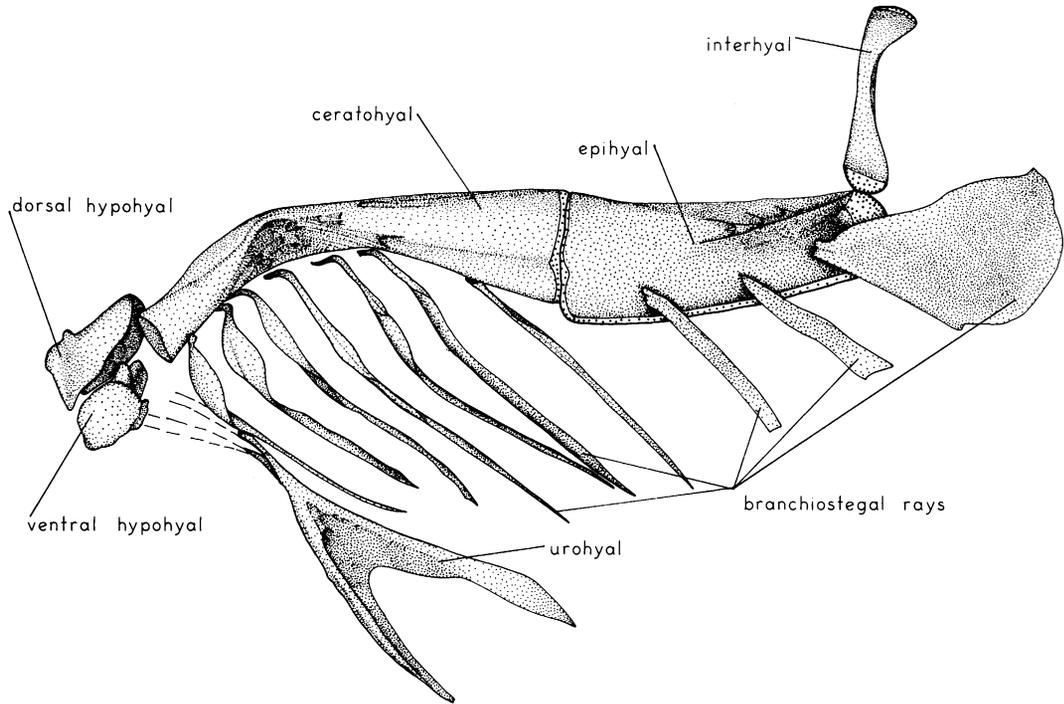
FIG. 73. Lateral view of the left side of part of the hyoid apparatus of *Argyropelecus aculeatus*, SL 49.5 mm., USNM 179056.
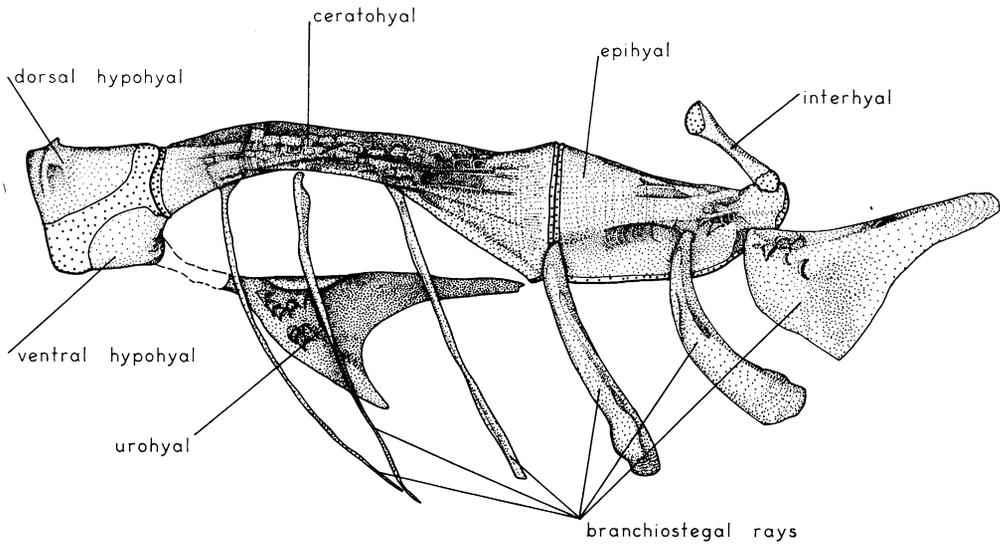
FIG. 74. Lateral view of the left side of part of the hyoid apparatus of *Sternoptyx diaphana*, SL 44.0 mm., USNM 192843.

epihyal. There are four, five, six, or seven branchiostegal rays on the epihyal in photichthyids, depending on the genus. Counts of 10 to 12 branchiostegal rays for *Vinciguerria* given by McAllister (1968) from the literature appear in error, for the single specimen of *V. lucetia* and all the specimens of the various species examined here and all the specimens of *V. lucetia* reported by Ahlstrom and Counts (1958) had 12. The other genus of photichthyid with a low branchiostegal ray number, *Ichthyococcus*, is reported to have 11 or 12 rays and I have confirmed this number. *Ichthyococcus* is further distinguished from the sternoptychid genera by having five rather than three branchiostegal rays on the epihyal. *Photichthys* had the greatest number of branchiostegal rays with a total of 15 along the ventral hypohyal and ceratohyal and seven on the epihyal. This indicates that *Photichthys* is a relatively primitive photichthyid, providing that the general rule proposed by Hubbs (1919) and McAllister (1968), that forms with a higher number of branchiostegal rays are generally more primitive, is correct. In this regard it should be noted that a survey of the osteology of *Photichthys* indicates that it is one of the more primitive stomiatoids in several characters; however, as noted in the Introduction, it does have three pectoral radials, presumably a more advanced number than the four radials found in almost all the gonostomatid genera.

In considering the stability of the above counts, the number of epihyal branchiostegal rays is more important than the total ray count because the number of rays on this bone are stable in all species and genera examined. When there is a variation of total ray count between the right and left side of a specimen or between specimens of a given species or genus, the anterior ray on the ventral hypohyal or ceratohyal is where the variation occurs. No variation was found in the epihyal count.

The shape and form of the lower hyoid bones is characteristic for all genera illustrated here (figs. 67–74). All the sternoptychid genera, exclusive of *Polyipnus*, *Argyropelecus*, and *Sternoptyx*, have a relatively short epihyal, its length invariably less than one-half the length of the ceratohyal (almost one-fourth the ceratohyal length in *Sonoda*). In *Polyipnus*, *Argyropelecus*, and *Sternoptyx* the epihyal is relatively long, being well over one-half the length of the ceratohyal. The ceratohyal of the sternoptychids exclusive of the hatchetfish genera is relatively slender, especially along its midportion. The anterior end is the largest where it abuts the cartilage of the hypohyals. In the hatchetfishes the posterior end is the largest, and the midsection of the ceratohyal is not so slender as in the other sternoptychid genera. *Polyipnus*, *Argyropelecus*, and *Sternoptyx* have a more pronounced arch in the ceratohyal. *Polyipnus* has a very distinctive ceratohyal that has been strengthened along its midportion by a thick, dorsal crest of bone that extends the entire length of the bone. The shape of the ceratohyal in sternoptychids reflects the presence of the branchiostegal photophores and the ventral border of the bone is arched to correspond with the dorsal border of the common gland of the branchiostegal photophores.

The hypohyals are variously ossified in the sternoptychids but are typically dorsal and ventral layers of bone surrounding the hypohyal cartilage. The dorsal hypohyal occasionally is very reduced (for example *Danaphos* and *Sonoda*). The ventral hypohyal in all species provides attachment for the sternohyoidus ligament (one on each side of the urohyal) and the bone remains well ossified. In figure 73 of *Argyropelecus* the hypohyals are shown without cartilage. Here the bony parts for the canal bearing the anterior hypobranchial artery can be seen. These bony sheaths of the canal are attached anteriorly to the ventral hypohyal where the artery exits the canal. This condition is found in all genera examined here. The hypohyals of *Polyipnus* are very deep and characteristic of all species (fig. 72).

The shape of the urohyal is characteristic of each genus and, like the ceratohyal, usually reflects the position of the adjacent, anterior photophores of the isthmus. Those genera with a deeply incised posterior margin of the urohyal have the anterior photophores of the isthmus encroaching upon the urohyal. The lower hyoid bones of *Valenciennellus* are not illustrated but they are very similar to those of *Danaphos*. Those of *Araiophos* are similar to those of *Thorophos*. Some sternoptychids exhibit some interesting variation in the size and shape of the urohyal and its point of attachment to the hypohyal. The large, flat, platelike urohyal illustrated in figure 72 for *Polyipnus asteroides* is characteristic of the genus. In some species the urohyal is considerably smaller, for example *Polyipnus unispinus*, but it still retains the broad,
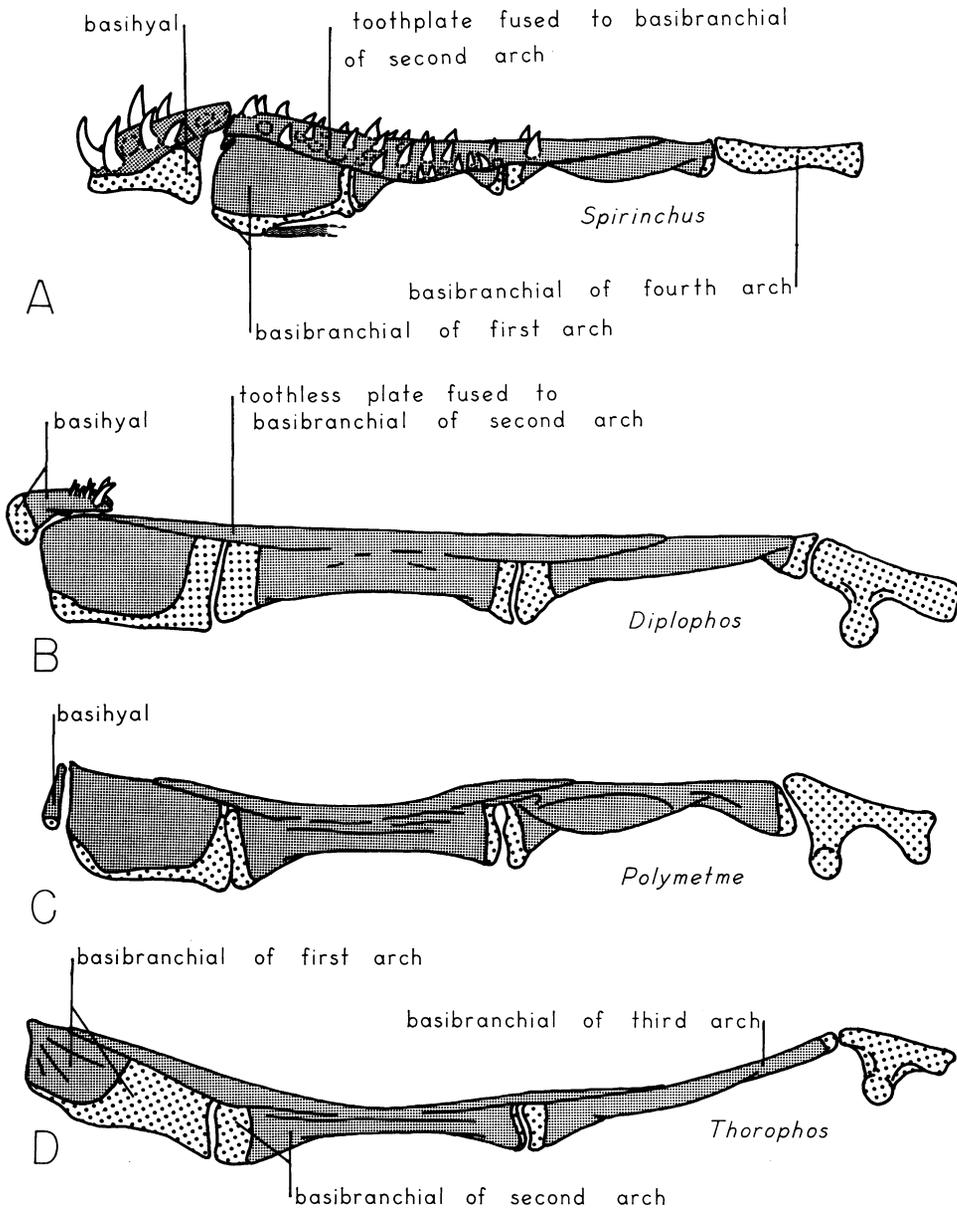
FIG. 75. Lateral view of basibranchial series. A. *Spirinchus thaleichthys*, SL 108.5 mm., USNM 104689. B. *Diplophos maderensis*, SL 104.0 mm., USNM 186364. C. *Polymetme corythaeola*, SL 174.0 mm., USNM 199507. D. *Thorophos euryops*, SL 44.7 mm., DANA 3736-VI. Anterior is to the left.

almost square profile. Both *Argyropelecus* and *Sternoptyx* have the posterior border of the uro-hyal deeply incised (figs. 73, 74) and in both genera this deep notch is associated with the anterior photophores of the isthmus.

BRANCHIAL APPARATUS

The branchial apparatus of osmerids may be considered relatively primitive for teleosts and therefore is compared herein with that of stomiatoids. The branchial arches of stomia-

toids lack a remnant of the fifth epibranchial and a separate fifth pharyngobranchial tooth plate.

The basibranchial series of *Spirinchus thaleich-thys* (fig. 75A) has a large basihyal cartilage capped by a heavily toothed, large basihyal tooth plate. The anterior three basibranchials are well ossified and the second is fused to an extensive, heavily toothed, tooth plate that extends anteriorly and posteriorly to cover both the anterior or first basibranchial and the third basibranchial bones. The tooth plate covers these bones so tightly that they look fused. However, careful dissection reveals that they are separate. This plate may be considered to be a fusion of three tooth plates, one each over the first three basibranchials, or it could be simply an extension of the second basibranchial tooth plate over the adjoining basibranchials. The fourth basibranchial is a bar of cartilage articulating posteriorly with the ceratobranchials of the fourth and fifth arches. The basibranchial series in stomiatoid fishes appear to be modifications of this basic plan found in *Spirinchus*.

According to Nelson (1970), the basihyal (=glossohyal) of stomiatoids is usually small, toothless, and at least sometimes with its long axis nearly vertical (see fig. 75C, *Polymetme corythaeola*). Actually in a large number of stomiatoids the basihyal is reduced and with a nearly vertical orientation. Exceptions to this condition exist. All sternoptychids have lost the basihyal as well as its tooth plate (see fig. 75D, *Thorophos euryops*). In both species of *Diplophos* examined, the basihyal is horizontal, of moderate size and toothed, a primitive situation for a stomiatoid (see fig. 75B, *Diplophos maderensis*). The basihyal and its tooth plate are absent in *Cyclothone* but it is present in all other gonostomatids (but often very small) and in the photichthyids. As *Cyclothone* is apparently a gonostomatid and has none of the other basic sternoptychid characters, the loss of the basihyal in *Cyclothone* seems to be independent.

The anterior three basibranchials are present in the Photichthyidae, Gonostomatidae, and Sternoptychidae. The elongate basibranchial tooth plate in stomiatoids appears to be formed from the second arch basibranchial tooth plate, not from the fused tooth plates of the first, second, and third arches. It is here called the expanded second arch tooth plate because it appears to have extended anteriorly and posteriorly dorsal to the basibranchials of the first and third arches. Presumably this is a primitive characteristic of stomiatoids. In some genera in both the Gonostomatidae and Photichthyidae there are large, usually lateral tooth plates with teeth superficial to part of the expanded tooth plate of the second basibranchial. These are not fused with the expanded, toothless basibranchial tooth plate below. In some genera, such as *Photichthys* and *Woodsia*, these may occur superficial to the entire basibranchial plate. They probably originated from hypobranchial tooth plates and represent a specialization. *Vinciguerria* is a problem in this regard. Members of this genus have large bilateral-toothed plates superficial to the cartilaginous fourth basibranchial The same kind of tooth structure occurs superficial to the posterior part of the third basibranchial. Immediately anterior to these tooth plates is another, median-toothed tooth plate. This plate appears to be the tooth plate of the third basibranchial and is separate from the expanded toothless tooth plate of the second basibranchial.

No extensive clusters of small tooth plates occur in most sternoptychids. *Argyropelecus* does have a large number of small tooth plates associated with the expanded plate of the second basibranchial and a few small tooth plates occur in some other sternoptychids, for example *Argyripnus*. In many genera of stomiatoids tooth plates and/or gill rakers are associated with the lateral margins of the expanded tooth plate of the second basibranchial. In some, such as *Sternoptyx*, these plates bear large teeth.

All gonostomatids, photichthyids, and sternoptychids have a ventral cartilaginous articular facet for the anterior end of the fourth ceratobranchial. This facet is absent in the Osmeridae (see fig. 75).

The hypobranchials, ceratobranchials, and epibranchials are similar in all sternoptychids, although the numbers of gill rakers and tooth patches, teeth and shape of the fifth ceratobranchial, and shape of the fourth epibranchial can be characteristic of genera and species (see figs. 76, 77, 78). As a group the sternoptychids have reduced tooth patches on the fifth ceratobranchial. *Sternoptyx* is an exception, having large teeth anteriorly near the fourth basibranchial. The photichthyid *Ichthyococcus* also has very reduced fifth ceratobranchial teeth, and in this genus gill teeth are reduced throughout the oral cavity. Most photich-
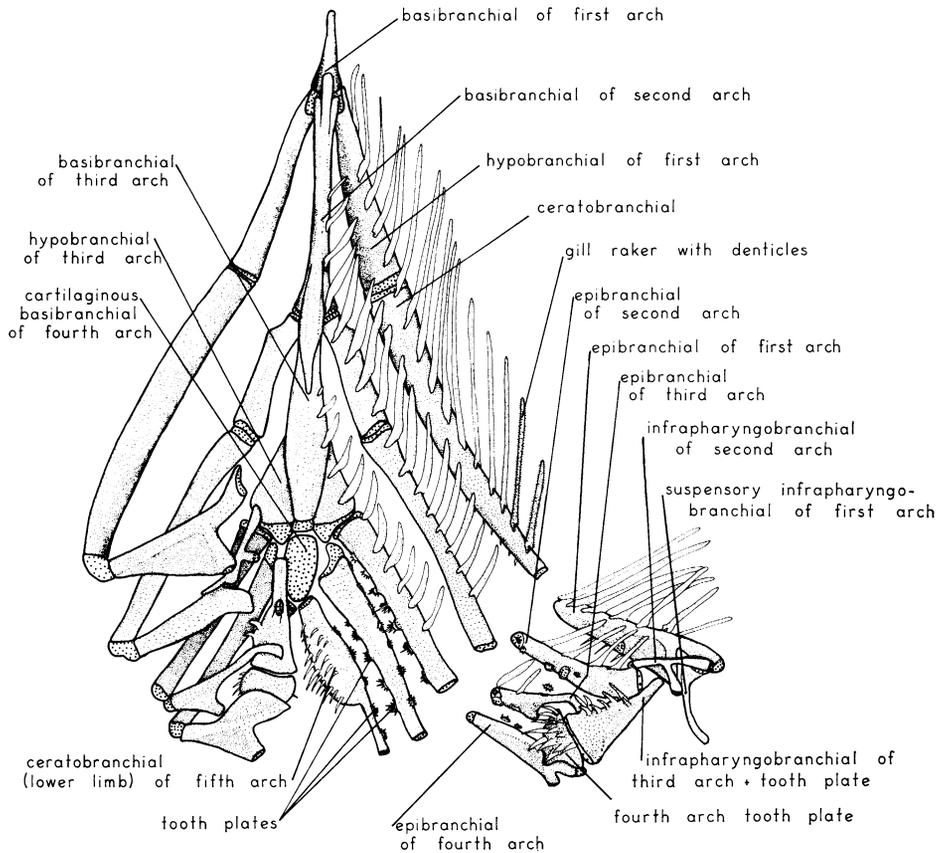
FIG. 76. Dorsal view of gill arches of *Maurolicus muelleri*, SL 45.5 mm., USNM 201138. Dorsal parts of right side shown in ventral view.

thyid genera have well-developed branchial teeth.

The infrapharyngobranchials of *Spirinchus thaleichthys* (fig. 79) are typical of osmerids and stomiatoids. The first arch infrapharyngobranchial is without attached teeth or tooth plates in all genera studied except *Gonostoma*, which has a small tooth plate lateral to the ventral end of the bone. This plate has probably migrated dorsally from the dorsal end of the epibranchial. Small isolated tooth plates associated with the first epibranchial are known in *Albula*, *Elops*, and *Megalops*. They are not known in any stomiatoid other than *Gonostoma*.

The second infrapharyngobranchial is without teeth in all sternoptychids but in the gonostomatids, photichthyids, and osmerids the condition is variable. *Spirinchus* has small, isolated tooth plates associated with the bone.

Osmerus lacks these. *Polymetme*, *Yarella*, *Ichthyococcus*, *Woodsia*, *Triplophos*, *Gonostoma*, and *Cyclothone* lack fused or isolated tooth plates. *Photichthys*, *Diplophos*, *Margrethia*, and *Bonapartia* have small, isolated tooth plates associated with the second infrapharyngobranchial. *Vinciguerria* and *Pollichthys* have a tooth plate fused to the second infrapharyngobranchial.

The third infrapharyngobranchial bears teeth in all nonastronesthoid stomiatoid genera except *Polyipnus*, *Argyropelecus*, *Sternoptyx*, *Sonoda*, *Ichthyococcus*, and *Photichthys*. These genera also lack isolated tooth plates associated with this bone.

The fourth infrapharyngobranchial is associated with an isolated large tooth plate in all genera examined. All genera lack a fifth infrapharyngobranchial tooth plate.
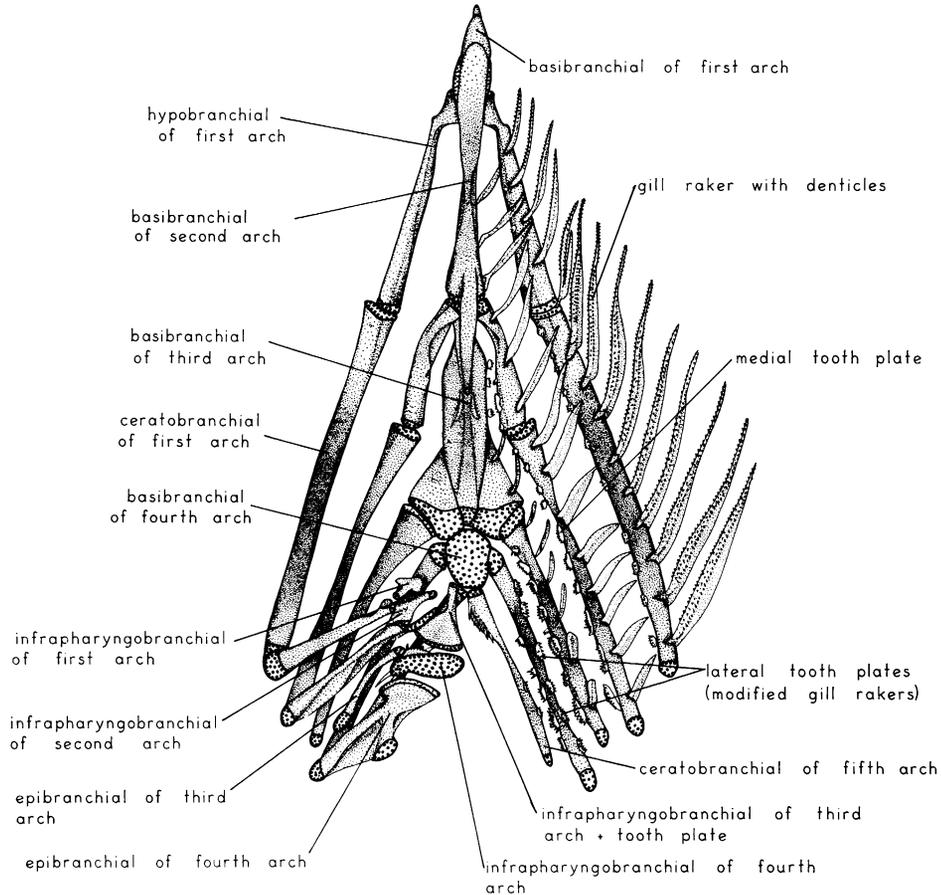
FIG. 77. Dorsal view of gill arches of *Sonoda megalophthalma*, SL 53.5 mm., USNM 201350.

OPERCULAR APPARATUS

Thorophos is the only sternoptychid genus with an opercular apparatus not appearing at least moderately advanced when compared with that of the osmerids and other relatively primitive teleosts. Comparison of figures 18 and 52 of *Thorophos euryops* with figures 2 and 3 of *Spirinchus* in Weitzman (1967a, pp. 510, 511) shows the opercle, subopercle, interopercle, and preopercle to be of approximately the same shape and profile. The dorsal border of the opercle of *Thorophos* is not so deeply notched as in *Spirinchus*, nevertheless this characteristic aspect of the stomiatoid-osmeroid opercle is present (cf. Weitzman, 1967a, pp. 529–530). The subopercle and interopercle of *Thorophos* are of about equal length. The preopercle is a moderately

curved bone forming an important brace for the remainder of the opercular bones, the dorsal portion of the hyoid arch, and the jaws. It bears a laterosensory canal its entire length and is without spines. Both species of *Thorophos* are nearly alike in their opercular apparatus.

The opercular apparatus of *Araiophos gracilis* (figs. 20, 54) is considerably modified. The opercle is reduced to a small, triangular bone that retains some evidence of a dorsal notch posterior to the opercular-hyomandibular joint. The subopercle is short, about one-half the length of the interopercle that retains a profile similar to that in *Thorophos*. The preopercle is reduced to a thin, arched strut that bears little evidence of a lateral line canal on its lateral surface. The opercular apparatus of *Araiophos*
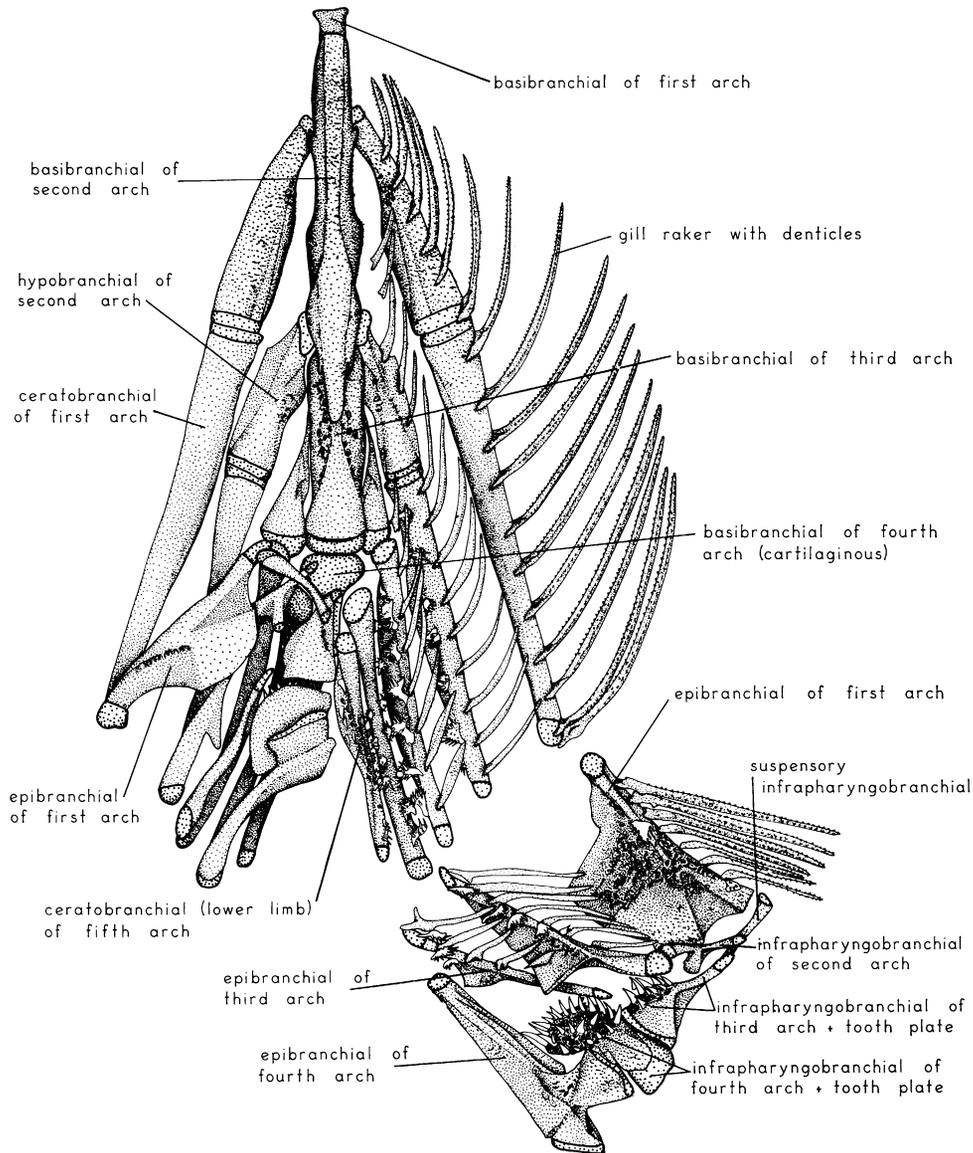
FIG. 78. Dorsal view of gill arches of *Polyipnus asteroides*, SL 58.3 mm., USNM 197542. Dorsal parts of right side shown in ventral view.

eastropas is very similar to that of *A. gracilis.*

The approximately rectangular opercle of *Maurolicus muelleri* (figs. 22, 56) bears a well-developed notch on its dorsal border just posterior to the opercular-hyomandibular articulation. The posterior border of the opercle has a characteristic scalloped appearance. The ventral border is slightly concave, and the rectangular subopercle contacts this opercular border along its entire length. The antero-dorsal corner of the subopercle bears a small spinous process, which is poorly developed or entirely absent in *Thorophos*. The interopercle is somewhat longer than the subopercle, which is correlated with the anterior position of the quadrate-angular joint. The preopercle con-

infrapharyngobranchial
of first arch

infrapharyngobranchial
of second arch

infrapharyngobranchial
of third arch

epibranchial
of first arch

area of tooth plate
fused to
infrapharyngobranchial

infrapharyngobranchial
of fourth arch

tooth plate of
fourth arch

epibranchial of fourth arch
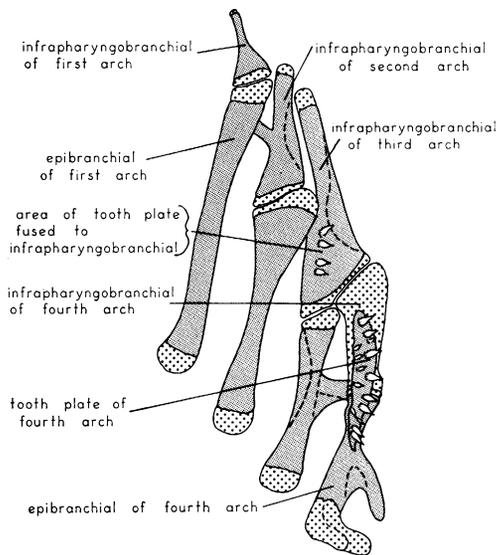
FIG. 79. Ventral view of the dorsal gill bars of *Spirinchus thaleichthys*, SL 108.5 mm., USNM 104689.

sists of two approximately equal limbs, almost at right angles to each other, and the bone bears an open, bony canal along its entire length for the laterosensory system.

The opercular bones of *Danaphos oculatus* and *Valenciennellus tripunctulatus* are very similar (figs. 24, 25, 58). The opercles of both are approximately rectangular in profile, and a notch posterior to the opercular-hyomandibular joint is moderately developed. The opercle of *Valenciennellus* has a longer vertical dimension. The subopercle of both genera is incompletely ossified in all cleared and stained specimens examined. The size of the membranous portion is variable within each species and usually the larger specimens have a more completely ossified subopercle. The anterior and dorsal borders are invariably ossified. No specimen of either genus has a spine on the anterodorsal corner of the subopercle. The anteroposterior length of the subopercle is a little more than one-half the length of the interopercle in *Danaphos* and a little less than one-half the same length in *Valenciennellus*. The interopercle is approximately crescentic in profile in both genera but in *Valenciennellus* the posterodorsal portion of the bone is somewhat developed into a separate process contacting the anterodorsal portion of the subopercle. In both genera the

preopercle bears an incompletely closed canal its entire length and is nearly intermediate in profile between that of *Maurolicus* and *Thorophos*.

The opercular apparatus of *Argyripnus atlanticus* (figs. 27, 60) and that of *Sonoda megalophthalma* (fig. 28) have several modifications. The dorsal border of the opercle of *Argyripnus* is similar to that of *Thorophos* in that the opercular bone extends a considerable distance dorsal to the opercular-hyomandibular joint. In addition, the dorsal profile of the opercle is gently convex in both *Thorophos* and *Argyripnus*. The notch posterior to the opercular-hyomandibular joint is present but relatively small in both *Argyripnus* and *Sonoda*. These two genera, like *Thorophos*, have a well-developed opercular spine that forms the distal attachment or insertion for the dilator operculi muscle. The dorsal border of the opercle of *Sonoda* is acutely angled in profile. Its ventral border is nearly straight and approximately parallel with the axis of the body. The ventral border of the opercle in *Argyripnus* is concave in profile.

The subopercle of *Sonoda* is rectangular, without a spine in its anterodorsal corner, and a little more than one-third the length of the interopercle. The same bone in *Argyripnus* is modified and bears a dorsal process that fits against the medial face of the lower half of the opercle. The anterior profile of the subopercle is notched and modified to receive the slender dorsal process of the interopercle. The greatest length of the subopercle about equals the length of the interopercle in *Argyripnus*. The interopercles of *Sonoda* and *Argyripnus* are very different in profile (compare figs. 27, 28). That of *Sonoda* is elongate, with the dorsal process somewhat more slender where it contacts the subopercle. The interopercle of *Argyripnus* is relatively short, especially the ventral portion. The dorsal part of the interopercle is modified into a slender process that contacts the anterior border of the subopercle. The spineless preopercle of both genera bears an open bony tube almost its entire length and the bone has a profile very similar to that of *Thorophos*.

The opercular bones of *Polyipnus asteroides* (figs. 30, 62) are greatly modified. The opercle is a relatively small, more or less rectangular bone with its anterodorsal border partially cut off just posterior to the opercular-hyomandibular joint. A sharp spine for the attachment of the dilator operculi muscle is absent and in its place

the opercle bears a lateral ridge. The opercle is strengthened by a cristate ridge extending from near the opercular-hyomandibular joint to near the midlength of the ventral border of the opercle. A notch posterior to the opercular-hyomandibular joint is absent. The ventral border of the opercle is nearly straight. The subopercle is a more or less triangular-shaped bone with a recess along the ventral portion of its anterior border for reception of a process of the interopercle that, to some extent, articulates with the lateral face of the subopercle. The greatest dimension of the subopercle is about three-fourths the greatest length of the interopercle. The interopercle is in two parts; a rather large, semi-circular body and a dorsal, flattened tabular process that contacts the incised portion and the lateral surface of the subopercle. All species of *Polyipnus* examined have similar opercles and subopercles. The preopercle also can be considered in two parts, a relatively slender dorsal ramus and a ventral, broad body. The posterior and ventral border of the preopercle bears a continuous, open laterosensory canal. Many species of *Polyipnus* bear a large preopercular spine. For example *P. tridentifer* has a large, ventrally directed spine with its axis oriented along the dorsal ramus of the preopercle. The posterior border of the preopercle bears a series of small spines in some species, for example *P. tridentifer* and *Polyipnis* sp. In *P. asteroides* the preopercular spines are poorly developed and only form a weakly dentate posteroventral border to the preopercle.

The opercular bones of *Argyropelecus aculeatus* (figs. 32, 64) are vertically elongate. The opercular spine is well developed, providing an important point of insertion for the dilator operculi muscle. The opercle is strengthened by a vertical longitudinal ridge originating at the opercular-hyomandibular joint where it is continuous with the dilator spine and extends ventrally over the midline of the bone. The profile of the opercle is approximately rectangular, with the anterodorsal border of the rectangle cut off. This latter area represents the area of the opercular notch in such sternoptychids as *Thorophos* and *Maurolicus*. The ventral border of the opercle is relatively straight, contrasted to the different shapes of the bone found in *Argyripnus* (fig. 60) and *Sternoptyx* (fig. 66). The subopercle is approximately triangular in all species of *Argyropelecus* and the

anterodorsal corner of the bone extends dorsally as a process in close contact with the ventroanterior border of the opercle. The interopercle and subopercle are of approximately the same size and triangular shape. The dorsal process of the interopercle is relatively elongate. The preopercle is rather characteristic in shape, consisting of a short anterior limb at right angles to an elongate dorsal limb. A laterosensory canal courses the length of the preopercle. The canal is completely enclosed in bone for part of the dorsal limb. The preopercle normally bears a large ventral spine in all species examined. This spine is a conic, sharp process in some species such as *A. pacificus*. Just dorsal to the base of the ventral preopercular spine is a posterior spine that is usually shorter than the ventral spine. This spine originates on the lamella of bone covering the laterosensory canal where the vertical and horizontal segments of the canal meet.

Sternoptyx diaphana has the most modified opercular bones of all the species considered here (see figs. 34, 66). The opercle is an elongate, roughly crescentic bone with a prominent, dorsally anterior process that articulates with the hyomandibular bone. The opercular spine extends laterally rather than anterodorsally, providing a relatively lateral attachment for the dilator operculi, and also providing more leverage for lateral rotation of the opercle around the opercular-hyomandibular joint. The ventral border of the opercle is strongly convex, almost lanceolate, and the dorsal border of the subopercle is tightly fitted and concomitant. This joint is characteristic for *Sternoptyx*. The interopercle of *Sternoptyx* suggests that of *Argyripnus* and *Polyipnus* in that the bone can be rather distinctly considered to have dorsal and ventral parts. The entire bone is relatively slender when compared with that in these two genera. The preopercle is similar to that of *Argyropelecus* with a very small anterior limb. A large spine extends ventrally from the posteroventral corner of the bone. A groove for the laterosensory canal extends the length of the bone and the crest lateral to this groove bears very small dentate spines. The opercular apparatus of *Sternoptyx* sp. is essentially the same as that of *S. diaphana*.

POSTCRANIAL AXIAL SKELETON

The sternoptychid-gonostomatid-photichthyid vertebral skeleton is of a relatively primitive

teleost form but in certain genera and certain groups of genera parts of the postcranial axial skeleton are specialized to an extreme degree. Some of these parts are the caudal skeleton, the neural and haemal spines, the anteriormost centrum, and the supraneurals. In some cases small size and apparent neoteny produce adults with a relatively poorly ossified axial skeleton accompanied by a lack of fusion of vertebral parts. Vertebral and rib numbers are important differences in some genera.

For purposes of description the vertebral skeleton is divided into two parts, those vertebrae exclusive of the caudal fin complex and the caudal complex itself, consisting of the first preural centrum, the ural centra, and associated structures. In the description below, the precaudal count is taken as including those vertebrae that do not bear a long, single haemal spine and/or are not directly associated with the anal fin pterygiophores. The anterior haemal spine is invariably associated with the anterior pterygiophore of the anal fin. The total vertebral count includes the caudal complex of preural and ural vertebrae as one.

The single usable specimen of *Thorophos euryops* has a precaudal count of 14 and a total vertebral count of 40. Six countable specimens of *T. nexilis* have a total of 45 and another specimen has 44 vertebrae. All specimens of *T. nexilis* counted had 16 precaudal vertebrae.

The first precaudal centrum of *T. euryops* (only one specimen) bears no ribs, and the first and sometimes the second centrum of *T. nexilis* lacks ribs. In both species the body of the first centrum is placed close to the basioccipital, there being no space between the centrum and basioccipital as reported for *Astronesthes* and several other genera of the Stomatoidea by Weitzman (1967b). The shape of the precaudal centra is very similar to that illustrated for *Argyripnus atlanticus* (fig. 80). The first 10 neural arch spines (not true neural spines but modified extensions of the arches) remain unfused to one another in *T. euryops*. The eleventh neural arch spine, which lies between the complicated first and second dorsal fin pterygiophores, is fully fused its entire length. The arches of the precaudal vertebrae appear weakly fused at their bases to the centra below. The autogenous parapophyses are similar to those illustrated in figure 80 but are confined to the anterior half of the centrum. There are 11 full-sized ribs and one short ventral (or pleural)

rib in *T. euryops*. *Thorophos nexilis* has 12 full-length ribs and one short rib. The short rib is absent on one side in some specimens. Dorsal or epipleural ribs appear absent. Epimerals are present but their number was not determined in *T. euryops*. There are eight well-ossified epimerals in a large specimen of *T. nexilis* (SL 65.8 mm.). The epimerals are not fused to the bases of the neural arches or body of the centrum as reported for *Astronesthes* by Weitzman (1967b). In the single specimen of *T. euryops* there is one "intermediate" precaudal vertebra (bearing no ribs or at most a very short rib segment and having no elongate haemal spine). In *T. nexilis* there is one in some specimens, two in others.

The shape of the caudal vertebrae of *T. euryops* and *T. nexilis* is similar to that illustrated for *Argyripnus atlanticus* (fig. 80), and all these vertebrae have the neural and haemal arches fused to their respective centra.

Supraneurals are present in both species of *Thorophos* and consist of rather slender, often bent, clavate rods of cartilage surrounded by bone. The "club end" of the rod is dorsal, just below the skin. The supraneurals are similar to those illustrated for *Argyripnus* (fig. 80). There are about nine supraneurals in *T. euryops* and at least six and probably more in *T. nexilis*. The X-ray negatives of *T. nexilis* are not fully satisfactory and the bone seems to have lost some calcium.

One dissected specimen of *Araiophos gracilis* has 20 precaudal and a total of 46 vertebrae. All specimens of *Araiophos eastropas* at hand have 44 vertebrae, 20 of them precaudal. Ahlstrom and Moser (1969) found 43 to 45 (usually 44) vertebrae in *A. eastropas*.

The structure of the precaudal vertebrae of *Araiophos* is basically similar to that of *Thorophos*. There is no space between the first centrum and the basioccipital. The parapophyses are very small and confined to the anteroventral borders of each centrum. Rib counts are not absolutely certain due to damage but the first vertebra is without pleural ribs and the next 15 appear to bear ribs in both species. The presence of epipleurals (or dorsal ribs) was not determined. The neural arches appear weakly attached by ligaments to pits on the surface of their respective centra. Epimerals are present in both species but their number could not be determined. The observable epimerals are attached to the centrum near the base of each neural
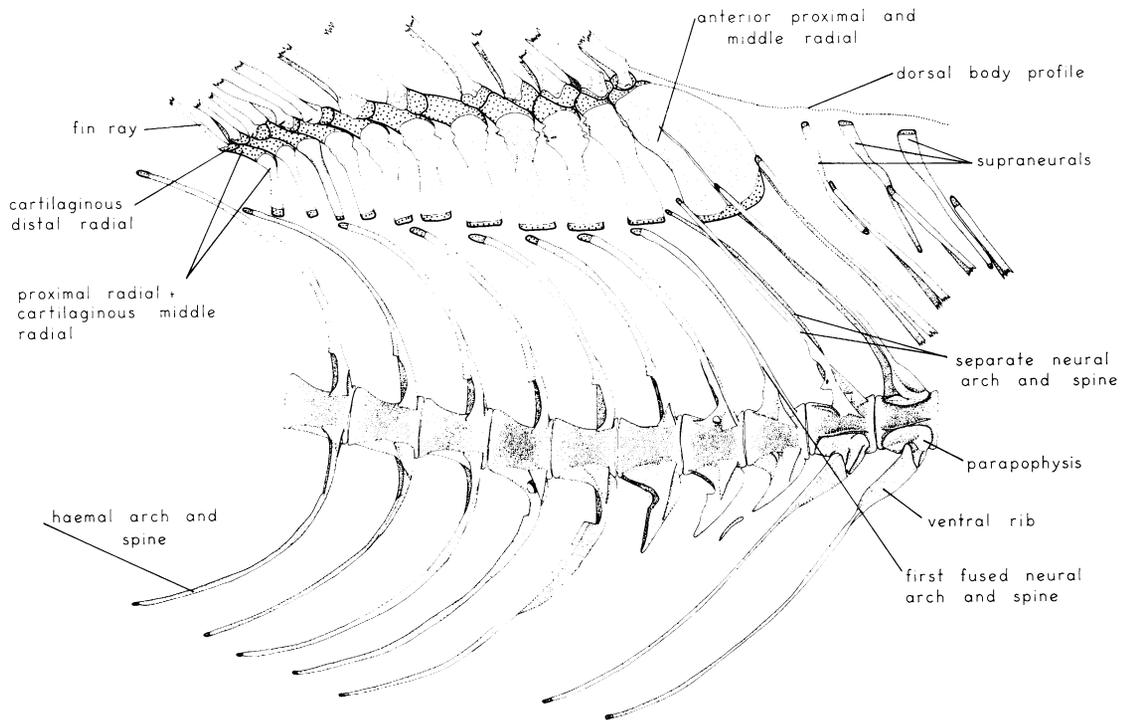
FIG. 80. Lateral view of the right side of the twelfth through the twenty-first vertebrae and dorsal fin of *Argyripnus atlanticus*, SL 57.0 mm., USNM 201351.

arch. In *A. gracilis* the seventeenth and in *A. eastropas* the eighteenth vertebra is the first to bear neural arch spines that are fused to each other.

The neural and haemal arches of the caudal vertebrae of both *Araiophos* species are fused, at least for the most part, to their respective centra. The neural arch of the twenty-third vertebra is the first to be associated with the anterior pterygiophore of the dorsal fin. Supraneurals are present in both species but their number could not be determined from the specimens at hand.

Four specimens of *Maurolicus muelleri* from the Straits of Messina (USNM 40070) have 15 precaudal and a total of 34 vetebrae. Another specimen from this lot has 14 precaudal and a total of 33 vertebrae. Several specimens from the Atlantic (USNM 201138) and South Pacific oceans (USNM 203269 and 203271) have a total of 32 to 33 vertebrae and 14 or 15 precaudal vertebrae. About one-third of the specimens have 32 vertebrae. Two specimens

from the Gulf of Elat (Aqaba) (USNM 203823) have 13 precaudal and a total of 31 vertebrae.

The anterior centrum of *Maurolicus* is closely articulated with the basioccipital, and all the neural arches are fused to their respective centra. The thirteenth neural arch spine is the first to fuse in all specimens except those from the Gulf of Elat (Aqaba) in which it is the eleventh neural arch spine. The first and second centra are without pleural ribs and the following 10 vertebrae bear elongate ribs except in the Elat specimens which have nine rib-bearing vertebrae. The parapophyses are small discs confined to the central constriction of the centrum except posteriorly where they are larger and cover part of the anterior half of each centrum appearing very much like those in figure 80 of *Argyripnus atlanticus*. Dorsal ribs or epipleurals are present on all ribs and continue posteriorly as well-ossified rods to at least the twentieth to twenty-first vertebra where they take their origin from haemal arches. It appears that the vestigial pleural ribs reported for
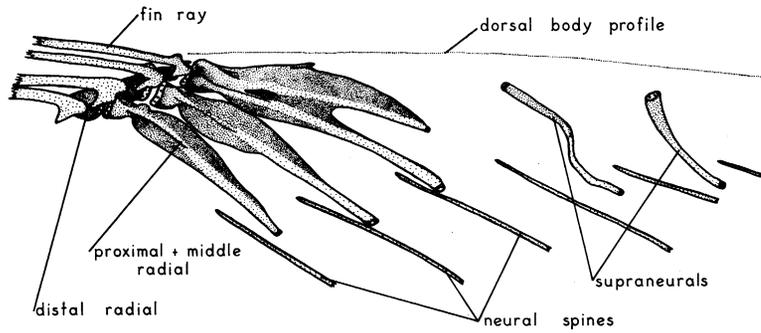
FIG. 81. Lateral view of the right side of the anterior base of the dorsal fin
and supraneurals of *Maurolicus muelleri*, SL 45.5 mm., USNM 201138.

Maurolicus by Baird (1971) are in fact dorsal ribs, for I could find no truly vestigial pleural ribs in the specimens examined for this report. Epimerals are present and articulate with the base of the neural arches anteriorly. At the thirteenth vertebra in specimens not from the Gulf of Elat (Aqaba), the epimerals gradually rise until their site of origin is at the middle of the neural arch. They finally terminate at the twentieth vertebra where they take their origin from the midlength of the neural spine. The shape of the precaudal and caudal vertebrae is similar to that of *Argyripnus atlanticus* (fig. 80). The specimens of *M. muelleri* from the Gulf of Elat had eight, whereas the rest of the specimens had nine supraneurals (see fig. 81 of *M. muelleri*). Baird (1971) used the term pterygiophores for the structures here called supraneurals.

Almost all specimens of *Danaphos oculatus* examined (from the southeastern Pacific Ocean) have 12 precaudal and a total of 38 to 39 vertebrae. One specimen has 13 precaudal vertebra. The neural arches and haemal spines of all vertebrae are weakly ossified but appear fused to the cylindrical, thinly ossified centra. The anterior three or four centra are moderately constricted at their midlength but the remainder of the centra are relatively unconstricted. The neural arches of the first six or seven vertebrae remain free from each other, the "spine" of the seventh or eighth neural arch is fused its entire length. The distal end of the first fused neural spine lies between the second and third or the third and fourth dorsal

fin pterygiophore. The first centrum is without pleural ribs and the second through the ninth bear moderately elongate ribs which are attached to small autogenous parapophyses placed along the anterior half of their respective centra. Neither epimerals nor dorsal ribs are ossified, and their presence as cartilaginous rods is doubtful. Six weakly ossified but well-developed cartilaginous supraneurals are present and shaped like those of *Maurolicus muelleri* (fig. 81).

Valenciennellus tripunctulatus has 12 precaudal and a total of 32 or 33 vertebrae. The neural and haemal arches are moderately well ossified and appear fused to their respective centra which are more constricted at their midlength than those of *Danaphos*. The first centrum does not bear ribs. The second through tenth vertebrae bear pleural ribs and small autogenous parapophyses attached to the anterior half of each centrum. The seventh neural arch spine is the first to be fused and the twelfth neural spine is the first to lie between dorsal fin pterygiophores. No epipleurals (dorsal ribs) and only about nine epimerals could be counted. Only one or two cartilaginous supraneurals were evident over the anterior end of the vertebral column.

The specimen of *Argyripnus atlanticus* examined has 16 precaudal and a total of 46 vertebrae. A specimen of an unidentified species of *Argyripnus* from the Indian Ocean (latitude 06°51'S longitude 39°54'E) has a precaudal count of 15 and a total count of 42. Two specimens of an unidentified species of *Argyripnus* from Hawaii
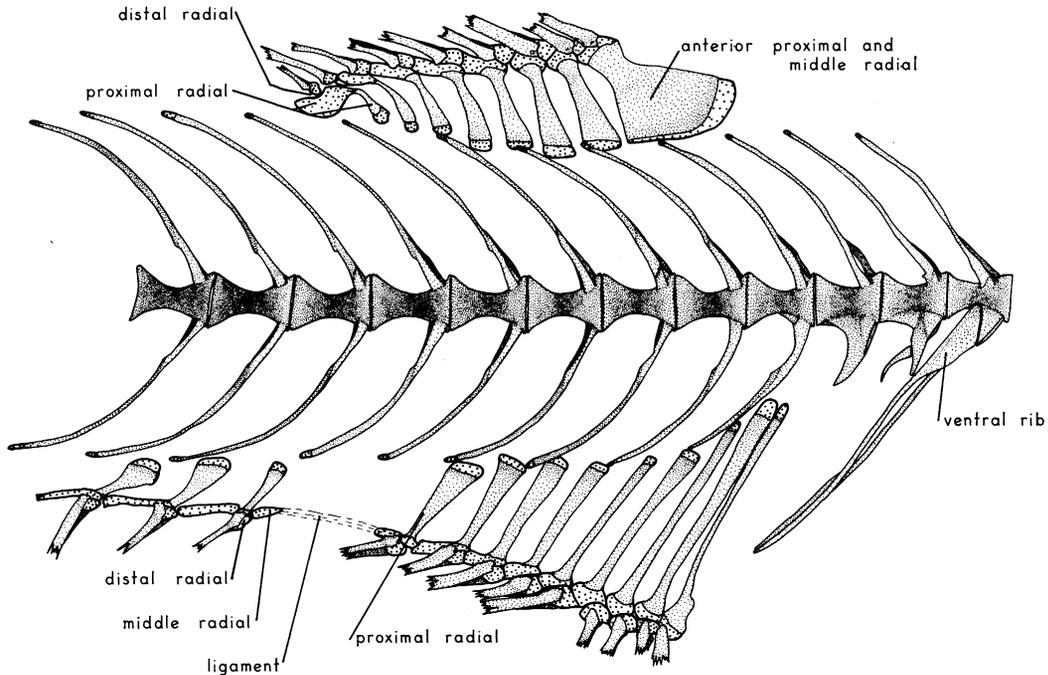
FIG. 82. Lateral view of the right side of the twelfth through the twenty-third vertebrae and the dorsal and anal fins of *Sonoda megalophthalma*, SL 53.5 mm., USNM 201350.

(USNM 126079) and a specimen from the Philippine Islands (USNM 135402) have 15 precaudal and a total of 44 vertebrae.

Figure 80 illustrates the twelfth through the twenty-first vertebrae of *Argyripnus atlanticus* and includes two typical precaudal vertebrae bearing autogenous parapophyses and pleural ribs. Three "intermediate" ribless vertebrae (classed as precaudals here) and five caudal vertebrae are also shown. The neural and haemal arches are well ossified and, with the exception of the first 12 vertebrae, fused to their respective centra. In *A. atlanticus* the fourteenth vertebra is the first to bear a fused neural spine and arch. As in most other sternoptychids the change between fused and unfused neural spines and arches is abrupt, the fourteenth spine being fused its entire length, the thirteenth not fused at all. The distal tip of the fourteenth neural spine lies between the proximal ends of the first and second pterygiophores of the dorsal fin. Five well-ossified epimerals are present (not shown in fig. 80). Posterior to these are two to three cartilaginous epimerals and posterior to this all

visual traces of epimerals disappear. There are ossified epipleurals (dorsal ribs) over all pleural ribs. These are not shown in figure 80. The shape of the nine to 11 supraneurals in *A. atlanticus* is similar to those of *Maurolicus muelleri*.

All specimens of *Sonoda megalophthalma* examined had 14 precaudal and a total of 40 vertebrae. Figure 82 illustrates three precaudal and nine caudal vertebrae of *Sonoda megalophthalma*. These vertebrae are very similar to those of *Argyripnus atlanticus* but more elongate. The anterior 10 neural arches are very weakly or not at all fused to their respective vertebrae in the cleared and stained specimen of *Sonoda megalophthalma* 53.5 mm. in standard length. All other neural and haemal arches are fused to the vertebrae. The eleventh neural spine is the first to be fused and the fusion is abrupt and complete. The first neural spine to lie between the anterior two pterygiophores of the dorsal fin is the fifteenth. There are two anterior vertebrae without pleural ribs followed by 10 vertebrae with large pleural ribs. There may be a small rib associated with the thirteenth vertebra.
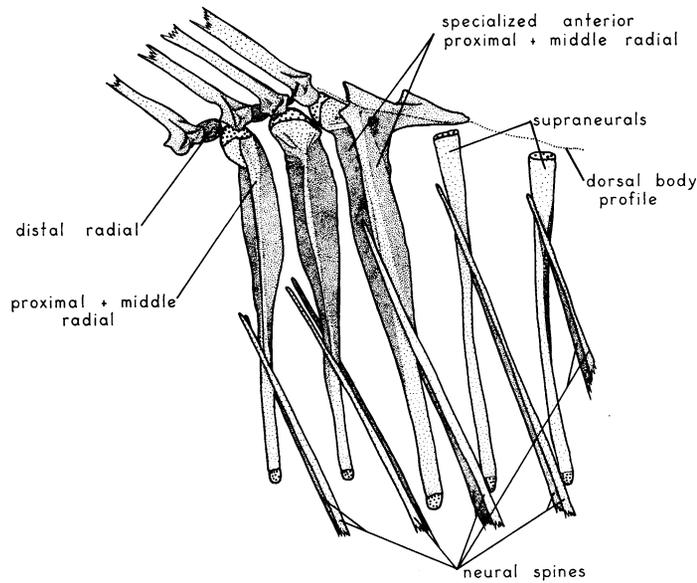
FIG. 83. Lateral view of the right side of the anterior base of dorsal fin and supraneurals of *Polyipnus asteroides*, SL 58.3 mm., USNM 197542.

Epimerals and epipleurals are present but they are not well ossified and their number could not be determined. There are at least seven partially ossified supraneurals similar in form to those of *Maurolicus muelleri*.

Total vertebral numbers in *Polyipnus* species examined cover a range from 32 to 35 (Baird, 1971, reported 31 to 36). Total vertebral numbers are relatively constant within a species. For example, of 45 specimens of *Polyipnus tridentifer* counted, five had 33, 37 had 34, and three had 35 total vertebrae. All specimens had 12 precaudal vertebrae. Of 12 specimens of *Polyipnus asteroides* counted, five had 32 and seven had 33 vertebrae. All specimens had 11 precaudal vertebrae. In *Polyipnus* precaudal vertebrae are considered to include the vertebra with a haemal spine immediately anterior to the anterior pterygiophore of the anal fin. Usually one vertebra anterior to this bears a short haemal spine and is equivalent to the "intermediate precaudal vertebra" of the nonhatchetfish sternoptychids. This gives a count equivalent to the count of precaudal vertebrae taken from the nonhatchetfish sternoptychids above. Several anterior neural arches of large as well as small specimens of *Polyipnus* are not fused to

their centra but are free and each lies in a fossa on the dorsolateral surface of its centrum. The neural arches of the first nine precaudal vertebrae of *P. asteroides* are free of the centra. The ninth may have a few lamellae of bone fused to the centrum but its main structure remains free and articulates in a fossa. The tenth neural arch is completely fused. In *P. tridentifer* the first anterior 10 neural arches are free or partially free from their vertebrae. The eleventh arch is completely fused to its centrum. In *P. asteroides* each neural arch (spine) of the anterior 11 vertebrae (12 in *P. tridentifer*) remains unfused to its counterpart of the opposite side. The twelfth arch in *P. asteroides* (thirteenth in *P. tridentifer*) is completely fused. Both species have expanded anterior plates around the bases of the arches and partially up the spinelike processes. The plates incline medially and come together anteriorly where usually they do not quite fuse to each other. These plates are absent distally and the neural spines are well separated (fig. 83 of *Polyipnus asteroides*) where the supraneurals and anterior three or four (in both *P. asteroides* and *P. tridentifer*) pterygiophores may pass between the separated spine halves. There are six large ribs in *P. tridentifer*. These begin on
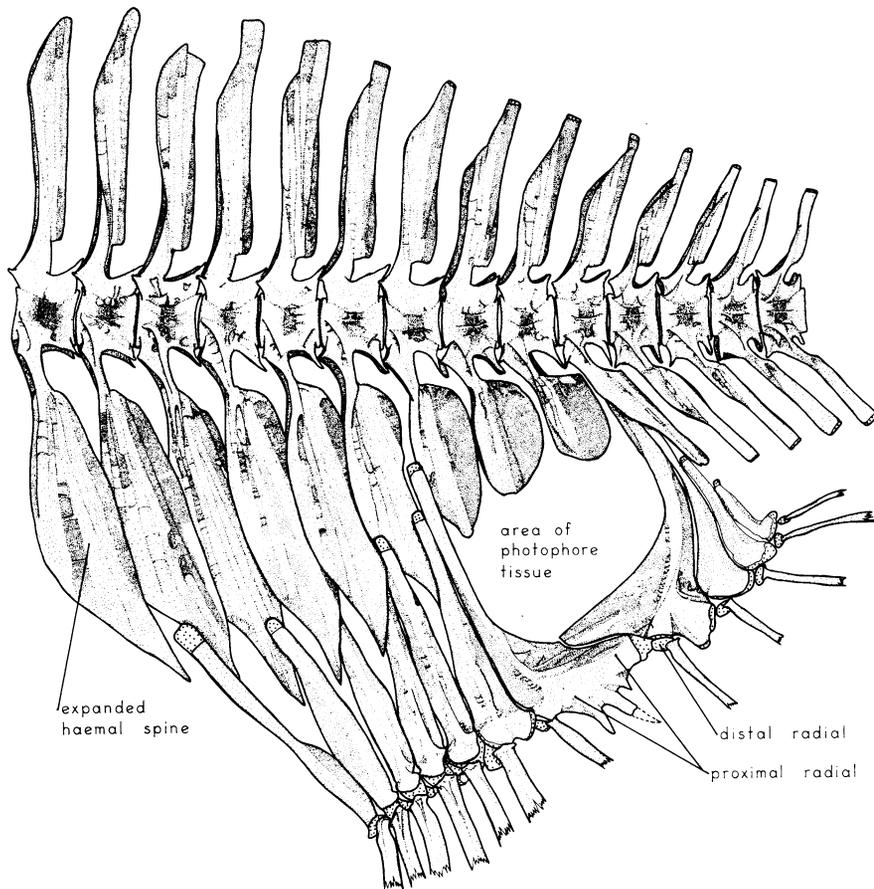
FIG. 84. Lateral view of the left side of anterior caudal vertebrae and anal fin of *Argyro-pelecus aculeatus*, SL 49.4 mm., USNM 179056.

the third precaudal centrum. The posterior two of these six ribs converge on the pelvic girdle where they support its lateral face. Posterior to the six large ribs are two short, relatively thin ribs. *Polyipnus asteroides* has the same number and arrangement of ribs. No epipleurals could be found on any specimens of *Polyipnus*. Epimerals are present on the bases of the neural arches of the second through the thirteenth or fourteenth vertebrae in *P. asteroides* and on the second through the ninth to eleventh vertebrae in *P. tridentifer*. The caudal vertebrae of all the species of *Polyipnus* examined have expanded neural and haemal spines similar to those illustrated for *Argyropelecus aculeatus* (fig. 84). However, the flattened bladelike projections are not so well developed in *Polyipnus*, and the

haemal blades never overlap as in *Argyropelecus*.

The supraneurals are quite large but not especially modified. There are five and usually six in both *P. asteroides* and *P. tridentifer*. The specialized anterior proximal and middle radial of the dorsal fin in all species of *Polyipnus* examined (see fig. 83) is a compound bone which may be formed by fusion of the anterior pterygiophore and the seventh supraneural. Eight supraneurals exist in *Argyropelecus*, whereas only six certain supraneurals exist in *Polyipnus*. This indicates, that perhaps at least the seventh has fused to the dorsal fin, especially because this element projects beyond the profile of the back of the modified supraneurals of *Argyropelecus* and *Sternoptyx*.

All the other species of *Polyipnus* examined
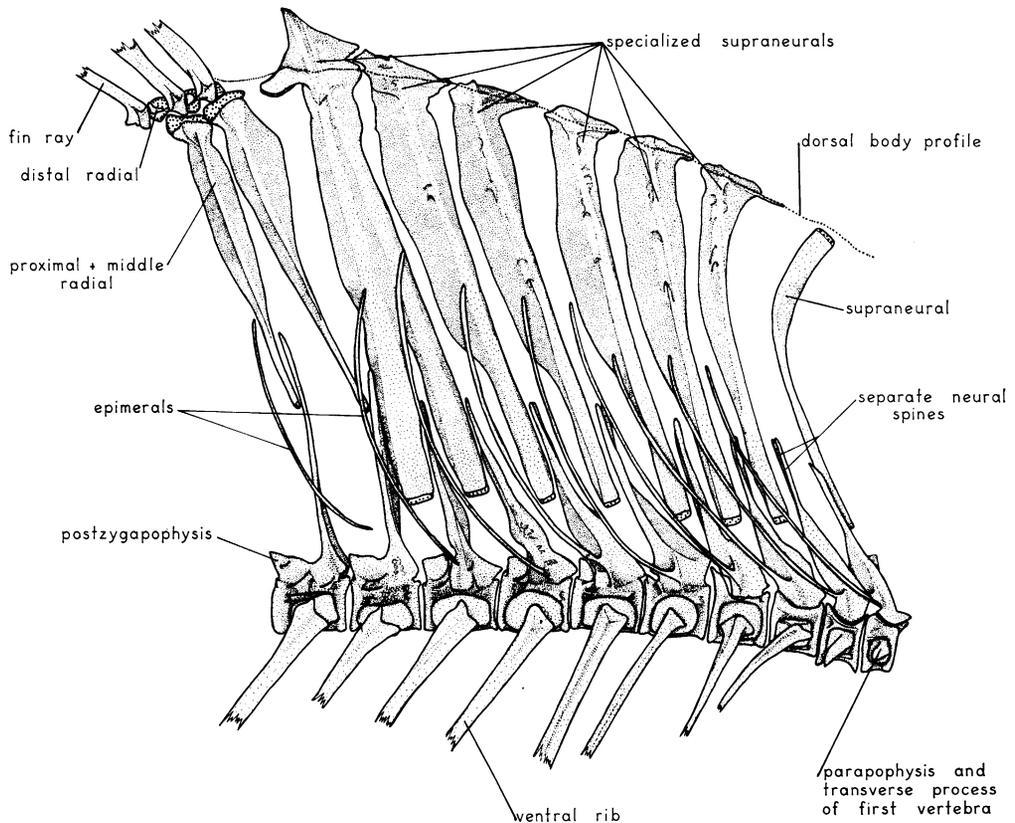
FIG. 85. Lateral view of the right side of the first 10 vertebrae and associated structures of *Argyropelecus affinis*, SL 58.2 mm., USNM 203258.

have vertebral and supraneural counts within the ranges for those given above for *P. asteroides* and *P. tridentifer*.

The total vertebral numbers in all *Argyropelecus* species examined varies from 34 to 40 (Baird, 1971, reported 35 to 40) with 14 or 15 precaudal and 21 to 24 caudal vertebrae. Of eight specimens of *Argyropelecus aculeatus* (USNM 196700) examined, one has a total of 34, five have 35, and two have 36 vertebrae. Three specimens of *A. affinis* have a total of 34 vertebrae. Three specimens of *A. hemigymnus* have 38 vertebrae, one has 37, two of *A. gigas* have 38. Several other species have a total vertebral count within the range of 35 to 37. The first two precaudal vertebrae are without ribs, the third bears a slender pleural rib. Following this, there are seven large ribs. The seventh large rib, attached to the parapophysis of the tenth vertebra, is thicker and stronger than the rest and supports the pelvic girdle. One and sometimes two vertebrae posterior to the tenth vertebra bear small, slender pleural ribs. This pattern is constant for all species examined. The neural spines remain separate in vertebrae one through nine (occasionally eight in *A. gigas*). The first or second vertebra following the supraneurals is the first to bear a fused neural spine (see figs. 85 of *A. affinis* and 86 of *A. aculeatus*). The number of anterior neural arches free from their associated precaudal centra varies, apparently usually being seven in *A. aculeatus* and *A. hemigymnus* but only two or three in *A. affinis* and *A. gigas*. There are nine or 10 epimerals fused to the bases of the neural arches in *A. aculeatus*, *A. hemigymnus*, and *A. affinis*. *Argyropelecus gigas* has eight and some other species, *A. olfersii* and *A. lychnus*, have 11 or 12.
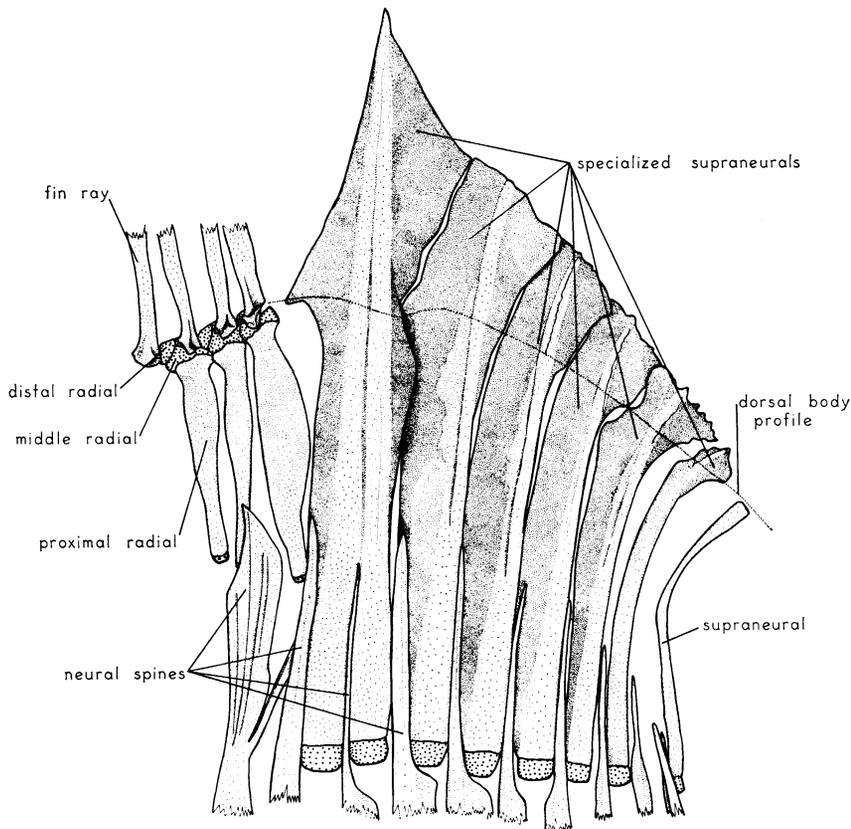
FIG. 86. Lateral view of the right side of the supraneurals and associated structures of
Argyropelecus aculeatus, SL 49.4 mm., USNM 179056.

In some species, *A. aculeatus* and *A. hemigymnus*, the first vertebra is without epimerals.

The caudal vertebrae of all species of *Argyropelecus* examined have greatly expanded haemal spines and moderately expanded neural spines (see fig. 84 of *A. aculeatus*). The neural and haemal spines of *A. affinis* are less expanded and more closely approach the condition described for *Polyipnus*. Note especially the differences illustrated for the neural spines associated with the dorsal fins in *A. affinis* (fig. 85) and *A. aculeatus* (fig. 86).

The supraneurals in *Argyropelecus* are advanced, and representatives of two basic types are illustrated, one in figure 85 of *A. affinis* and the other in figure 86 of *A. aculeatus*. All species of *Argyropelecus* investigated had eight supraneurals. In all cases the anterior supraneural was relatively unmodified and much like those

in the "maurolicids" and *Polyipnus*. The remainder were advanced into what has been called the dorsal blade. This compound structure consists of seven supraneurals, the posterior two supraneurals being fused to each other distally. All these modified supraneurals project above the profile of the back, the posterior elements projecting the greatest distance. The supraneurals of *A. affinis* project less far and each element is less expanded and articulates at a greater distance from its neighbor than those in *A. aculeatus*. Those of *A. aculeatus* are more advanced and more lightly bound by connective tissue to the unfused neural spines at their bases. None of the supraneurals appear fused to the dorsal fin as may be the case in *Polyipnus*.

In *Sternoptyx diaphana* there are 29 to 31 vertebrae (Baird, 1971, reported 28 to 31 for the genus *Sternoptyx*), the most frequent number
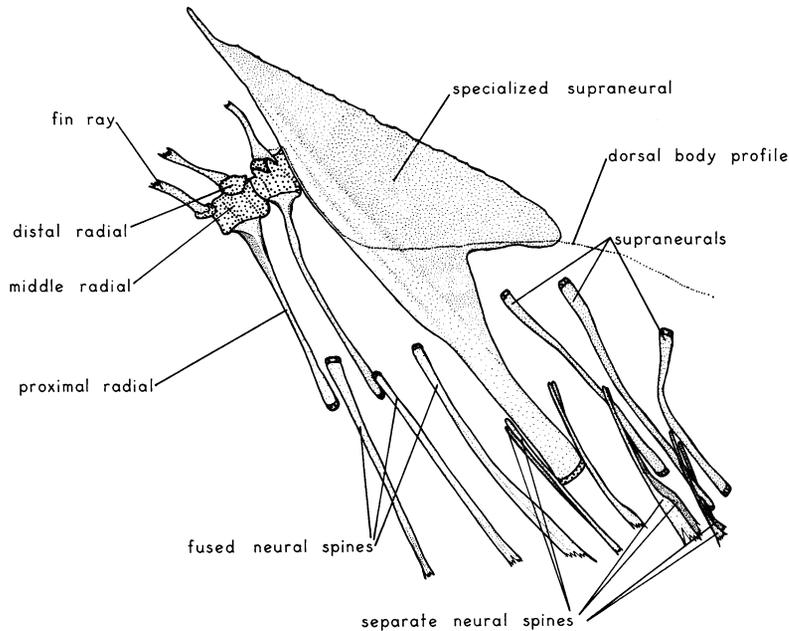
FIG. 87. Lateral view of the right side of the supraneurals and associated
structures of *Sternoptyx diaphana*, SL 44.0 mm., USNM 192843.

being 30 in the specimens examined. Eleven or
12 of these are precaudal. The single specimen
of *Sternoptyx* sp. had 30 vertebrae, 11 of them
precaudal.

All neural and haemal arches are fused with
their centra, and there are either six or seven
anterior neural spines that remain separate
from each other. The last unfused neural arch
(spine) is either that immediately anterior to
the specialized supraneural (dorsal blade) or
that just posterior to the blade (see fig. 87).
There are no epimerals and the first and second
vertebrae are without ribs or intermuscular
bones of any sort. The third through tenth
vertebrae bear a total of eight pleural ribs,
those of the ninth and tenth vertebrae support
the pelvic girdle. Five of these pleural ribs are
large and extend to the ventral body wall, these
are on vertebrae six to 10. There are one or two
small pleural ribs posterior to the tenth vertebra.
There are no dorsal ribs (epipleurals). The distal
ends of both the slender neural and haemal
spines are expanded and do not come to a point
as do the neural spines associated with the
supraneurals. The neural and haemal spines do
not bear expanded bases as in *Polyipnus* and
Argyropelecus.

There are four supraneurals in *Sternoptyx*. The
anterior supraneural is difficult to see in X-ray
negatives because it lies between the two post-
temporal and supracleithral bones. The pos-
terior, fourth supraneural is the only advanced
member of the series, and it bears a large,
bladelike portion external to the body of the
fish and immediately anterior to the dorsal fin.

CAUDAL SKELETON

The caudal skeleton of gonostomatids, pho-
tichthyids, and sternoptychids is quite diverse at
the generic level and, in addition, somewhat
variable among species of a given genus. Even
specimens of a single species will vary some-
what in fusion of hypural bones. Nevertheless
the caudal skeleton is a useful structure for
interpreting relationships among stomiatoid
genera. In order to understand the caudal skele-
ton of the sternoptychids it is necessary to dis-
cuss a few problems in homology and note the
caudal structure found in some gonostomatids
and photichthyids.

Weitzman (1967a, p. 523, fig. 15) published
an illustration of the relatively primitive caudal
skeleton of *Polymetme corythaeola*. In this species
there are two elongate, free, cylindrical epurals.

The gonostomatids *Margrethia obtusirostra* and the species of *Diplophos*, have three cylindrical epurals, a condition common among primitive teleosts (Patterson, 1968) and therefore probably primitive for a stomiatoid. *Polymetme*, a photichthyid with its two cylindrical radials is more advanced in this regard. The epurals of sternoptychids are variable; they are never ossified except in *Polyipnus*, *Argyropelecus*, and *Sternoptyx*, and they may be absent (in *Araiophos*). There is usually only one cartilaginous plate present anterior to the uroneural. Patterson (1968, pp. 220–221) reviewed the possible homologies of epural elements and concluded that they are the homologues of the anteriorly placed supraneurals rather than radial elements. His reasons were based on the differences between the simple joints between the epurals and the procurrent caudal fin rays and the more complex joints of the radials of the dorsal fin. He also noted that epurals appear to be equivalent to detached true neural spines and therefore serial homologues of supraneurals. In sternoptychids, the epurals if truly present, appear to be derived from elements that appear to be radials or at least serve functionally as radials. These usually cartilaginous elements are called radials here or epurals when placed immediately anterior to the uroneural (see figs. 88–93). These radial cartilages are between the neural and haemal spines and sometimes distal to the spines. In the gonostomatid *Cyclothone acclinidens* there is one large epural cartilage, very much like that in *Danaphos oculatus* (fig. 91), and *Thorophos euryops* (fig. 88). In all genera of gonostomatids other than *Cyclothone* and in the photichthyids the epurals are elongate as in *Polymetme*. In *Cyclothone signata* there are two small, cartilaginous dorsal radial elements between the terminal neural spine and the uroneural. Each looks much like the single element in *Sonoda megalophthalma* (fig. 93). In some specimens of *C. signata* these cartilages fuse dorsally. The epural of *Thorophos euryops* (fig. 88) looks as though it was formed from two "epural" or radial cartilages. It is difficult to distinguish epurals from radials in sternoptychids and gonostomatids and epurals may simply be modified radials.

One or more free or fused uroneurals are present in gonostomatids and most sternoptychids. In sternoptychids the uroneural is fused to the centrum and sometimes even to the

epurals (*Sternoptyx*). A urodermal (as defined by Patterson, 1968, p. 221) is present in the osmerid *Spirinchus*; however, none was found in stomiatoids. The absence of this very superficial bony element in the primitive stomiatoid caudal skeleton such as that of the gonostomatid *Margrethia* and the photichthyid *Polymetme* may not be real but may be due to damage by net rolling during capture.

In all adult stomiatoids examined (see lists in Weitzman, 1967a and 1967b as well as the present list), the first preural centrum and the first ural centrum appear fused. The shape of the centrum associated ventrally with the terminal haemal spine and first two hypurals of *Danaphos* (fig. 91) certainly indicates that two centra are involved with this bone. The second ural centrum is often fused with the first preural and ural centra in some genera with otherwise primitive teleost caudal skeletons, for example *Margrethia*, or it may be separate, for example *Polymetme*. In *Triplophos* the second ural centrum is quite large and the articulation between it and the combined first ural centrum and preural centrum anterior is quite mobile. The large uroneural above is not fused to either central body. This fish has a slender, tapering tail and the mobility at this joint is probably a functional adaptation. Some gadoid fishes with slender, tapering tails have a very similar arrangement. In other cases, photichthyids and gonostomatids have a small, free second ural centrum and it appears to have little functional significance.

The haemal spine of the first preural centrum, that is the parahypural, and the two hypural bones associated with the first ural centrum (hypurals one and two) are often fused to a single bone in gonostomatids, photichthyids, and sternoptychids. They are primitively separate in a few genera such as *Polymetme* and *Margrethia*. The third through the sixth hypurals are fused or partially fused in many genera of the Gonostomatidae and Photichthyidae but are separate in those possessing relatively primitive caudals such as *Polymetme* and *Margrethia*.

Although most of the skeleton of *Thorophos* (fig. 88) is relatively primitive in both species, the caudal skeleton is modified by having the combined first preural centrum and first ural centrum fused with the parhypural and with hypurals one and two. In addition, the haemal spine and the first and second hypurals are fused
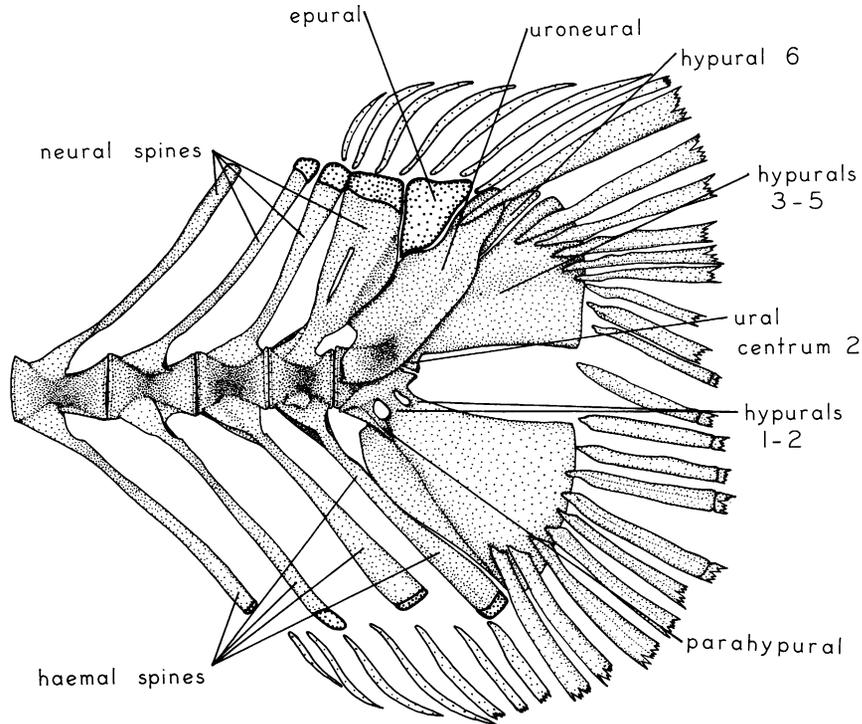
FIG. 88. Caudal skeleton of *Thorophos euryops*, SL 44.7 mm., DANA 3736-VI.

to each other except for a small area near their bases. Hypurals three through five are fused to each other and to the second ural centrum, which is not fused to the first ural centrum. Hypural 6 is autogenous. Only one large uroneural is present and this appears to be free of the first ural centrum. The uroneural may be fused to ural centrum two. The single, platelike, cartilaginous epural appears to be formed from two fused cylindrical cartilages. No other dorsal or ventral radial elements are present.

The caudal skeleton of *Araiophos* (fig. 89) has the preural centrum and ural centra one and two fused to a single element. Hypurals one and two and the parahypural are free from their associated centra but all are fused to one another. Hypurals three and four are fused to each other but free from the ural centra. The autogenous fifth and sixth hypurals are partially covered by two uroneurals. The largest seems fused in part to the ural centra. No radials or epurals are found.

In *Maurolicus* (fig. 90) the first preural and both ural centra are fused to a single element

plus the parahypural and the first two hypurals. The presence of a first uroneural is questionable but a second uroneural is present. Hypurals three and four are fused to each other but free from ural centra. Hypural five is partially fused to three and four. Hypural six is autogenous. There is a single, relatively elongate cartilaginous epural. Anterior to this, between the neural spines of the second through fifth preural centra, are large cartilaginous dorsal radials. There are no radials in the ventral part of the caudal skeleton. The ventral procurrent fin rays are restricted anteriorly to make space for photophores. The haemal spines of the fourth and fifth preural vertebrae are shortened to make room for photophores.

Baird (1971) noted the similarity between the caudal skeleton of *Maurolicus* and that of *Vinciguerria* as reported by Weitzman (1967a). As mentioned above the hypurals are often fused to a single bone in stomiatoids and it appears that this may be a common tendency in stomiatoids. This characteristic is probably independently acquired and therefore not very
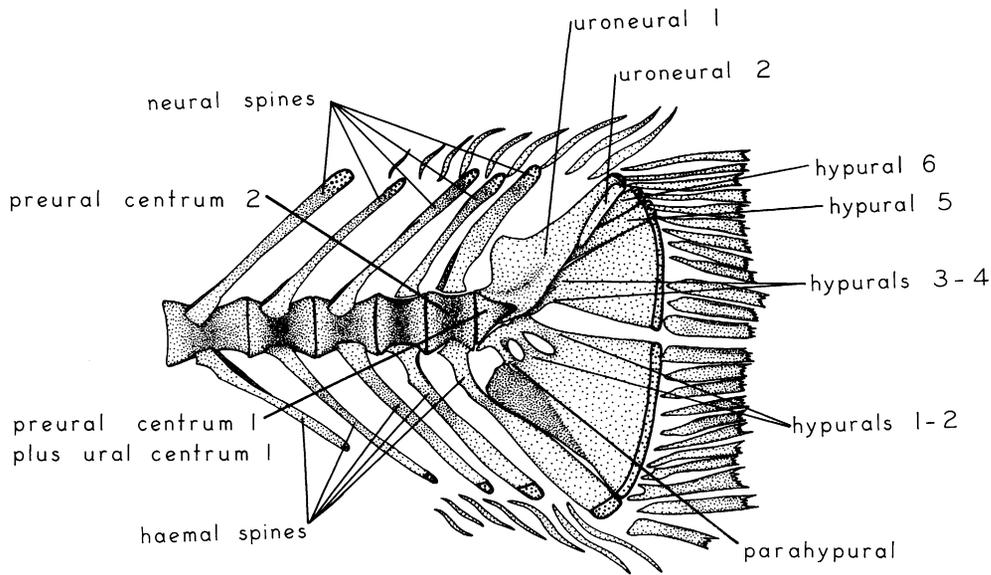
FIG. 89. Caudal skeleton of *Araiophos gracilis*, SL 25.7 mm., FMNH 73902.

useful for understanding phylogenetic relationships in these fishes.

The caudal skeletons of *Danaphos* and *Valenciennellus* are essentially the same. The first preural and ural centra are fused to each other but free from the combined first two hypurals and parahypural (see fig. 91). Hypurals three through five are fused to a single element in adults and free from the second ural centrum which is free from the first ural centrum. There appear to be one or possibly two small ural centra dorsal to the upturned ural centrum two. The sixth hypural is autogenous. An opisthural cartilage is present and well developed. There appear to be three uroneural elements. None are fused to ural centra but two are partially fused to each other. These uroneural elements occur in the morphological position of the first uroneural. It is probable that these elements (in the illustrated specimen) represent broken fragments of the first uroneural, the damage sustained by net rolling during capture. In some specimens they are fused to a single element forming uroneural one. There is one large, platelike epural. A small radial element lies anterior to the distal tip of the neural spine of the second preural centrum. Procurrent fin rays are partially missing in the specimens of *Danaphos* at hand.

The caudal skeletons of *Argyripnus* (fig. 92) and *Sonoda* (fig. 93) are similar in general pattern but show several differences. Both have the ural centra and the first preural centrum fused to a single element. In *Sonoda* hypurals one and two plus the parahypural are fused to a single element that itself forms a synostosis with the centra. In *Argyripnus* hypurals one and two are fused to each other but free of the ural centrum. The parahypural is autogenous as are hypurals three through six in both genera. There appear to be two large uroneurals in *Sonoda* fused to a single element, whereas there appears to be only one large uroneural in *Argyripnus*. Both genera have a series of rather irregular dorsal and ventral radials associated with the procurrent fin rays. The dorsal terminal one of these is equivalent to an epural. In *Sonoda* the first six preural haemal spines support the caudal fin, whereas in *Argyripnus* it is the first five. Haemal spines anterior to these are shortened to make room for ventral photophores.

Polyipnus asteroides (fig. 94) has the first preural and all ural centra fused to a single element. The parahypural is co-ossified with the fused first and second hypurals only at its base. The combined element is free of the fused centra. Hypurals three through six are autogenous and separate from each other. Baird (1971)
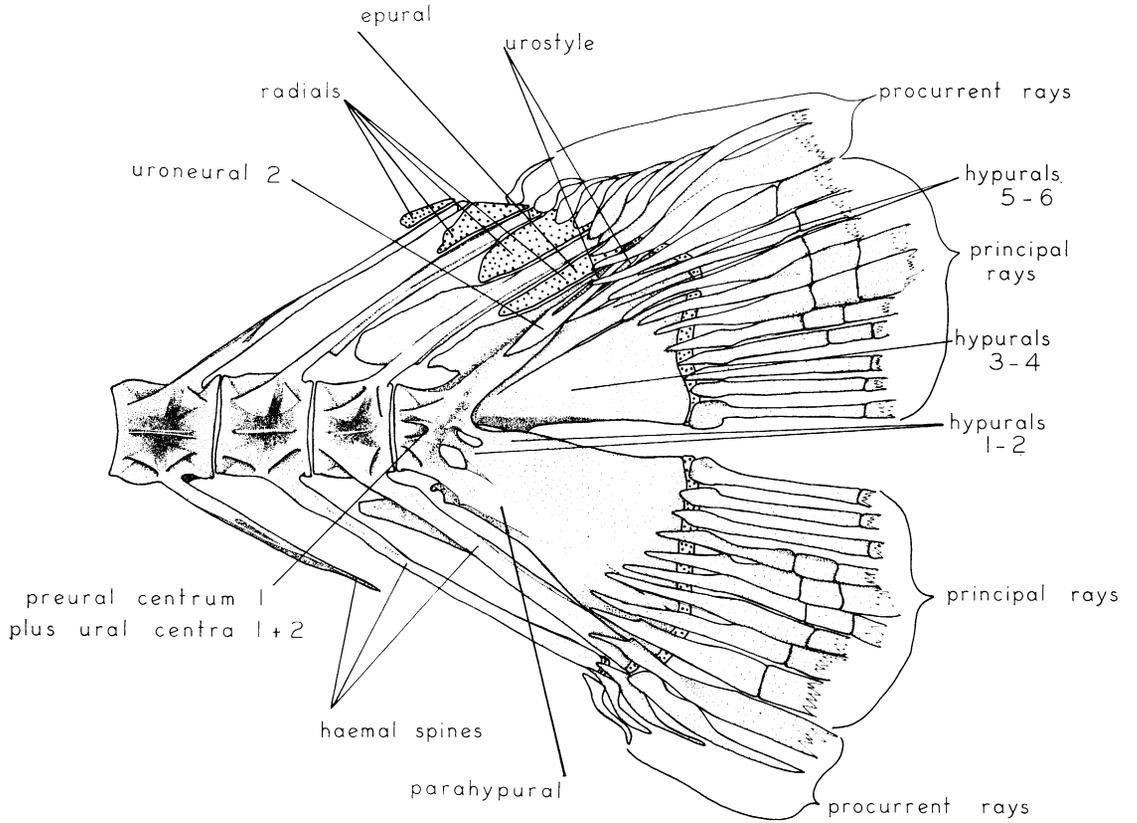
FIG. 90. Caudal skeleton of *Maurolicus muelleri*, SL 45.5 mm., USNM 201138.
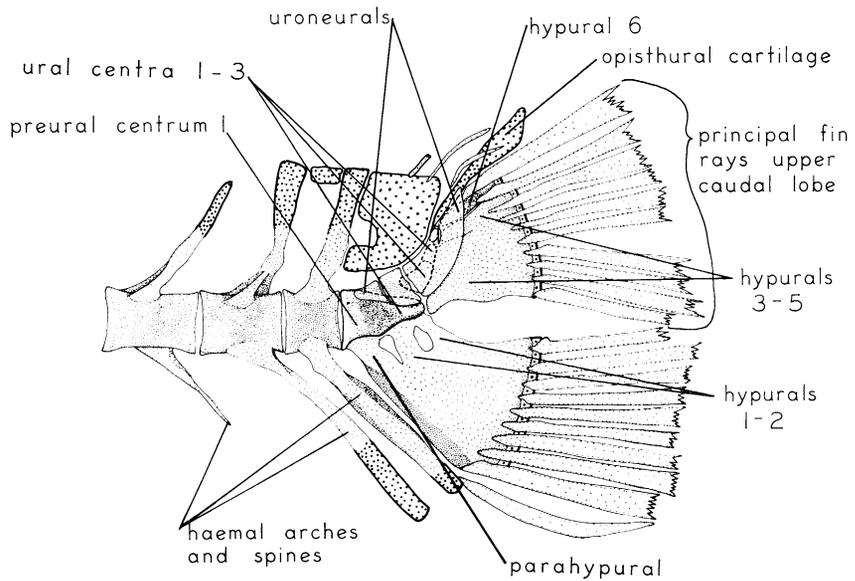
FIG. 91. Caudal skeleton of *Danaphos oculatus*, SL 34.5 mm., USNM 203261.
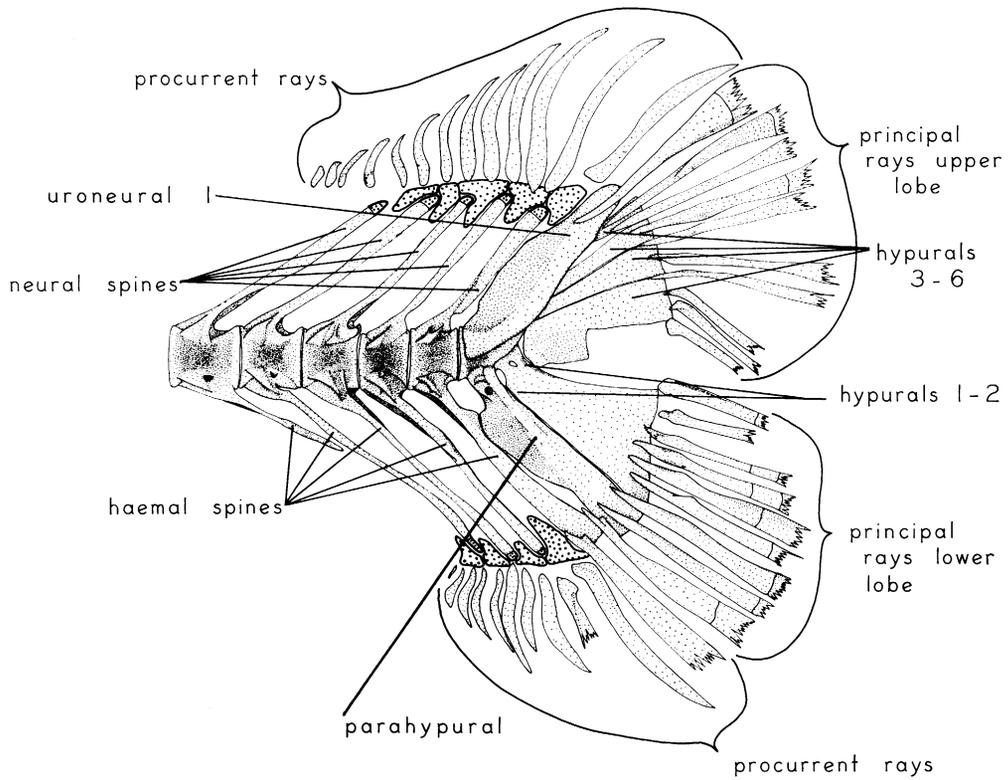
FIG. 92. Caudal skeleton of *Argyripnus atlanticus*, SL 57.0 mm., USNM 201351.
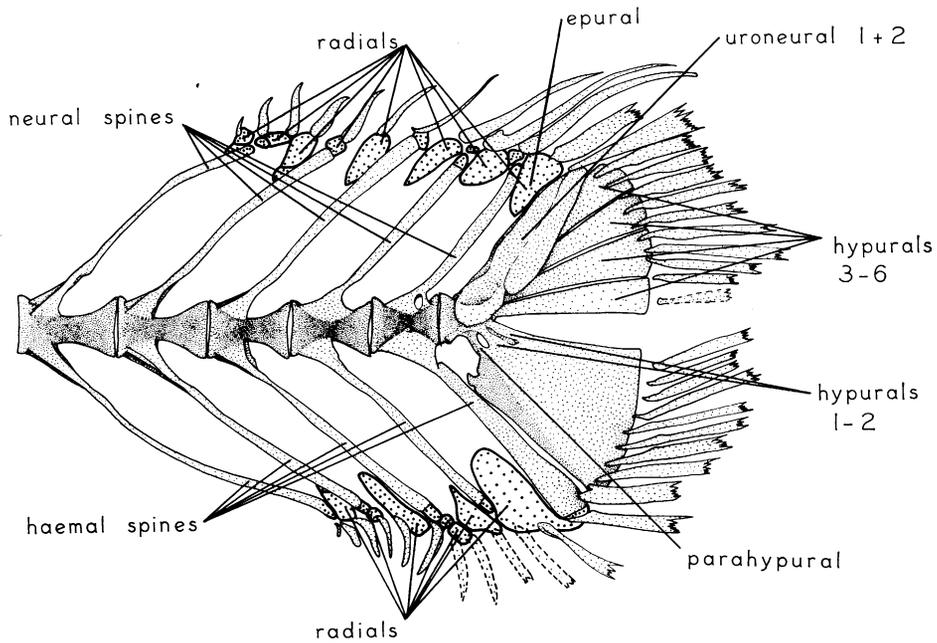
FIG. 93. Caudal skeleton of *Sonoda megalophthalma*, SL 53.5 mm., USNM 201350.
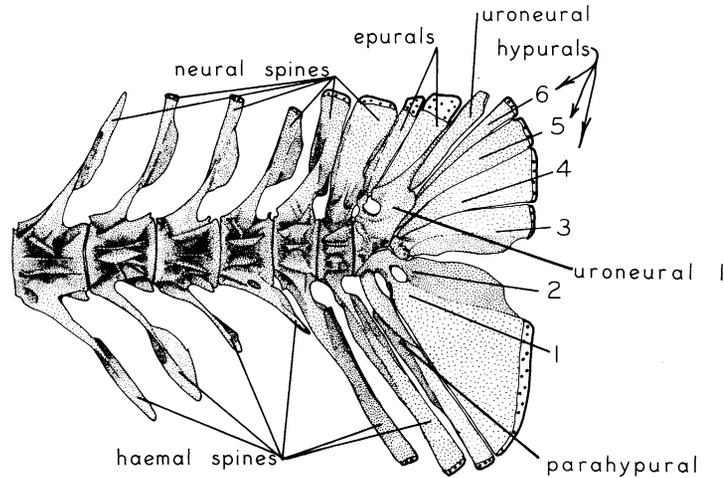
FIG. 94. Caudal skeleton of *Polyipnus asteroides*, SL 58.0 mm., USNM 197452.

reported hypurals three, four, and five fused in *Polyipnus asteroides* (mislabeled three and four in Baird's paper). There is one free uroneural and two epurals. The neural spines of preural vertebrae two and three are expanded and these two vertebrae also bear elongate haemal spines associated with caudal fin rays. Haemal spines anterior to these are shortened to accommodate light organs. *Polyipnus* sp. has the same arrangement as *P. asteroides* but *P. laternatus* has hypurals three and four fused to each other and *P. tridentifer* has three and four fused along their posterior length and only a single epural bone.

Baird (1971, fig. 1D) illustrated the caudal skeleton of *Polyipnus asteroides* but appears to have mislabeled the uroneural as the sixth hypural and considered the posterior epural as a uroneural. Baird's interpretation of the numbering of the hypurals in *Polyipnus asteroides* differs from the numbering adopted here. Compare figure 94 with that of Baird's cited above.

In *Argyropelecus aculeatus* (fig. 95) the first preural centrum and the ural centra are fused. The first and second hypurals are co-ossified but free from the centra. The haemal spine of the parahypural is autogenous. The co-ossified third through fifth hypurals are free from the ural centra. Also the sixth hypural is autogenous. There is one large, flattened bony epural and the neural spine of the second preural centrum is flattened and expanded. The

haemal spines of the second and third preural vertebrae are elongate and support the caudal fin, whereas the haemal spines anterior to this are shortened to accommodate light organs. *Argyropelecus pacificus* and *A. gigas* have the first and second hypurals free of each other. In one specimen of *A. gigas* the fourth and fifth hypurals are fused, in another they are not. *Argyropelecus hemigymnus* is also somewhat variable, if all the specimens at hand are the same species. One specimen from the North Atlantic Ocean has the co-ossified haemal spine of the first preural centrum and the first and second hypurals free of the centra, whereas a second specimen from the southeastern Pacific Ocean has them fused. The specimen which has these elements fused to centra also has co-ossified hypurals three through six fused to the ural centra. The other specimen has only hypurals three through five co-ossified and has all its hypurals free of the centra. There are no free uroneurals in any specimens of *Argyropelecus* examined.

Sternoptyx diaphana has a very peculiar upturned caudal skeleton (fig. 96). The entire group of caudal elements are co-ossified to a single bone and only a single, large epural seems to be represented in this complex. As in the other sternoptychid genera, only the first, second, and third preural haemal spines are utilized in caudal support and the second preural neural spine is broad and flat and involved in
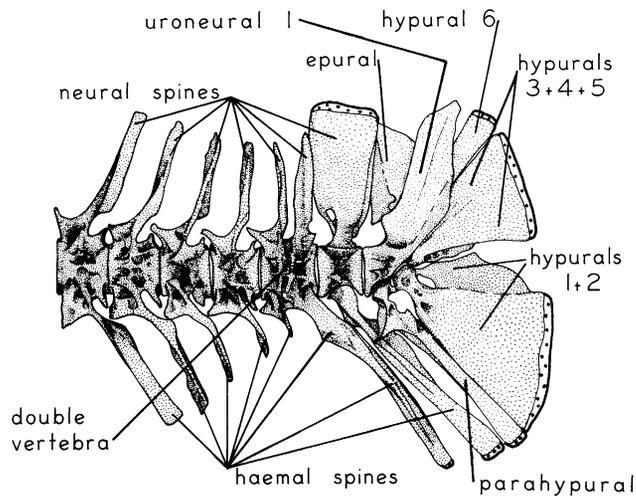
FIG. 95. Caudal skeleton of *Argyropelecus aculeatus*, SL 49.5 mm.,
USNM 179056.

caudal fin support. The neural spine of the third preural vertebra is short and directed posteriorly where it contacts the anterior edge of the neural spine just posterior. This condition is also found in *Argyropelecus* but the neural spine of preural centrum three is longer than in *Sternoptyx*.

DORSAL, ANAL, AND ADIPOSE FINS

In comparison with the dorsal and anal fins of other teleosts, those of stomiatoids, especially of some sternoptychids, are highly advanced. In the anal fin some of these specializations appear associated with the AC row of photophores.

In many salmoniforms and other teleosts all except the first one or two anterior dorsal and anal fin pterygiophores consist of three radials in a series. The proximal and middle radials are medial cartilaginous structures usually surrounded and partially replaced by bone except at their distal and proximal ends. The distal radial is a more or less spherical cartilage that ventroanteriorly articulates with the distal end of the middle radial and lies between the proximal bases of the fin ray halves. It is ossified by two ossification centers, the apex of each usually forming the attachment for the pteroradial ligament. This ligament (one on each side) extends from the ossification center of the distal radial anteriorly to the medial base of the proximal ray half of the ipsilateral ray segment just anterior. Thus this ligament extends

from one segmental fin ray structure to the next. These ligaments between the basal structures of the fins occur in both the dorsal and anal fins and do not appear homologous to the inter-filamenti analis muscles found between the bases of the fin rays in the anal fin of *Onco-rhynchus tshawytscha* by Greene and Greene (1915). The pteroradial ligament is found in at least a few other fish groups where it may contain a few muscle fibers. In specimens of *Elops saurus* the ligaments, one on each side, extend between the lateral surfaces of the distal radials. In osmerids, gonostomatids, and photichthyids it passes between the posterior spinous process of each ray half and the lateral surface of the distal radial behind. In *Salmo gairdneri* it follows the same pattern as in osmerids.

The pterygiophores of the sternoptychid dorsal and anal fins are often similar to those of the osmerids, but in many of the gonostomatids, photichthyids, and sternoptychids, most if not all of the proximal and middle radials of a given pterygiophore may be fused to one another. Often the area of fusion between medial and proximal radials forms a saddle-shaped joint surface for the reception of the distal radial of the pterygiophore series just anterior (see fig. 82).

The pterygiophores of the anal fins of sternoptychids are frequently shortened to accommodate the AC photophore row. In some cases specialized groups or clusters of photo-
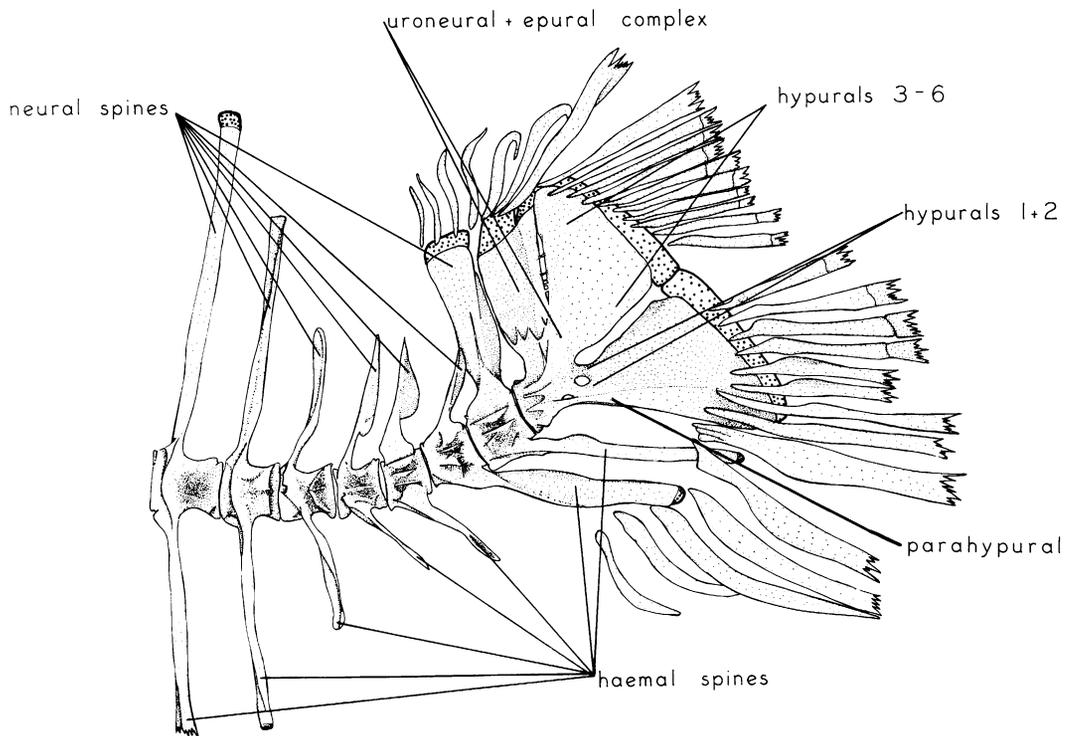
FIG. 96. Caudal skeleton of *Sternoptyx diaphana*, SL 44.0 mm., USNM 192843.

phores are associated with a hiatus or spatial reorientation of the pterygiophores.

An adipose fin is present in most sternoptychid genera. The fin is usually short based in the gonostomatids and in most photichthyids and is invariably long based when present in the sternoptychids, except *Thorophos*.

The dorsal fin of *Thorophos euryops* consists of 12 rays and 11 pterygiophores, each with its proximal and middle pterygiophores fused. The anterior pterygiophore appears to consist of two pterygiophores fused at their distal ends and it bears the anterior two fin rays, similar to the situation in *Maurolicus muelleri* (fig. 81). The posterior terminal dorsal fin ray is single, not double or split to its base.

The anal fin has 29 rays and 28 pterygiophores, all having their middle and proximal portions fused to each other. The posterior terminal fin ray is not divided to its base. There is no hiatus between the pterygiophores, which are relatively short, extending only to the distal tips of the haemal spines. Here they end as blunt, somewhat laterally flattened clavate rods similar

to the structure labeled proximal radial in figure 82 of *Sonoda megalophthalma*.

The adipose fin is present and relatively short based for a sternoptychid (see fig. 1).

Thorophos nexilis has dorsal and anal fin structures almost exactly like those of *T. euryops* except for the number of rays and pterygiophores—eight rays and seven pterygiophores in the dorsal and 38 rays and 37 pterygiophores in the anal fin. The terminal ray is not divided in either fin. An adipose fin was reported absent by Myers (1932) and Grey (1960a). All specimens examined are severely abraded by the action of the net and the adipose fin is present in only one specimen where it is represented by basal fragments. In figure 2 the fin is shown as reconstructed by dotted line. The adipose fin is missing on the specimen illustrated.

Grey (1961) reported 13 to 14 dorsal fin rays in *Araiophos gracilis*. The specimen at hand has the posterior part of the dorsal fin missing. The anterior pterygiophore bears two fin rays but appears to consist of a single cartilaginous rod rather than two fused rods as in *Thorophos* and

Maurolicus. The remaining proximal and distal pterygiophores are fused and cartilaginous each bearing a distal radial on its dorsoposterior end.

The anal fin has 17 rays, two associated with the anterior pterygiophores and one undivided on the posterior pterygiophore. There are 16 very short pterygiophores, with the dorsal end of each not reaching dorsally beyond the distal end of the haemal spines. There is no hiatus in the serial regularity of the pterygiophores and the proximal and middle radials are fused to each other. The anal fins are undivided their entire length, as in figure 4 of *A. eastropas.* An adipose fin is absent in the specimen at hand. Grey (1961) reported it in some cases present.

Araiophos eastropas has dorsal and anal fins identical with those of *A. gracilis* except for fin ray numbers, having 18 to 20 in the dorsal fin and 20 to 23 in the anal fin according to Ahlstrom and Moser (1969). The specimens at hand have 18 (17 in fig. 4) dorsal fin rays and 17 pterygiophores. The posterior terminal dorsal fin ray is undivided. The adipose fin was reported absent by Ahlstrom and Moser (1969) and is absent in all specimens at hand.

According to Grey (1964), *Maurolicus muelleri* has a total dorsal fin ray count of 10 or 11. The specimens examined here conform to this count except that of five specimens from the Red Sea (USNM 203823), two had nine rays and three had 10. There are invariably two rays associated with the first pterygiophore (see fig. 81) and one fewer pterygiophore than fin rays. The posterior terminal ray is not split to its base. The middle and proximal radials are fused in all pterygiophores.

Grey (1964) recorded 19 to 23 anal fin rays, and all specimens examined here are within this range. The posterior terminal ray is not split to its base. All pterygiophores have their middle and proximal radials fused. However, the portion of the pterygiophore representing the middle radial remains unossified, its cartilage fused with that of the proximal radial. The un-ossified portion at the posterior end of the fin is relatively elongate, equaling between one and one-and-one-fourth of the total pterygiophore length. Only the anterior two pterygiophores have their proximal tips in contact with more than the distal tips of the haemal spines.

The adipose fin is present and long based in all specimens. It equals or slightly exceeds the length of the base of the dorsal fin.

All specimens of *Danaphos oculatus* have six dorsal fin rays (see also Grey, 1960a). There are five cartilaginous pterygiophores; the anterior one supporting two fin rays appears to consist of two pterygiophores. All proximal and middle radials are fused, and the anterior two ptery-giophores are fused at their proximal and distal ends. Thus the anterior pterygiophore structure supports three fin rays. The remaining three pterygiophores are fused to each other at their distal ends. The distal radials remain cartilaginous in all specimens examined. All fin rays are ossified and the posterior terminal ray is not split to its base.

The anal fin as reported by Grey (1960a) usually has 24 to 25 fin rays but the specimen drawn here (fig. 6) has 23. The entire ptery-giophore series is cartilaginous but all pterygio-phores are separate from each other. All proximal and middle radials are fused, the elongate, cylindrical middle radials being half as long as the relatively short, flattened, platelike proximal radials. The anterior few pterygiophores have a more usual, approximately cylindrical appear-ance, with the anterior two pterygiophores extending dorsally beyond the distal ventral tips of the haemal spines. The posterior terminal fin ray is not split to its base.

The adipose fin is very long based, being almost five times as long as the short-based, rayed dorsal fin.

Grey (1964) reported seven to 10 dorsal fin rays for *Valenciennellus tripunctulatus* and 12 for *V. stellatus.* I can confirm Grey's counts for *V. tripunctulatus* and find that there is one less pterygiophore than fin rays in all specimens examined. The anterior pterygiophore bears two rays despite the fact that it does not appear to consist of two pterygiophores and is slender, similar to the remaining posterior pterygiophores. All pterygiophores are ossified although only weakly so and each consists of a fused middle and proximal radial. The posterior terminal fin ray is not split to its base and is supported by its own pterygiophore.

The anal fin of *Valenciennellus tripunctulatus* is essentially similar to that of *Danaphos* and only the anterior six or seven pterygiophores exhibit evidence of ossification, the proximal portions being ossified. All specimens examined confirm Grey's range of anal fin ray counts of 22 to 25. There is one less pterygiophore than fin rays and the anterior pterygiophore bears two rays. The

posterior terminal anal fin ray is not split to its base. Proximal and middle radials are fused and only the anterior four pterygiophores extend farther dorsally than the distal tips of the haemal spines. The posterior middle radials are cylindrical and constitute about one-fourth to one-half the entire length of the pterygiophore. The proximal radials are cylindrical, not laterally compressed, spatulate structures as in *Danaphos*.

The adipose fin is long based, its base is somewhat more than twice the length of that of the relatively short dorsal fin.

Grey (1964) reported 11 to 14 dorsal fin rays in *Argyripnus* and the specimens examined here confirm her counts. The dorsal fin of *A. atlanticus* at hand (see fig. 80) has 12 dorsal fin rays, the posterior terminal ray not split to its base. There are 11 pterygiophores, the anteriormost bearing two rays. The well-ossified proximal and the middle cartilaginous radials are fused in a continuous cartilaginous rod, the ventral end of which is surrounded by the bone of the proximal radial. The distal radials remain unossified. The anterior pterygiophore is an expanded plate.

The anal fin of *Argyripnus atlanticus* examined has 15 plus nine rays. Grey (1964) found a range of 13 to 15 plus nine in 14 specimens of *A. atlanticus*. There are 24 pterygiophores, each consisting of a proximal ossified portion and a middle cartilaginous, cylindrical rod very similar to the structure illustrated for *Sonoda* in figure 82 except that in *Argyripnus* the cartilage of the proximal and middle radials is fused. The hiatus between the two portions of the anal fin in *Argyripnus* is much like that illustrated for *Sonoda*. The anterior part of the especially elongate middle radial appears to be entirely ligamentous rather than cartilaginous as in *Sonoda*. The posterior part in *Argyripnus* is of cartilage. The second cluster of AC photophores lies dorsal to the anal fin hiatus but partially covers the proximal radials of the pterygiophores just anterior to the hiatus.

A somewhat long-based adipose fin is present in *Argyripnus*.

Grey (1964) reported eight to nine dorsal fin rays in *Sonoda* and specimens of *Sonoda megalophthalma* examined here have nine rays, the posterior terminal ray not being split to its base. There are eight pterygiophores, each consisting of fused proximal and middle radials. The distal radials are not ossified.

The anal fin of *Sonoda* has eight to 10 plus 14 to 16 fin rays according to Grey (1964). The specimens of *Sonoda megalophthalma* examined here have nine plus 15 rays, the last not split to its base. There are nine plus 14 pterygiophores, with two fin rays on the anterior pterygiophore. The ray of the ninth pterygiophore extends from the base of the tenth pterygiophore, and the ray count according to Grey and me is included in the count posterior to the hiatus, whereas its pterygiophore is counted anterior to it. The middle radial that spans the hiatus and belongs to the ninth pterygiophore and ray is cartilage at both ends but ligamentous in the middle.

All specimens of *Sonoda* were damaged in the dorsal area of the caudal peduncle and the presence or absence of an adipose fin could not be determined.

The dorsal fin of *Polyipnus asteroides* has 14 rays and 14 pterygiophores, counting the complex anterior pterygiophore that apparently consists of a fused pterygiophore and supraneural (see fig. 83 and discussion on p. 419). All proximal (ossified for the most part) and middle pterygiophores (cartilaginous) are fused. The posterior dorsal terminal fin ray is divided to its base (double) and the posterior pterygiophore supports no fin rays nor a distal radial. The pteroradial ligaments are strongly developed. All other species of *Polyipnus* examined have similar dorsal fin structures and differ only in number of serial elements.

The anal fin of *P. asteroides* has 15 fin rays and 15 pterygiophores, the posterior terminal pterygiophore not supporting a fin ray. The terminal fin ray is divided or split to its base. As in the dorsal fin, the proximal and middle radials are fused. Anteriorly the middle radials are not so prominent as posteriorly, the cartilage of the middle radial being mostly included within the ossified distal head of the proximal radial. Posteriorly the prominent cylindrical cartilage of the middle radial extends posteroventrally to contact the distal radial very similar to the situation in the posterior pterygiophores of the dorsal fin. Between the proximal shafts of the eighth and ninth proximal anal fin radials is a space for the deep structures of two AC (anal) photophores. This hiatus between radial shafts was present in all species of *Polyipnus* examined and is somewhat similar in appearance to that illustrated for *Argyropelecus aculeatus* (fig. 84). As in the dorsal fin the distal radials are mostly cartilage, each capped laterally by a small

sheath of bone forming the attachment for the prominent pteroradial ligament. The other species of *Polyipnus* examined differ only in having different fin ray and pterygiophore counts.

The length of the base of the adipose fin, when present, varies in *Polyipnus* from relatively short in *Polyipnus* sp., to quite long in *P. matsubarai*.

The dorsal fin of *Argyropelecus aculeatus* (fig. 86) has nine fin rays and nine pterygiophores. The anterior pterygiophore bears two distal radials and two fin rays; the posterior, very short pterygiophore bears no distal radial or fin ray. The terminal fin ray is not divided to its base. The distal end of each proximal radial is club-shaped and filled with a semispherical mound of cartilage, part of which is probably derived from the middle radial. The distal cartilaginous end of each pterygiophore articulates directly with the same structure anterior and posterior to it. The pterygiophores of the base of the dorsal fin are thus in a closely fitting series and closely bound by ligaments. The pteroradial ligaments are moderately well developed posteriorly, but appear weakly developed on the first five or six rays. The posterior terminal pterygiophore consists of an arched bar of cartilage with a weakly ossified surface.

The dorsal fins of *Argyropelecus affinis*, *A. gigas*, and *A. hemigymnus* are very similar to that of *A. aculeatus* differing only slightly in number of fin rays. In *A. gigas* the fibers of the well-developed posterior pteroradial ligaments are primarily crossed, that is, the fibers coming from a right basal fin ray half cross those coming from the left and attach to the left side of the distal radial posterior to the fin ray half. In *A. aculeatus* and *A. affinis* a few fibers appear crossed but never the major share.

The 11 anal fin pterygiophores of *Argyropelecus aculeatus* (fig. 84) are modified and bear 12 rays. The first pterygiophore bears two rays, the next 11 bear one each. The first six pterygiophores are much like those of the dorsal fin but the seventh and eighth are modified, having a space between them for deep structures of the AC or anal photophores. The distal end of the seventh pterygiophore is enlarged and bears three to four spinous processes. Its distal end is cartilaginous and is in contact with the cartilaginous distal radial bearing the eighth fin ray. The posterior terminal fin ray is not divided to its base. Of the other species examined, *A. hemi-*

gymnus has the hiatus between the sixth and seventh pterygiophores. Both *A. gigas* and *A. affinis* have it between the seventh and eighth pterygiophores. None of the other species examined have spinous processes on any pterygiophore. The hiatus between the pterygiophores in species of *Argyropelecus* other than *aculeatus* is not associated with a distinct gap in the fin rays.

Argyropelecus gigas has the pterygiophore anterior and posterior to the hiatus least modified of any species examined and in fact has an anal fin more like that of *Maurolicus* than that of any other species of *Argyropelecus*. Pteroradial ligaments are well developed in the anal fin of all species examined and the ligaments do not cross. However, the ligaments near the posterior end of the fin converge on the anterior end of the distal radial just posterior of rather than to the lateral surface of the radial. In some cases, for example *A. affinis*, the pteroradial ligaments of each side converge, and by the time they reach the distal radial appear to be one ligament.

The adipose fins of all species of *Argyropelecus* are long based.

The dorsal fin of *Sternoptyx diaphana* is highly modified (fig. 87). There are nine or 10 dorsal fin rays and nine or 10 pterygiophores. The first pterygiophore bears two distal radials and fin rays. The second ray and radial articulates with the dorsal surface of the second pterygiophore but is actually part of the first pterygiophore series. The third dorsal fin ray, part of the second pterygiophore-radial series, sits between and articulates with both the second and third pterygiophores. Only the proximal radial of each pterygiophore is ossified, the cartilaginous middle radial being fused with the internal cartilage of the proximal radial. The middle radial is laterally compressed and its anterior face articulates with the posterior face of the next anterior middle radial. The anterior face of the middle radial of the most anterior pterygiophore articulates with the posterior groove of the specialized supraneural. The distal radial remains unossified and supports the fin ray. The posterior pterygiophore does not bear a distal radial or fin ray but the fin ray and radial of the antepenultimate pterygiophore articulates with the dorsal surface of the ultimate or most posterior pterygiophore. The last fin ray is not split to its base.

The dorsal fin of *Sternoptyx* sp. is like that of *S. diaphana*.

The anal fin of *Sternoptyx* is more modified than that of any other genus examined for this report. The anterior four pterygiophores are especially modified (fig. 112). The anterior pterygiophore, as in some species of *Polyipnus*, bears an external spine (preanal spine of Schultz, 1961), which projects beyond the rest of the ventral body profile (see fig. 10 of *Polyipnus*, figs. 13, 112 of *Sternoptyx*). This spine is bilateral as is the anterior flat plate or lamella along the anterior border of the distal one-third to one-half of the pterygiophore. The articular head of the pterygiophores, bearing segments of both the proximal and cartilaginous radials, is fused with the main body of the pterygiophore (primary proximal radial) and bears three fin rays and two distal radials. The second pterygiophore consists of a distal "head" portion of the proximal radial and the cartilage of the middle radial. This structure has a flattened base that is firmly applied to the posterior surface of the shaft of the anterior pterygiophore. Although the joint between the two pterygiophores is tight and syndesmotic, the two pterygiophores are easily separable and there is no fusion between the two bones. The third pterygiophore is similar to the second but here the shaft of the proximal radial attaches to the shaft of the anterior pterygiophore. The shaft of the proximal radial of the fourth pterygiophore and the shaft of the anterior pterygiophore become parallel and closely applied to each other for most of their proximal length. They do not fuse. The proximal ends of the shafts of the fifth and sixth proximal radials also parallel each other, are closely bound together, and in turn are loosely bound to the shafts of the proximal radials of the first and fourth pterygiophores. Between the sixth and seventh pterygiophores is a large hiatus seen as a transparent area below the light organ in figure 13. The cartilage of the middle radials of the entire fin are cylindrical rods that abut each other producing a continuous series of cartilages along the base of the fin (see figs. 13, 112). The distal radials are elongate, heart-shaped cartilages when viewed ventrally, with the broad end of the heart lying between the fin rays. The anterior, tapering end is attached to the noncrossed pteroradial ligaments of each side. This ligament is not shown in figure 112 but its position can be seen ventral to the middle radial cartilages in figure 13. The muscles of the anterior half of the anal fin are almost complete-ly covered by the main muscular body mass, leaving the elongate portions of the pterygiophores of the fourth, fifth, and sixth pterygiophores accompanied only by the tendons from these muscles to the fin rays and by skin and membranous connective tissue. The shafts of the pterygiophores posterior to the hiatus between the sixth and seventh pterygiophore are accompanied by fin muscles and do not appear transparent in figure 13. The large body area anterior to them is transparent. There are 15 fin rays and 13 pterygiophores in the specimens examined. As noted above, the anterior pterygiophore bears the muscles and tendons of the first three fin rays. Each remaining pterygiophore bears one fin ray and its distal radial. These are seated on the ventral surface of the middle radial just posterior except for the posterior terminal ray which is seated against its own pterygiophore.

The adipose fins of both forms of *Sternoptyx* examined are long based.

PECTORAL FIN AND GIRDLE

Of the bony structures examined, the pectoral girdle and fin rays appear to have undergone relatively less modification than most in tracing the specialization of structures in gonostomatid and sternoptychid stomiatoids.

The pectoral girdle of *Thorophos euryops* (fig. 97) is like that of the osmerid *Spirinchus* in many respects. The posttemporal (fig. 18) is well formed, with a strong lower limb and bears no laterosensory canal. The posttemporal of *Spirinchus* and other osmerids (see Weitzman, 1967a, p. 510, fig. 2) has a similar shape, and bears no laterosensory canal. Extrascapulars appear absent in *Thorophos* but may have been lost as a result of rough treatment in the trawl net. Several extrascapulars are present in osmerids with a similar distribution as illustrated by Rembizewski (1964, p. 279, fig. 10). Some stomiatoids do have extrascapulars, for example *Polymetme* (see Weitzman, 1967a, p. 520, fig. 13). The supracleithrum of *Thorophos* is present, strongly developed, and not fused with the posttemporal. The lateral surface of the supracleithrum in osmerids bears an elongate, almost vertically oriented fossa for the laterosensory canal, but there is no canal in *Thorophos*. The cleithrum is an elongate bone, well ossified, with a prominent notch along its posteroventral border to allow freedom of movement for the
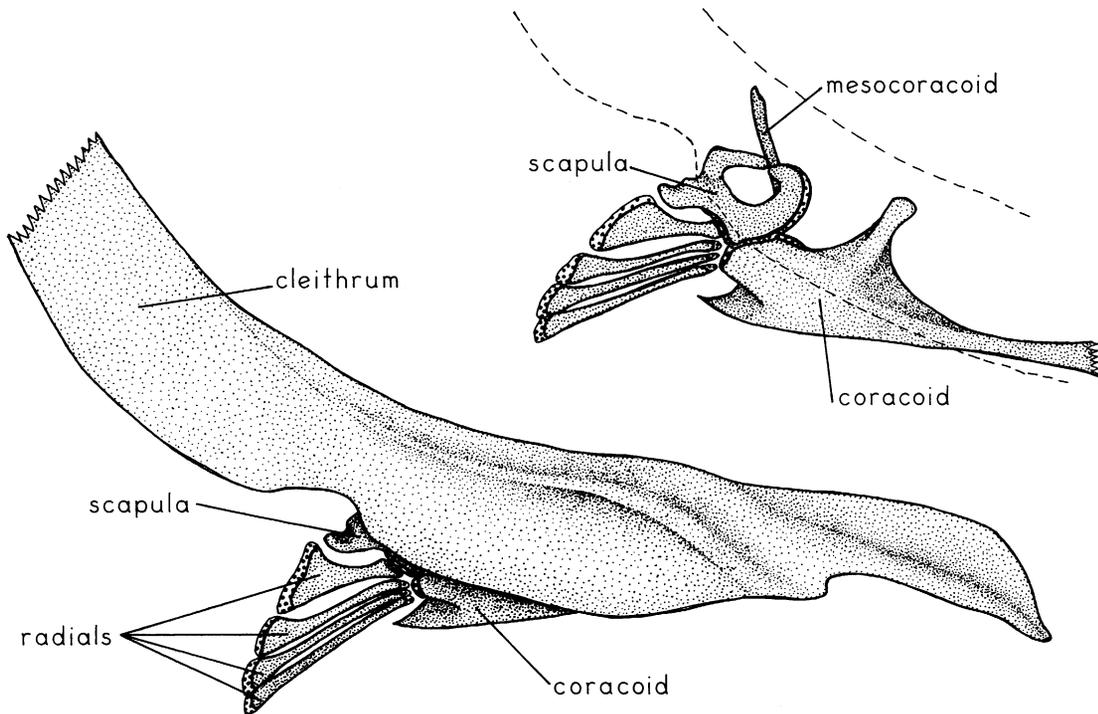
FIG. 97. Lateral view of the ventral portion of the right pectoral girdle of *Thorophos euryops*, SL 44.7 mm., DANA 3736-VI. Upper right shows position of cleithrum as dotted outline.

dorsal rays of the pectoral fin. This notch is absent in osmerids which have a cleithrum bent almost at right angles at the position of the pectoral fin rays. A coracoid, mesocoracoid, and scapula are present, the last having a prominent scapular foramen (see fig. 97). These structures are well developed in the osmerids examined, but differ in shape and development in keeping with the more angular shape of the cleithrum. Four pectoral radials are present, the ventral three being relatively elongate, the dorsal one somewhat triangular in shape. There are 13 pectoral fin rays.

The posttemporal of all specimens of *Araiophos* examined was missing or damaged. The bone, however, is present, has both lower and upper limbs, and contains no laterosensory canals. Extrascapulars could not be found in either species of *Araiophos*, probably because of extensive damage to the area. Unfortunately, the shape and size of the supracleithrum could not be determined because of damage. The supracleithrum is present and probably relatively

strong for there is space for it in the damaged tissue between the posttemporal and cleithrum of one of the specimens of *Araiophos eastropas*. This specimen retains a fragment of the supracleithrum just lateral to the dorsal limb of the cleithrum. The cleithrum and remainder of the pectoral girdle is intact in the specimen of *Araiophos gracilis* (fig. 98). This species has a vertically elongate, slender cleithrum consisting of thin bone applied to the thick lamella of cartilage that bears the coracoid along its ventromedial border and the scapula along its dorsolateral border. The scapular foramen and the notch in the lateral border of the cleithrum are absent. No mesocoracoid was found. There are four radials, large and elongate, of cartilaginous rods and thinly surrounded with bone. Seventeen fin rays are present in *Araiophos gracilis*; Ahlstrom and Moser (1969) reported 16 to 18 pectoral fin rays in *Araiophos eastropas*. The primary pectoral girdle of *A. eastropas* is almost an exact duplicate of that in *A. gracilis*.

The dorsal portion of the pectoral girdle of
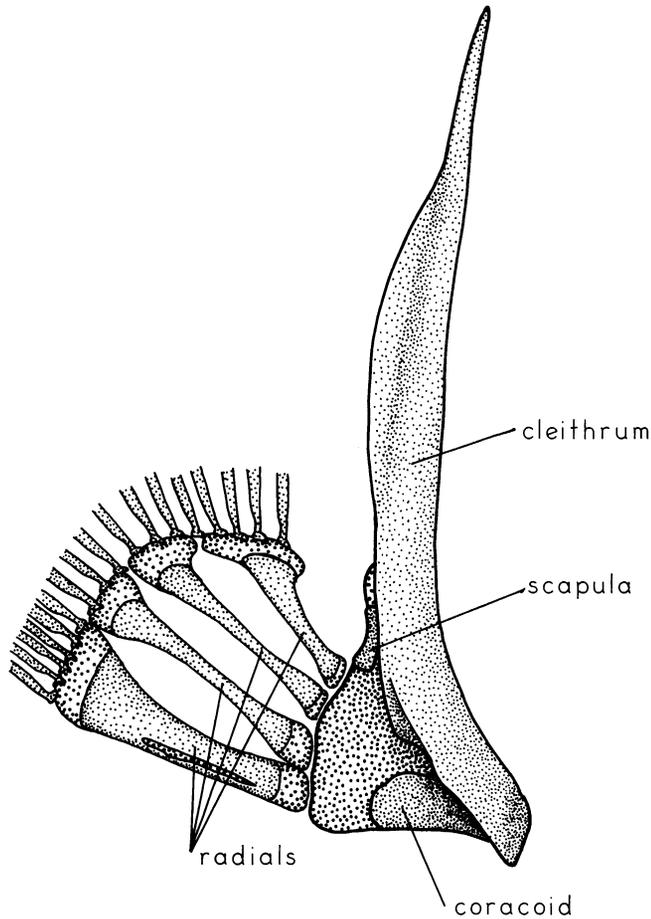
FIG. 98. Lateral view of the primary right pectoral girdle of
Araiophos gracilis, SL 25.7 mm., FMNH 73902.

Maurolicus muelleri is very much like that of
Thorophos euryops. The posttemporal (see fig. 22)
has both limbs well developed and has no
laterosensory canal. Extrascapulars appear to
be absent. The supracleithrum is a strong bracing
bone between the posttemporal and cleithrum
and lacks a laterosensory canal in all specimens
examined. The ventral one-third of the cleith-
rum has a short, rather modified shape with a
large notch for the fin rays (see fig. 99). The
coracoid, mesocoracoid, and scapula are all
present and well ossified. The scapular foramen
is large and completely surrounded by the scap-
ula. There are four radials, the ventralmost
being the longest, the dorsalmost the shortest.
There are 15 pectoral rays (16 in two specimens,
USNM 203823).

Danaphos and *Valenciennellus* have very similar
pectoral girdles and are described together (see
figs. 24, 25, 100). The posttemporals have both
dorsal and ventral limbs well developed and
there is no laterosensory canal included in any
pectoral girdle bone. Extrascapulars appear to
be absent. A supracleithrum is present. The
cleithrum is a relatively slender bone, its an-
terior half arching over the large mass of the
abductor muscles of the pectoral girdle and the
photophore cluster (IP series) superficial to
them. The coracoid is extremely large and plate-
like, serving the origin of the abductor and ad-
ductor muscles. The mesocoracoid and scapula
are present but small. The scapular foramen is
well developed and surrounded by bone. The
notch for the fin rays in the pectoral girdle is
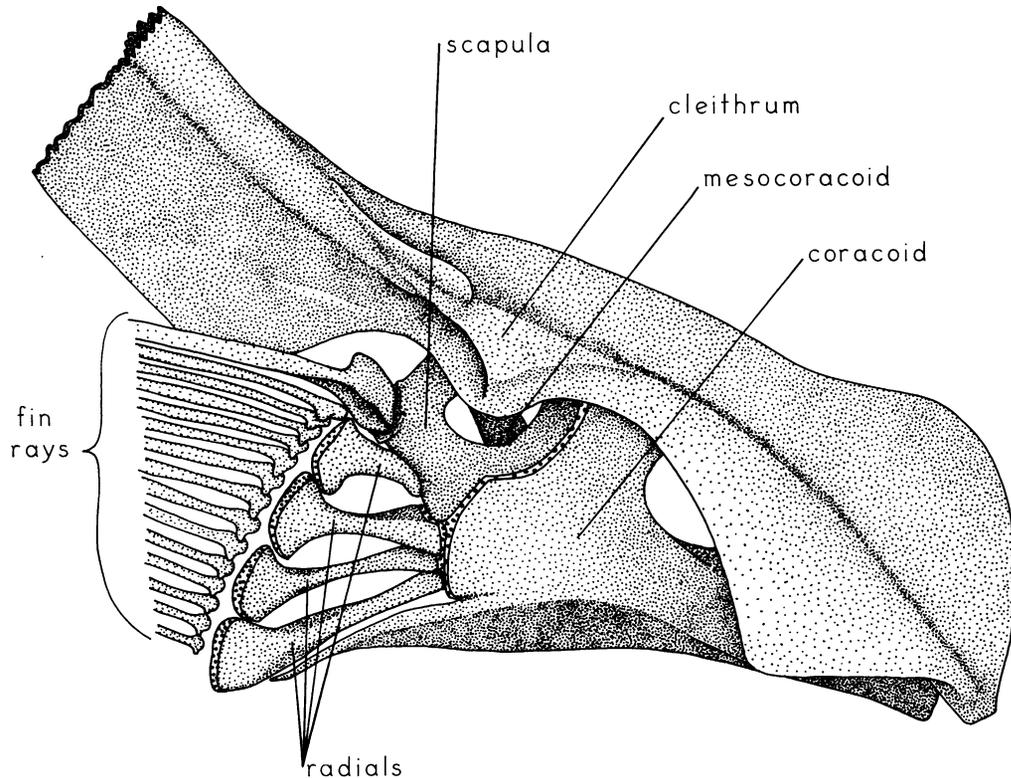
FIG. 99. Lateral view of the ventral portion of the right pectoral girdle of *Maurolicus muelleri*, SL 45.5 mm., USNM 201138.

prominent. There are four radials, the ventral radial being elongate, the dorsalmost very short. There are 15 pectoral rays in *Danaphos* and 16 to 17 in *Valenciennellus*.

The bones of the pectoral girdle of *Sonoda* are more slender than those of *Argyripnus*. Compare the dorsal portion of the pectoral girdles in figures 27 and 28. The dorsal limb of the post-temporal in *Argyripnus* has bladelike processes which are absent in *Sonoda*. The lower limb is slender in both genera. The supracleithrum is almost a simple, narrow rod in *Sonoda* with little evidence of the broad, expanded posterior border found in *Argyripnus*. Both genera appear to lack extrascapulars and no evidence of a laterosensory canal is found associated with the bony substance of the posttemporal or supra-cleithrum in either genus. The cleithrum of both *Argyripnus* (fig. 101) and *Sonoda* has a large notch for the pectoral fin rays. The anterior portion of the cleithrum that lies dorsal to the abductor

pectoral muscles is especially short and broad in *Argyripnus* but relatively long and slender in *Sonoda*. Coracoids, mesocoracoids, and scapu-lae are well developed in both genera, and the scapular foramen is present, almost completely surrounded by bone. Four radials are present in both genera, and there are 17 pectoral fin rays in *Argyripnus atlanticus*, 14 in *Sonoda megalophthalma*.

All the species of *Polyipnus* examined have a pectoral girdle essentially like that of *Polyipnus asteroides* (see figs. 30, 102). The posttemporal is especially modified in *Polyipnus* with a strong upper limb bearing a small to large, single to multiple, posterior spinous process. This spine is single and small in *P. asteroides*. The lower limb of the posttemporal is broad and flat near its junction with the upper limb and tapers to a point. The lower limb is elongate in all species examined. The short process that ordinarily contacts the lateral dorsal surface of the supra-cleithrum is elongate and contacts the cleithrum
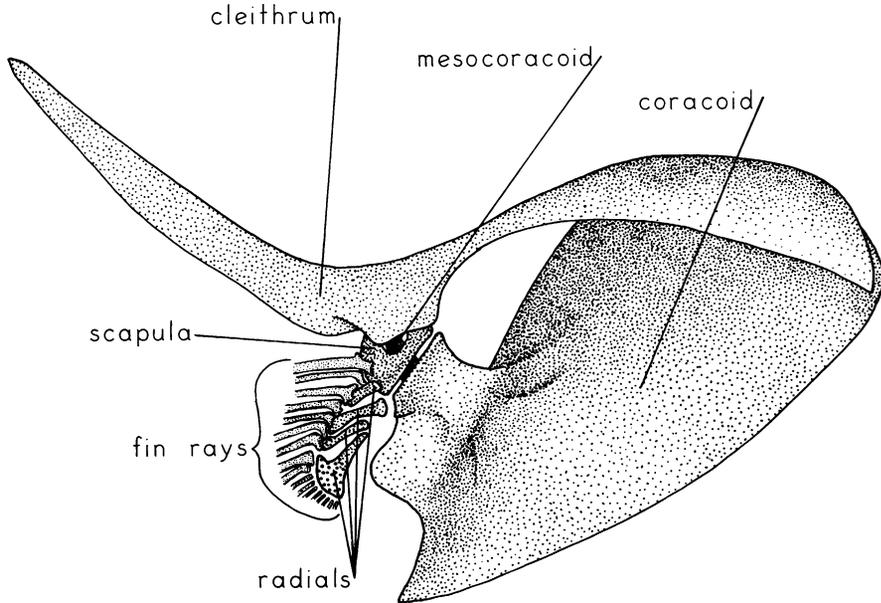
FIG. 100. Lateral view of the primary right pectoral girdle of *Danaphos oculatus*, SL 34.5 mm., USNM 203261.

in the same manner as the supracleithrum probably would if it were present. Probably this elongate ventral process of the posttemporal represents the supracleithrum fused with the posttemporal and is so labeled in figure 30. No extrascapulars are present and no laterosensory canal is associated with the bony substance of the posttemporal or its supracleithrum-like portion. The upper limb of the cleithrum is long and slender, the ventroanterior limb short and broad, with prominent striae on its lateral surface (see fig. 102). The pectoral fin notch in the cleithrum is very large. A coracoid, mesocoracoid, and scapula are present. The scapular foramen is incompletely surrounded by bone of the scapula. Four radials are present. *Polyipnus asteroides* has 14 pectoral fin rays.

All the species of *Argyropelecus* have similar pectoral girdles. The posttemporal is prominent and well ossified, but the lower limb is reduced and often unossified; however, the ligament between the posttemporal and intercalar remains strong regardless of the completeness or absence of the lower limb (see fig. 32). As in *Polyipnus*, the ventral process of the posttemporal appears fused with the supracleithrum and articulates with the dorsal end of the cleithrum.

The posterior spine of the postemporal remains relatively simple and small, not greatly elaborated as in some species of *Polyipnus*. There appear to be no extrascapular bones and no direct association between the bone of the posttemporal and laterosensory canal. The ventral end of the elongate cleithrum (see fig. 103) is typical for all species of *Argyropelecus* and is characterized by the great elaboration of the notch for the fin rays and the development of a large postero-ventral process on the anteroventral border of this notch. The anterior part of the cleithrum above the abductor muscles is deeply arched and relatively slender. The anterior spinous process of the cleithrum was called the preabdominal spine by Schultz (1961, 1964). There are nine or 10 pectoral fin rays in the specimens of *Argyropelecus aculeatus* and 11 in those of *Argyropelecus affinis* examined. A coracoid, meso-coracoid, and scapula are present and well ossified. The scapular foramen is prominent and almost completely surrounded by the scapula. There are four radials, two having their proximal ends articulating with the scapula, not one as in all the genera discussed so far. The third radial (counting from the dorsalmost) articulates with both the scapula and coracoid.
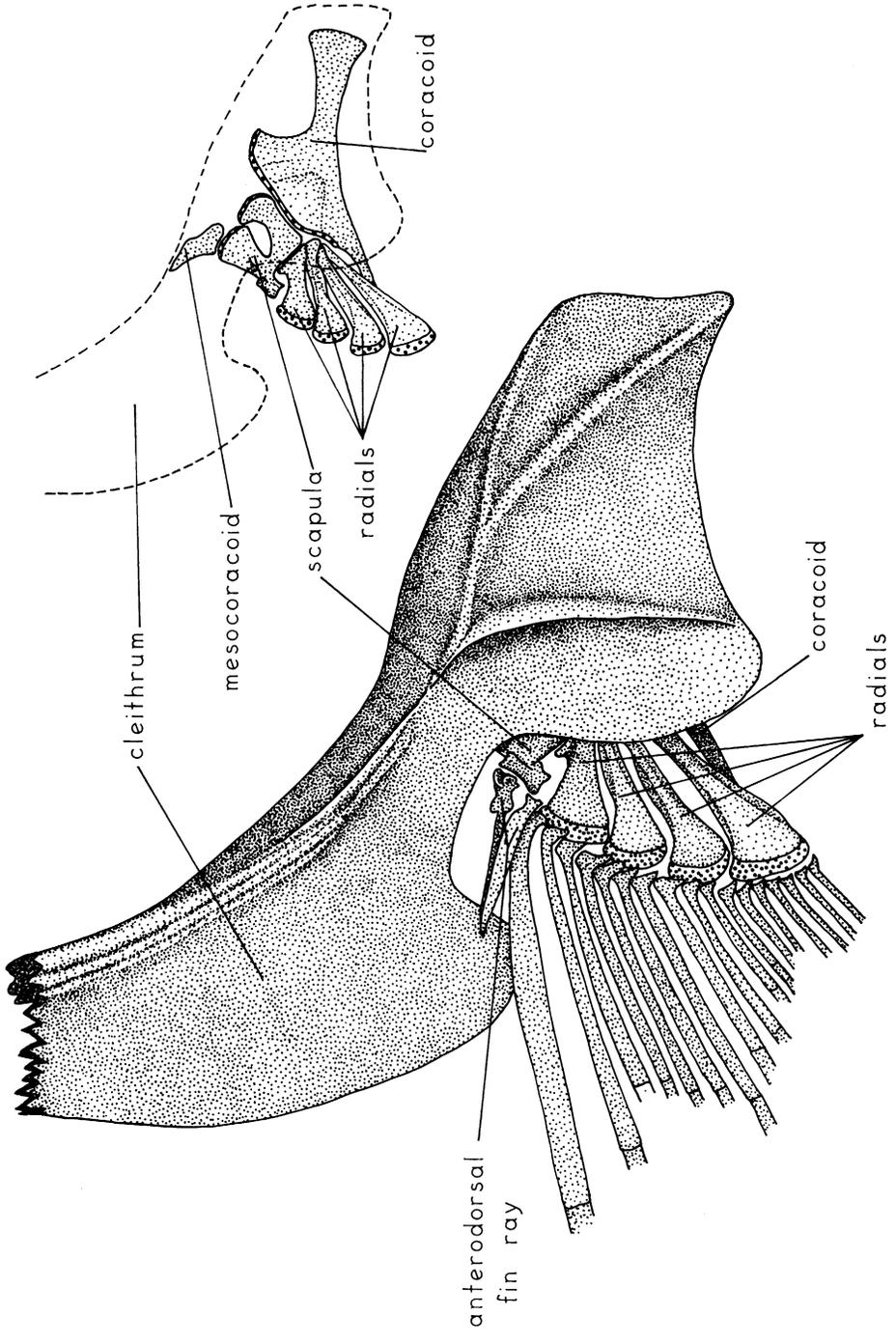
Fig. 101. Lateral view of the ventral portion of the right pectoral girdle of *Argyripnus atlanticus*, SL 57.0 mm., USNM 201351.
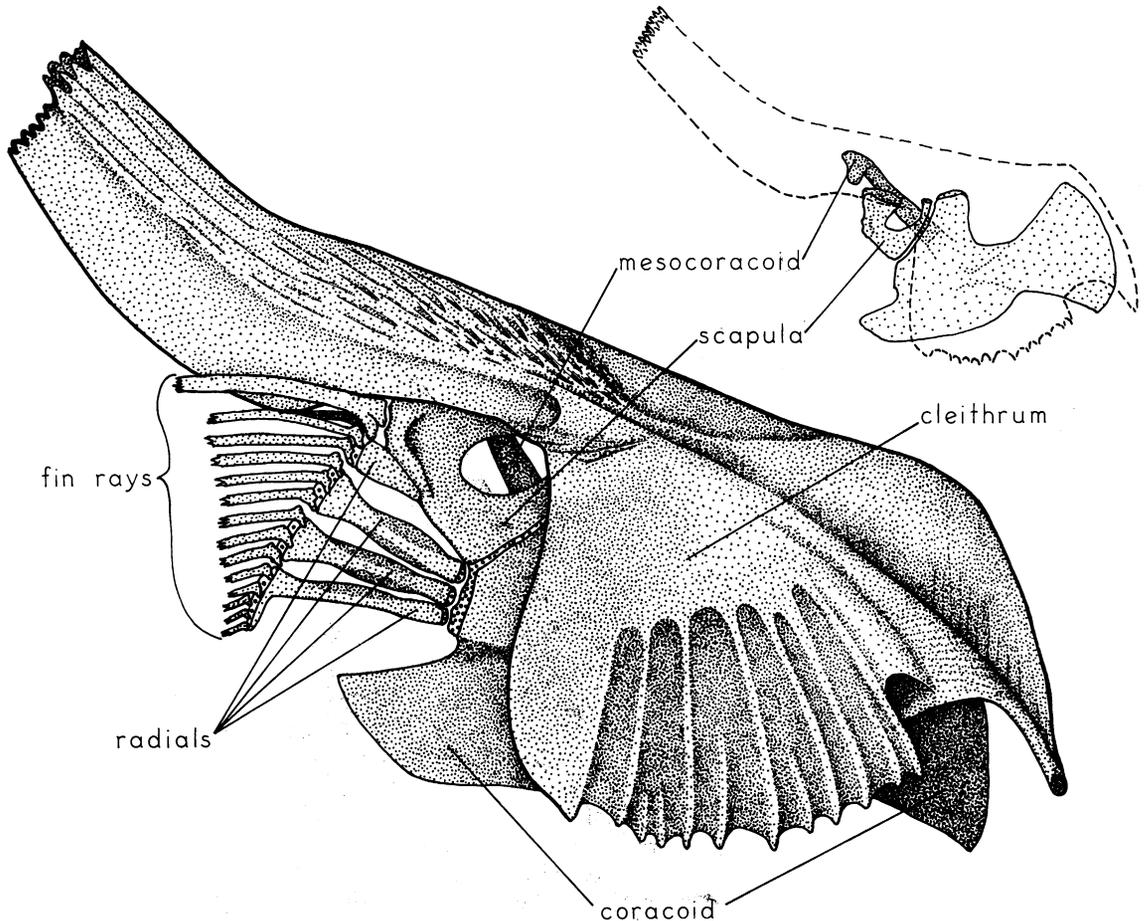
FIG. 102. Lateral view of the ventral portion of the right pectoral girdle of *Polyipnus asteroides*, SL 58.3 mm., USNM 197542.

All specimens of *Sternoptyx* examined have very similar pectoral girdles (see figs. 34, 104). The posttemporal is a V-shaped bone consisting of the two well-ossified limbs. Extrascapulars are absent, and there is no evidence of a latero-sensory canal in either the posttemporal or supracleithrum. The supracleithrum (fig. 34) is a very large, elongate, bladelike bone with a strengthening ridge through the center of its vertical axis. It is completely separate from (not fused to) the posttemporal but articulates with it. It broadly overlaps the elongate upper limb of the cleithrum. The cleithrum completely lacks the elongate recurved anteroventral border of the fin ray notch found in *Argyropelecus*. The anterior portion of the cleithrum is strongly

arched and terminates in a spine called the preabdominal spine by Schultz (1961, 1964). The coracoid is almost entirely in view in figure 104 and its narrow support for the slender mesocoracoid can be seen just anterior to the scapula. The scapula is small and does not enclose a scapular foramen; however, it does articulate with all four pectoral radials, only the fourth (ventralmost) partially articulates with the coracoid. There are 11 pectoral fin rays in the specimens of *Sternoptyx diaphana* examined.

PELVIC FIN AND GIRDLE

The pelvic girdle of both species of *Thorophos* (see fig. 105) is very similar to that of the osmerid *Spirinchus thaleichthys* illustrated by
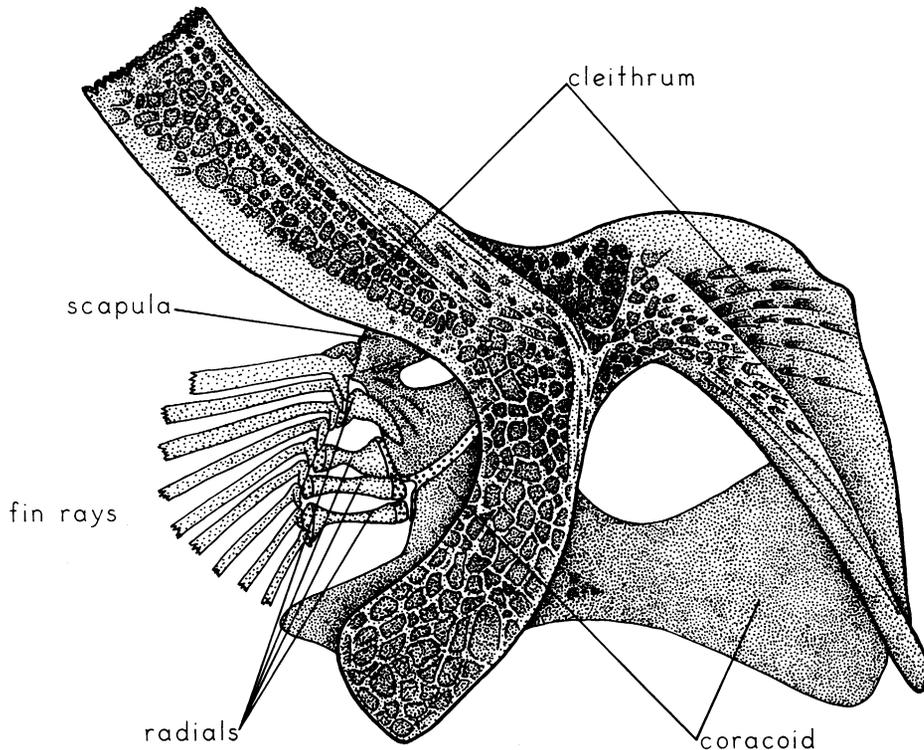
FIG. 103. Lateral view of the ventral portion of the right pectoral girdle of *Argyropelecus aculeatus*, SL 49.4 mm., USNM 179056.

Weitzman (1967a, p. 513). The cartilaginous ischial plate surrounded by bone and with its posterior ischial process is very similar to that of *Spirinchus*, more so than that of the photichthyid *Polymetme* illustrated by Weitzman (1967a, p. 524). A pubic plate is only slightly developed, occurring basally in the notch between the ischial plate and the pubic process. The iliac process is entirely cartilaginous in *Thorophos* and without a spinous process. Three radials are present, only the medial elongate radial being ossified. There are seven fin rays.

The pelvic girdle of *Araiophos gracilis* is entirely of cartilage, or if covered by a thin layer of bone this was not detected by alizarin staining. The pelvic girdle of each side is triangular with well-developed pubic and ischial processes, the entire structure having a shape much like that of *Thorophos*. The cartilaginous ischial plate and process is represented by a rod of cartilage continuous posteriorly with the body of the pelvic bone. The anterior half of the ischial plate is a

rod of cartilage extending anteriorly and lying medial to the medial border of the body of the pelvic girdle. Three cartilaginous radials are present, the medial being relatively elongate. There are five pelvic rays in *Araiophos gracilis*, and Ahlstrom and Moser (1969) reported five pelvic rays in *Araiophos eastropas*.

The pelvic girdle of *Maurolicus muelleri* (fig. 106) is similar to that of *Thorophos* except that the ischial plate is modified, more elongate, and its anterior process does not extend anteriorly. Three radials are present, all well ossified and the medial radial is not elongate.

Danaphos oculatus and *Valenciennellus tripunctulatus* have similar pelvic girdles. That of *Danaphos* (fig. 107) has prominent pubic and iliac processes. The ischial plate is greatly enlarged and bears a small posterior iliac process and a large anterior iliac process. A pubic plate appears absent and the only ossification obviously present centers around the pubic process. The exact line where bone ends could
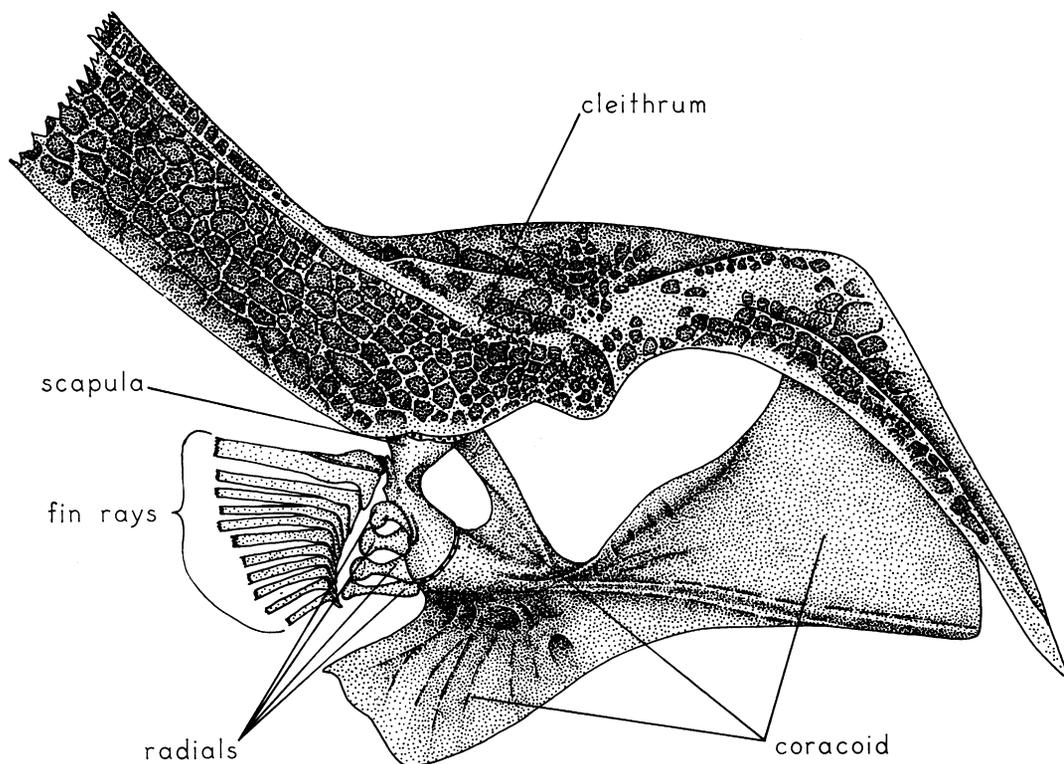
FIG. 104. Lateral view of the ventral portion of the right pectoral girdle of *Sternoptyx diaphana*, SL 44.0 mm., USNM 192843.

not be determined from gross inspection. There are six radials and seven fin rays. *Valenciennellus* also has six radials and seven fin rays, has a pubic plate, and an ischial plate proportionally about half the size of that of *Danaphos*.

Argyripnus atlanticus (fig. 108) has no ischial spine but has a prominent ischial plate. The pubic plate and process are well ossified. There are seven fin rays and six radials.

Sonoda megalophthalma (fig. 109) has a very similar pelvic girdle but has a cartilaginous ischial process, six fin rays, and six radials.

All species of *Polyipnus* examined have similar pelvic girdles (see fig. 110 of *Polyipnus asterioides*). All the pelvic girdles discussed above lie flat, that is, with the pubic process extending anteriorly, the ischial process medially, and the iliac process laterally. The flattened plane of the pelvic girdles lies in the rounded, relatively flat plane of the body wall. In *Polyipnus*, *Argyropelecus*, and *Sternoptyx* the body is very compressed and the ventral region bladelike. In *Polyipnus* the

pelvic girdle has rotated so that the dorsal, flat side of the girdle faces laterally, the pubic process dorsally, the iliac process anteroventrally, and the ischial process posterodorsally. The pubic process is well ossified, very strong, and in close association with the posterior two of the six enlarged pleural ribs. There is a very prominent iliac spine (postabdominal spine of Schultz, 1961, 1964) projecting ventrally and protruding beyond the surrounding body wall. The iliac spines of each pelvic bone lie adjacent to each other so that two spines will be found on inspection of the fish. Six radials are present and seven fin rays were found on all species examined.

The pelvic girdle of all the species of *Argyropelecus* examined is essentially similar to that of *A. aculeatus*. The pelvic bone is vertically oriented with the pubic process extending dorsally, the ischial process posterodorsally, and the iliac process ventrally. The degree of dorsal and posterior orientation of the ischial process varies with the species, being more
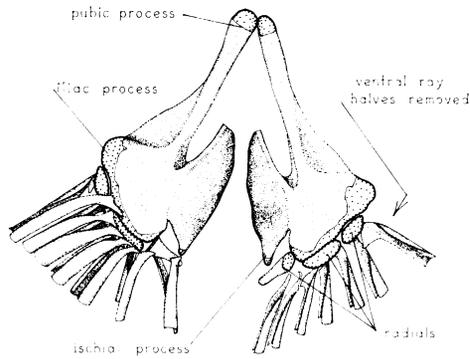
FIG. 105. Ventral view of the pelvic girdle of *Thorophos euryops*, SL 44.7 mm., DANA 3736-VI. Ventral ray halves removed from the left side of the fish (right side in the illustration) exposing the radials.

FIG. 106. Ventral view of the right side of the pelvic girdle of *Maurolicus muelleri*, SL 45.5 mm., USNM 201138. Part of the ventral half of the ray halves have been removed to expose the radials.

FIG. 107. Ventral view of the right side of the pelvic girdle of *Danaphos oculatus*, SL 34.5 mm., USNM 203261. Ventral ray halves removed.

FIG. 108. Ventral view of the pelvic girdle of *Argyripnus atlanticus*, SL 57.0 mm., USNM 201351. The ventral ray halves of the right side (left side in figure) have been removed.

FIG. 109. Ventral view of the pelvic girdle of *Sonoda megalophthalma*, SL 53.5 mm., USNM 201350. Part of ventral ray halves removed from right side (left side in figure).
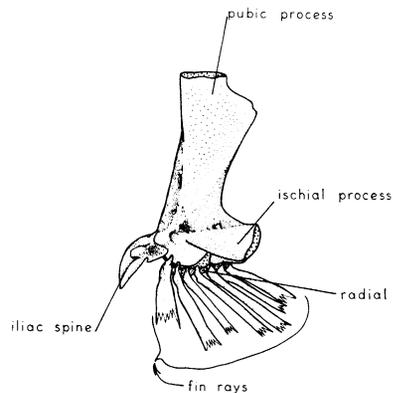
FIG. 110. Lateral view (corresponds to ventral view in figs. 104–106) of the left half of the pelvic girdle of *Polyipnus asteroides*, SL 58.0 mm., USNM 197542.
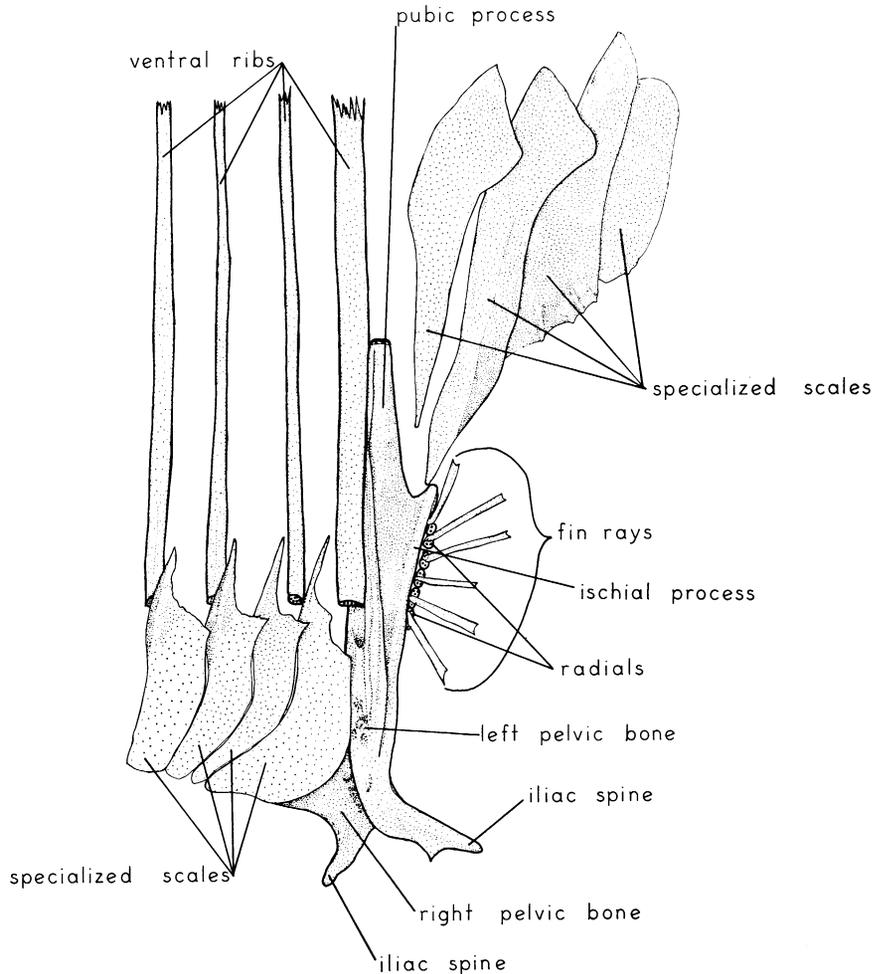
FIG. 111. Lateral view of the pelvic girdle and associated structures of *Argyropelecus aculeatus*, SL 49.4 mm., USNM 179056.

dorsal in *A. aculeatus* and more posterior in *A. affinis*. The iliac spine (=postabdominal spine of Schultz, 1961, 1964) protrudes beyond the body wall and may extend posteriorly, ventrally, or anteriorly (see variation in figs. 11, 12, 111). Usually the iliac spine of each side extends in a different direction and the pelvic bones of each side are separate. However, as reported by Baird (1971), the pelvic bones are fused in *A. hemigymnus*. In this species the iliac spines appear to have fused to a single median element, the remainder of the girdles of each side remaining separate. Anteriorly and posteriorly the pelvic girdle is closely associated with sharp,

specialized scales or scutes of the abdominal floor (see fig. 111). There are six radials and six fin rays. One of the large ribs, the seventh and last (attached to the parapophysis of the tenth vertebra) parallels the pubic process and forms an important structural union with the pelvic girdle, being bound by fibrous connective tissue and helping to maintain the rigid nature of the ventral part of the body.

Sternoptyx has a peculiar pelvic girdle (see fig. 112), dorsally oriented as in *Polyipnus* and *Argyropelecus*, but with a relatively elongate pubic process associated with two large ventral ribs (the sixth and seventh from the ninth and tenth vertebrae

respectively). The ischial process and an iliac spine are well developed, the former posterodorsally, the latter anteroventrally oriented. There is only one pelvic radial and five pelvic fin rays. Baird (1971) reported the pelvic bones (basipterygia) to be fused in *Sternoptyx*. All specimens examined here had the pelvic bones of each side separate; however, a little anterior to a point midway between the extreme ends of the ischial process and iliac spine, the pelvic bones are closely bound together by connective tissue and appear as one bone unless pried apart.

RELATIONSHIPS OF THE STERNOPTYCHIDAE AND STERNOPTYCHID GENERA

FAMILY STERNOPTYCHIDAE

THE STERNOPTYCHIDS REPRESENT a distinct stomiatoid lineage of the Gonostomata and for purposes of a diagnosis can be separated from all other stomiatoids by the possession of three branchiostegal rays on the epihyal and four pectoral fin radials. The first of these characters used alone will distinguish them from all other stomiatoids except the highly derived melano-stomiatid genus *Bathophilus* Regan and Trewavas.

The sternoptychids as defined here include relatively primitive stomiatoid genera, for example *Thorophos*, as well as some of the most highly advanced stomiatoids known, for example *Polyipnus*, *Argyropelecus*, and especially *Sternoptyx*. Despite the great difference in morphology among sternoptychids, some unique, apparently advanced characters are found in them all, indicating a common ancestry. All sternoptychids have 10 branchiostegal rays except *Sternoptyx* which has six. All sternoptychid genera have three branchiostegal rays on the epihyal. These are never slender, threadlike rays as in some of the Photichthya (specifically the superfamily Stomiatoidea). The primitive versus advanced nature of the low branchiostegal ray count in sternoptychids is debatable, but I believe it probably represents an advanced condition.

Of the other Gonostomata, gonostomatids have a total of 12 to 16 branchiostegal rays, with four, five, or six on the epihyal, depending upon the genus. The Photichthya have a wide variation in branchiostegal rays with 11 to 22 in the Photichthyidae. In this family there are four, five, six, or seven on the epihyal, depending upon the genus. The number of branchiostegal rays varies greatly in the superfamily Stomiatoidea, again depending upon the genus, sometimes with more than 22 and often at least 10 on the epihyal. For example in *Astronesthes* there are as many as 24 and in *Heterophotus* there are 28 branchiostegal rays. Some of the more advanced genera of the Stomiatoidea such as the melano-stomiatids and malacosteids have reduced numbers of branchiostegal rays. For example *Bathophilus* has only three epihyal rays and has a total of 10 rays. *Eustomias* with four epihyal rays has a total of about 13 branchiostegal rays. *Photostomias* Collett and *Aristostomias* Zugmayer have four epihyal rays but the posterior of these has migrated posteriorly on to the ventral base of the interhyal. Idiacanthids have five epihyal rays, stomiatids seven, and chauliodontids six. Many of the stomiatoid counts of branchiostegal rays taken from the literature and published by McAllister (1968) are in error, not being based on alizarin preparations.

McAllister (1968) noted that the high number of epihyal branchiostegal rays in some stomiatoids suggests their derivation from elopoids which also have a high number of epihyal rays. If one examines the epihyal branchiostegal rays of the relatively primitive stomiatoid genera in the Gonostomatidae (*Triplophos* with five, *Diplophos* with four) and the Photichthyidae (*Vinciguerria*, *Polymetme*, *Yarrella*, and *Pollichthys* all with four), it seems likely that early stomiatoid ancestors had a relatively low epihyal branchiostegal ray count and that this low count is inconsistent with elopoid counts. Counter to McAllister's belief that a high epihyal branchiostegal ray count is primitive, in stomiatoids a very high count may be advanced, for it is in the otherwise derived genera of the Photichthya that high counts occur. Sternoptychids may either retain a relatively primitive and low number of epihyal branchiostegal rays for stomiatoids or more probably have actually reduced the primitive count of four or five to three. The trend in the Photichthya seems to have been to increase in some cases the numbers of epihyal branchiostegal rays. A similar argument might also be valid for the total branchiostegal count. Certainly the reduced count of six total rays in *Sternoptyx* is advanced for sternoptychids and for stomiatoids as a whole. It is here assumed that the branchiostegal ray count of 10 for sternoptychids is a moderate, but nearly constant, advanced con-

dition and serves to relate the various sternopty-
chid genera.

Sternoptychids also have a small and stable
number of branchiostegal photophores, almost
all genera having six. *Sonoda* rarely has seven and
Sternoptyx has three, corresponding to its reduc-
tion in ceratohyal branchiostegal rays. All
genera of the Photichthyidae have eight or
sometimes seven (in *Vinciguerria*) branchio-
stegal photophores. Gonostomatids have a low
of eight branchiostegal photophores but with
up to 16 in *Diplophos*. The branchiostegal
photophore count in the Stomiatoidea varies,
much as the branchiostegal ray count with a
generally high count of 15 to about 24 in the
Astronesthidae. Certainly whatever arguments
may be valid for the advanced versus primitive
nature of low or high branchiostegal ray counts
are also valid for branchiostegal photophore
counts.

The photophores of sternoptychids are
clumped or united into common specialized
organs, whereas they are separated in all other
stomiatoid groups. In addition, Bassot (1966)
noted that the photophores of a few sternopty-
chids (*Maurolicus*, *Argyropelecus*, and *Sternoptyx*)
are histologically similar (Alpha type). He
considered the Alpha type of photophores
advanced compared with the photophores
found in the Gonostomatidae.

The branchial arches of sternoptychids are
characteristic and derived. The basihyal (glosso-
hyal) is absent. Among the gonostomatids only
Cyclothone, a possible relative of *Gonostoma* and
advanced in many characters, lacks this bone,
and is severely reduced in all and possibly
absent in some of the superfamily Stomiatoidea.
There is a general trend in the stomiatoids to
have a reduced basihyal. A basihyal is present in
all photichthyid genera. The basihyal is tooth-
less in all stomiatoids except for the gonosto-
matid *Diplophos* which has the bone exception-
ally large for a stomiatoid and horizontally
placed rather than small and tipped antero-
ventrally as in almost all other stomiatoid
genera having this bone. The bone is of moder-
ate size but toothless in *Triplophos*, *Photichthys*,
and *Woodsia*, all relatively primitive stomiatoids
in other ways also. The large, toothed basihyal
in *Diplophos* is undoubtedly primitive for the
suborder Stomiatoidei. The absence of the
basihyal in the Sternoptychidae is a derived
character.

An anterior myodome bone is present in the
young at least of some gonostomatids and
photichthyids. This bone is invariably absent in
the sternoptychids and the loss represents an
advanced state but not an exclusive one.

The infrapharyngobranchial of the second
gill arch is toothless in all sternoptychids as it is
in many stomiatoids. In some of the relatively
primitive gonostomatids (*Margrethia*, *Bonapartia*,
Diplophos) and photichthyids (*Vinciguerria*, *Pho-
tichthys*, *Pollichthys*) it is toothed. The bone is
toothed in osmeroids. The loss of teeth on this
bone in sternoptychids is an advanced but not
exclusive character.

Upper jaw ligaments are most useful in de-
fining genera and groups of genera in stomia-
toids but are not very helpful in defining higher
categories. Excluding the Stomiatoidea, in which
these structures are greatly modified, some inter-
esting results can be found in comparing
sternoptychids, gonostomatids, and photich-
thyids. Osmeroids and several other teleosts
plus the photichthyid *Polymetme* have a maxillary
proethmoid ligament. It is absent in all other
photichthyids, all sternoptychids and gonosto-
matids. Presumably this ligament was present in
stomiatoid ancestors but has been lost in most
modern genera.

All sternoptychids except *Sternoptyx* have the
parietals separated from one another by the
supraoccipital. No gonostomatid or photich-
thyid has the parietals separated, and pre-
sumably the separation is an advanced character
common to most sternoptychids. There is a
tendency for reduction of the parietals in the
superfamily Stomiatoidea (see Weitzman,
1967b). In *Sternoptyx* the parietals are only par-
tially separated, and presumably this contact be-
tween the parietals is secondarily reacquired,
having been lost early in the evolution of the ster-
noptychid line. Baird (1971) believed the meeting
of the parietals in *Sternoptyx* may be a primitive
character at least for a relationship based on
Sternoptyx, *Argyropelecus*, and *Polyipnus* as a
group. In any relationship between these three
genera or the remaining sternoptychids as
considered here, I believe it best to consider the
character advanced, for it is rather difficult to
believe that the ancestors of *Sternoptyx*, which
were probably close in structure to *Sonoda* and
Argyripnus, retained parietals in contact, where-
as all other known Recent sternoptychids have
them separated.
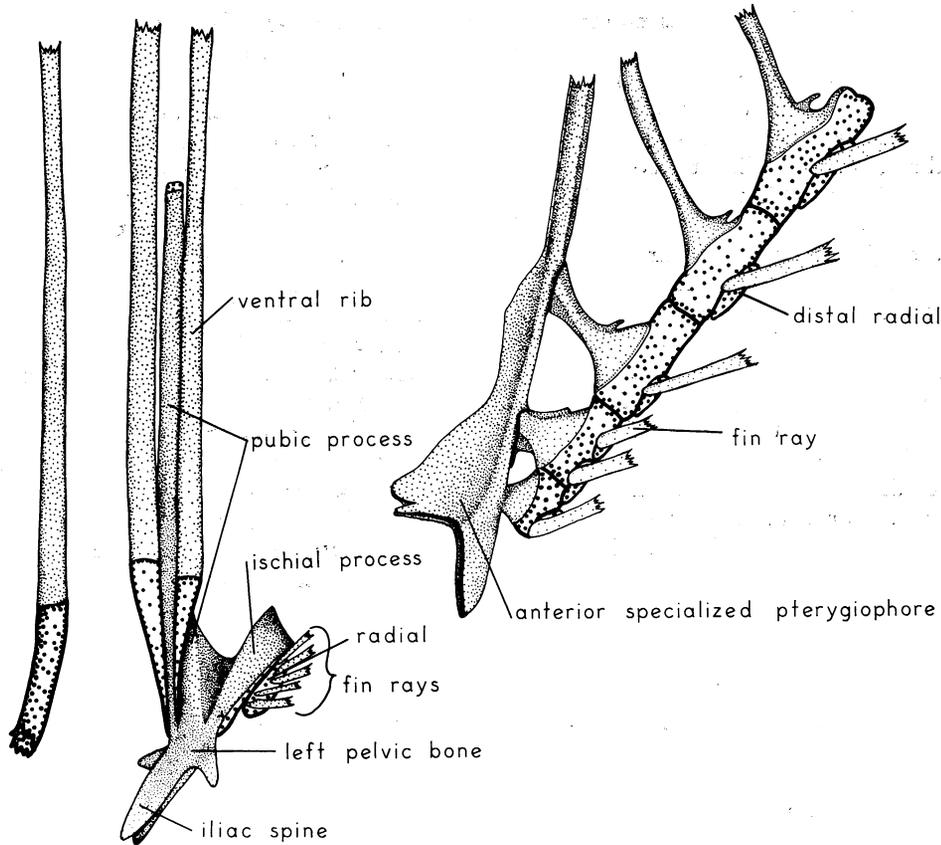
FIG. 112. Lateral view of the pelvic girdle and associated structures including the anterior
end of the anal fin in *Sternoptyx diaphana*, SL 44.0 mm., USNM 192843.

The terminal dorsal and anal fin rays of sternoptychids are never divided or split to their bases except for *Polyipnus* which may be atavistic in this character. In the gonostomatids and photichthyids the terminal fin rays are various, sometimes divided, sometimes not, but always consistent in one fin in any given species. In some species the dorsal fin will have divided terminal rays, whereas the anal fin will have a single ray. It is impossible at the present time to be certain of the advanced versus primitive nature of these structures in stomiatoids.

All sternoptychids, except *Thorophos*, with an adipose fin have that fin relatively long based (compare figs. 2–13). Even the adipose fin in *Thorophos* is long based in that it is not constricted at its base. All other stomiatoids except the photichthyid *Ichthyococcus* (fig. 16) have it short based (see figs. 14, 15) when it is present. A

long-based adipose fin is undoubtedly advanced (perhaps neotenic) for stomiatoids. The possession of a long-based adipose fin by the sternoptychids and *Ichthyococcus* is here considered convergent because in certain advanced characters *Ichthyococcus* is a typical photichthyid.

Finally, no sternoptychid was found to have mesopterygoid teeth. These teeth are found in several genera of relatively primitive gonostomatids and photichthyids.

STERNOPTYCHID GENERA

On the basis of a wide variety of advanced characters, the 10 sternoptychid genera can be arranged into several groups, each representing a probable evolutionary line (see fig. 113). In the treatment of these groups below, advanced and exclusive characters in common with the member genera of a group are discussed. These
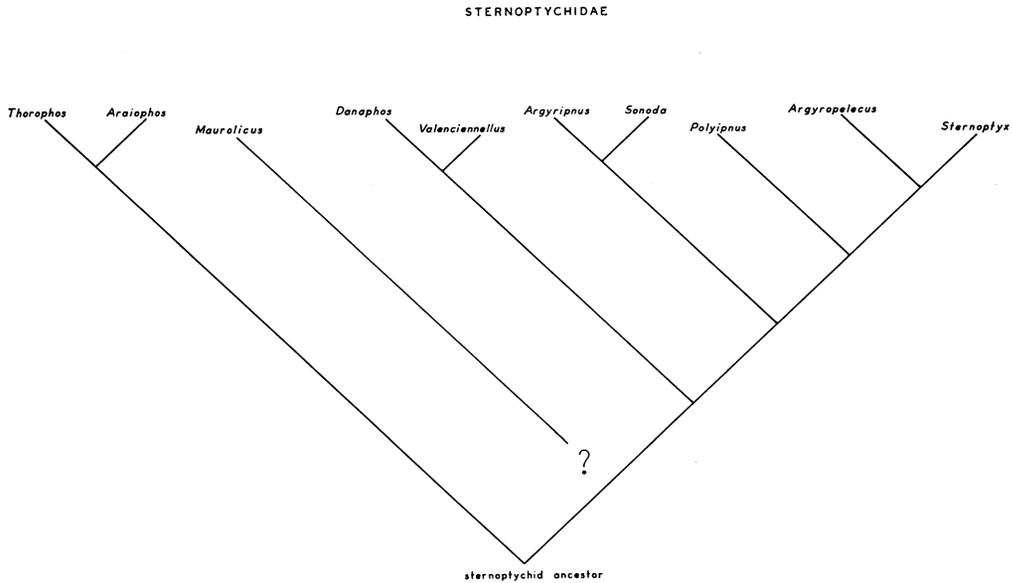
STERNOPTYCHIDAE

FIG. 113. A phylogeny of the Sternoptychidae.

characters are used to relate the genera to their respective groups. Primitive characters in common with member genera also are discussed. These characters are not used to relate these fishes at the group level discussed here but to indicate the relative primitive aspects of the group in question. Characters of uncertain primitive or advanced nature are treated but not used to relate genera or groups. The genera within each group are compared for differences and an attempt is made to deduce their primitive or advanced state relative to each other.

THOROPHOS AND ARAIOPHOS

Thorophos and *Araiophos* appear more closely related to each other than either is to any other sternoptychid genus. Of the two, *Araiophos* is the more advanced, lacking an adipose fin and having a reduced bony skeleton in the adult, suggesting neoteny. The genus *Neophos* is placed in the synonymy of *Thorophos* (see Appendix).

For the most part, characters held in common by *Thorophos* and *Araiophos* are primitive for stomiatoids and therefore cannot be used to relate these fishes to any particular stomiatoid line but are useful in indicating that both genera are relatively primitive sternoptychids.

Advanced characters common to *Thorophos* and *Araiophos* but not present in other sternopty-

chids are rather few and not too convincing. The exoccipitals of both genera do not enter the border of the posttemporal fossa. In all other sternoptychid genera except *Sternoptyx* which has a greatly modified posttemporal fossa, the exoccipital enters the posttemporal fossa. In gonostomatids and photichthyids a small section of the exoccipital enters the fossa border. Its absence from the fossa in *Thorophos* and *Araiophos* is an advance perhaps indicating a common ancestry. In any event comparison of figures 17 and 19 shows that the ethmoid region and upper jaws of these two genera are very similar in appearance. They are not similar to the form of the jaws in any other sternoptychid nor that in any gonostomatid or photichthyid. It seems likely that the similarity between these two genera in jaw structure is due to a close phylogenetic relationship.

Similarities of the skulls of *Thorophos* and *Araiophos* (compare figs. 17–20) are many. This is especially apparent if one compares the skulls of these two genera with skulls of other sternoptychids, photichthyids, and gonostomatids. Even in details of the supraethmoid, pterotics, frontals, and upper and lower jaws (compare figs. 52, 54) the two genera are similar. These details may be slight specializations associated in these genera only and thus indicate relationship.

Primitive characters or character complexes found in *Thorophos* and *Araiophos* are here defined as those shared with gonostomatids and/or photichthyids only, and those shared not only with these families but also with one or a few other apparently relatively primitive sternoptychid genera. Primitive characters in common with Gonostomatidae and Photichthyidae but not found in other sternoptychid genera are a relatively shallow longitudinal frontal fossa, in contrast to the deep or even tubelike fossa found in other sternoptychid genera. This fossa is shallow in most gonostomatids and photichthyids. The mesopterygoid of both genera is quadrangular, as is the usual case in the gonostomatids and photichthyids. It is triangular in all the remaining sternoptychids, an advanced character that may unite all these remaining genera. The adductor recess is near the posterior one-third or one-fourth of the mandible in the less specialized genera of the Gonostomatidae and Photichthyidae. It is near the posterior one-third in *Thorophos* and *Araiophos* and slightly posterior, or near, or anterior, to the middle of the mandible in the remainder of the sternoptychids. The urohyal is of moderate length and its posterior border is deeply incised in *Thorophos* and *Araiophos*. It is elongate and deeply incised in most gonostomatids and photichthyids. In most sternoptychids, except *Argyropelecus* and *Sternoptyx* (in which it is relatively moderate in size and incised but unique in shape), the urohyal is either small and incised or large and not incised. In urohyal size and shape *Thorophos* and *Araiophos* appear more primitive than other sternoptychid genera in which the urohyal is advanced in various ways.

Certain primitive sternoptychid characters are found in *Thorophos* and *Araiopohos* and shared with either *Maurolicus* or in some cases other sternoptychid genera. For example, as in the gonostomatids and photichthyids, *Thorophos*, *Araiophos*, and *Maurolicus* retain a primitive number of three pelvic radials. All other sternoptychid genera have six or, in the case of *Sternoptyx*, only one. Also *Thorophos*, *Araiophos*, and *Maurolicus* are the only sternoptychid genera to retain both anterior and posterior supramaxillaries. Several genera of photichthyids and gonostomatids have both supramaxillaries. The sagitta of *Araiophos* is unknown but that of *Thorophos* and *Maurolicus*, especially that of the latter, is more primitive than that of any other sternoptychid

for which the structure is known. *Maurolicus* retains the large rostrum found in many gonostomatids and photichthyids and teleosts in general. Of the sternoptychids, *Thorophos*, *Araiophos*, and *Maurolicus* retain the relatively primitive elongate posterior process of the supraethmoid found in gonostomatids and photichthyids, even though the supraethmoid of *Maurolicus* is laterally compressed.

Thorophos, *Araiophos*, *Argyripnus*, and *Sonoda* also exclusively share several characters, most of them primitive for stomiatoids. All have a broad ethmoid cartilage as in most gonostomatids and photichthyids, the laterally compressed ethmoid region of *Maurolicus*, *Danaphos*, and *Valenciennellus* being advanced. Palatine teeth are retained in *Thorophos*, *Araiophos*, *Argyripnus*, *Sonoda*, *Polyipnus*, *Argyropelecus*, and *Sternoptyx*. The ectopterygoid is elongate-triangular and of moderate size in *Thorophos*, *Araiophos*, *Argyripnus*, and *Sonoda*, similar to that of relatively primitive gonostomatids and photichthyids. The maxillary of *Thorophos*, *Araiophos*, *Argyripnus*, and *Sonoda* does not have a sharp angle in its ventral border as does that of *Maurolicus*, *Danaphos*, *Valenciennellus*, and many species of *Polyipnus*. The sharp angle is probably an advanced character and may be independently derived in these genera, except for the closely related *Danaphos* and *Valenciennellus*.

A few other features, mostly external, indicate the relatively primitive nature of *Thorophos* and *Araiophos* compared with other sternoptychids. For example, in common with many gonostomatids and photichthyids, they retain a relatively elongate body shape and less deep head. For sternoptychids, *Thorophos* has a relatively short-based adipose fin, approaching that of some gonostomatids and photichthyids more than any other sternoptychid and most probably is a primitive feature. The adipose fin is missing in *Araiophos*, an advanced character. *Thorophos* and *Araiophos* also have relatively primitive and simple photophore arrangement for a sternoptychid (compare figs. 2–13). *Thorophos* and *Araiophos* retain more primitive characters than any other sternoptychid genera and therefore may be considered the most primitive members of the family.

The following characters common to *Thorophos* and *Araiophos* are difficult to interpret. *Araiophos* and *Thorophos* are the only sternoptychid genera lacking crossed portions of the premaxillary-proethmoid ligament. This liga-

ment is commonly present in photichthyids and gonostomatids, where it is crossed or uncrossed. The lack of a crossed segment in *Thorophos* and *Araiophos* may or may not be a specialization. *Thorophos* and *Araiophos* lack radial elements in the caudal fin. All other sternoptychid genera except *Polyipnus*, *Argyropelecus*, and *Sternoptyx* have these cartilages. These elements are also present in some gonostomatids and photichthyids. Although the distribution of these structures in stomiatoids follows a mosaic pattern, within families their presence or absence seems correlated with other characters relating genera. For example, the genera *Polyipnus*, *Argyropelecus*, and *Sternoptyx* can be related on the basis of several advanced characters (see below) and these genera lack caudal fin radials. The problem of the possible advanced versus primitive nature of caudal radial cartilages in stomiatoids remains unsolved at this time. These structures are not known with certainty in other teleosts yet they are structures that one would expect to find in primitive teleosts. Their appearance in certain genera of stomiatoids remains enigmatic.

Most gonostomatids and photichthyids have the dorsal fin origin in advance of the anal fin. This is true of all sternoptychid genera except *Thorophos*, *Araiophos*, *Valenciennellus*, and *Sonoda* which have the anal fin origin in advance of the dorsal fin origin. Apparently the forward position of the anal fin is an advanced character that appears independently in some stomiatoid genera for there is much other evidence that these four genera do not share an "immediate" common ancestor. Even so, *Thorophos* and *Araiophos* probably do have one and in any case an anterior anal fin in common between these two genera certainly does no damage to the concept that these fishes are related. If the character is advanced it may be considered a reinforcement of the hypothesis that *Araiophos* and *Thorophos* are closely related.

Thorophos has few advanced characters not found in *Araiophos*. It appears to be the only genus in Gonostomata or the Photichthyidae with median teeth on the vomer. Presumably this is advanced for a stomiatoid. It is also the only sternoptychid with a slender posterior supramaxillary except *Sternoptyx*, in which the condition is somewhat different and undoubtedly independently derived. The caudal skeleton of *Thorophos* may be more advanced than that of *Araiophos*, but see discussion below.

In most characters in which they differ, *Thorophos* is primitive relative to *Araiophos*, which seems definitely neotenic. The following characters appear advanced for *Araiophos*. *Thorophos* has two moderate-sized lateral parasphenoid wings, *Araiophos* one small wing, the latter presumably a specialization for stomiatoids. *Araiophos* has a very small, apparently advanced basisphenoid, *Thorophos* a moderate-sized basisphenoid similar to that found in gonostomatids. The palatine has a two-headed, relatively primitive shape in *Thorophos*, whereas in *Araiophos* it is a rectangular bar of cartilage (possibly neotenic) with a ventral toothed bone. *Thorophos* has a complete orbital ring of four bones, whereas *Araiophos* has only two infraorbitals, none posterior to the eye. The condition of orbital bones in *Araiophos* appears advanced relative to *Thorophos*, but that of *Thorophos* is advanced relative to the Gonostomatidae and Photichthyidae, *Thorophos* having a reduced number of separate orbital bones as do all sternoptychids.

The opercular apparatus of *Thorophos* is well ossified, the bony parts covering the gill apparatus completely. That of *Araiophos* is reduced and modified and the individual bones have modified shapes (compare figs. 18, 20) compared with *Thorophos* and the gonostomatid and photichthyid genera. The hyomandibular bone of *Thorophos* is relatively long, being about one-half the length of the cranium. The hyomandibular bone of *Araiophos* is about one-fourth the cranial length. The articulation between the opercle and the hyomandibular bone is near the dorsal one-third of the hyomandibular length in *Thorophos* and at about one-half the hyomandibular length in *Araiophos*. Comparison with other stomiatoids indicates that the low position of this articulation and the relatively short length of the hyomandibular in *Araiophos* is advanced. Some sternoptychids, the hatchetfish genera, have the hyomandibular bone modified in the opposite direction, with the bone elongate.

Although *Araiophos* may in part be juvenile or larval in form, it is not a neotenic *Thorophos*, for it has a few nonneotenic specializations which differentiate it from *Thorophos*. *Araiophos* more frequently has the photophores clustered into groups than *Thorophos* (compare figs. 2–4). *Araiophos* has an increased number of precaudal (abdominal) vertebrae (20 rather than the 14 to 16 in *Thorophos*) together with at least two more

rib-bearing vertebrae. *Araiophos* has a longer-based dorsal fin and a shorter anal fin than those of *Thorophos*. *Thorophos* has a better developed coronoid tooth "platform" on the dentary than *Araiophos*. All of these characters for *Thorophos*, except the length of the base of the anal fin, appear primitive when these two genera are compared with the gonostomatids.

The relative primitive versus advanced nature of the caudal skeleton is difficult to interpret in these two genera. *Thorophos* has one platelike epural and *Araiophos* has no epural, the latter apparently an advanced condition. The caudal skeleton of *Araiophos* has undergone a little less fusion than that of *Thorophos* (compare figs. 88, 89). The fused parahypural and hypurals one and two are free of the preural centrum and the ural centra in *Araiophos*, but fused in *Thorophos*, seemingly a derived condition for *Thorophos*. Hypurals three, four, and five are fused in *Thorophos* but five remains autogenous in *Araiophos*. *Araiophos* retains a second uroneural. It is either lost or fused to the first in *Thorophos*. In the sum of characters the caudal skeleton of *Araiophos* looks less advanced than that of *Thorophos* but it may retain fewer fused elements simply because this small, neotenic fish may not grow large enough for fusion to take place, the caudal skeleton returning to a "less advanced" state. In any event it seems best not to utilize the caudal fin in evaluating the relative advanced versus primitive states of these two genera.

An attempt to consider the remaining sternoptychid genera as a sister group with the group containing *Thorophos* and *Araiophos* was not very successful. There are many characters in which the *Thorophos-Araiophos* group is primitive and in which the remaining sternoptychid genera are advanced; however, the latter genera are usually advanced in a variety of different directions, and if their ancestors once had somewhat advanced characters in common, these former similarities have been obscured by subsequent evolution. There are a few unique advanced characters common to *Maurolicus*, *Danaphos*, *Valenciennellus*, *Argyripnus*, *Sonoda*, *Polyipnus*, *Argyropelecus*, and *Sternoptyx* but their real significance is in doubt. They are treated below in order of descending reliability, but I consider them all of questionable value.

The adductor pocket of the mandible is nearer to the middle or anterior part of the mandible than to the posterior one-third or one-fourth as it is in *Thorophos*, *Araiophos*, the gonostomatids, and photichthyids. There seems to be a clear trend to move the position of this pocket anteriorly in sternoptychids compared with other stomiatoids. *Thorophos* and *Araiophos* are exempt. Possibly such a shift could be convergent among these fishes, but probably the shift is suggestive of a trend based on relationship.

The cranium bears a deep, longitudinal frontal fossa. This is common to all sternoptychids except *Thorophos* and *Araiophos*, which have a condition like that of the less advanced genera of the Gonostomatidae and Photichthyidae. The crania of the several sternoptychid genera advanced in this direction are widely different and advanced in different ways and it is quite possible that this deepening of the fossa is convergent. Again, all the sternoptychid genera except *Thorophos* and *Araiophos* have a triangular-shaped mesopterygoid. It is quadrangular in the latter two genera and in most gonostomatids and photichthyids. Again, however, such a shape could be due to convergent alteration associated with the different kinds of head modification in these genera.

Another character, the failure of the entrance of the exoccipital bone to contribute to the border of the posttemporal fossa may be advanced or primitive for *Thorophos* and *Araiophos*. It does enter into the border in all the remaining sternoptychids except *Sternoptyx* which has the fossa highly altered and filled with the intercalar. In some but not all gonostomatids the exoccipital may enter the fossa a slight amount. The primitive versus advanced nature of the character thus appears indeterminate.

With three characters of the above being only possibly meaningful it is difficult to place confidence in a sister group containing all sternoptychid genera except *Thorophos* and *Araiophos*. The main problem with regard to such a group is *Maurolicus*, which, if it is related more closely to the remaining sternoptychid genera than to *Thorophos* and *Araiophos*, had its advanced characters showing this relationship highly modified by subsequent evolution. Also, *Maurolicus* appears to have diverged so early that it retains several primitive characters not found in the remaining Recent genera, *Danaphos*, *Valenciennellus*, *Argyripnus*, *Sonoda*, *Polyipnus*, *Argyropelecus*, and *Sternoptyx*. These remaining Recent genera may be the sister group of *Maurolicus* (see below). In addition, *Maurolicus*

appears to have some primitive characters not found in *Thorophos* and *Araiophos* indicating that the last two genera are in some ways more advanced than *Maurolicus*. See the discussion below under *Maurolicus*.

MAUROLICUS

The advanced characters of *Maurolicus* are many, several being shared by other sternopty-chid genera. Of the relatively unique characters perhaps the capsular ethmoids are the most peculiar. These are united dorsally but remain free of the supraethmoid dorsal to them. Only *Argyripnus*, *Polyipnus*, and *Argyropelecus* have capsular ethmoids, and in these genera these bones, if really present, are fused to the supra-ethmoid. The presence of capsular ethmoids should be considered primitive, for they are found in gonostomatids and photichthyids. However, their fusion to one another below the supraethmoid is advanced. The vomer is very advanced and extends dorsally a relatively long distance to contact the narrow, elongate supra-ethmoid. The sagitta has a primitive, elongate rostrum but lacks a postcaudal trough. The only other sternoptychid genera lacking a postcaudal trough are *Polyipnus*, *Argyropelecus*, and *Sternoptyx*. In these genera the rostrum is reduced or highly modified, and the entire otolith is so modified that it may be safe to conclude that the loss of the postcaudal trough is independent of the loss in *Maurolicus*. Much other evidence from other character complexes support such a conclusion. *Maurolicus* has a long, slender palatine with a modified posterior head unlike that of any other stomiatoid. The ectopterygoid is very large, forming at least one-half of the palatal arch rather than a small, triangular portion as in most sternoptychids. The maxillary is a highly modified broad, flattened bone with a sharply angled ventroanterior border, the teeth being borne posterior to the angle. The mandible is very deep, the greatest depth being more than four times the depth of the dentary just posterior to the symphysis. Only *Polyipnus* among the stomiatoids has a mandible approaching that of *Maurolicus* but the similarity is probably conver-gent. The coronoid "platform" of the dentary is well developed but advanced by being toothless. The preopercular angle is abrupt and nearly at 90 degrees rather than much less. Only *Sternoptyx* and *Argyropelecus* among the Gonostomata have such a sharp preopercular angle.

Maurolicus is a relatively derived sterno-ptychid, but it retains a few quite primitive characters, most of them shared with *Thorophos* and *Araiophos*. These characters, presence of three pelvic radials, retention of anterior and posterior supramaxillaries, a well-developed rostrum on the sagitta, and an elongate posterior supraethmoid process, are primitive stomiatoid structures and do not necessarily indicate any close relationship with *Thorophos* or *Araiophos*. Further possible primitive characters are crossed premaxillary-proethmoid ligaments in *Maurolicus*, very similar to those found in the photich-thyid *Vinciguerria*. *Danaphos* and *Valenciennellus* have two separate premaxillary-proethmoid ligaments, one on each side, one crossed, and the other uncrossed. Of the sternoptychids only *Argyropelecus* has both of these ligaments and they are joined on the premaxillary. In the other genera either one or the other of these ligaments is present. In gonostomatids and photichthyids, one or the other or both of these ligaments is present. Possibly the presence of both should be considered primitive. *Maurolicus* has one cylin-drical epural, rather than a flat plate. This character is only shared with some species of *Polyipnus*. Cylindrical epurals are present in gonostomatids and photichthyids and the character should be considered primitive for stomiatoids as it is found in many other fishes. A mesopterygoid fenestra is absent. This is also true for gonostomatids and photichthyids and therefore seems a primitive character relative to *Thorophos*. It is also absent in *Polyipnus*, *Argyro-pelecus*, and *Sternoptyx*. The significance of the character is uncertain. A crista superior is present in the sagitta of *Maurolicus* (also in *Danaphos* and *Valenciennellus*, but in no other sternoptychids).

Maurolicus seems to share a few advanced characters with *Danaphos* and *Valenciennellus*. All three have relatively narrow ethmoid regions (compare figs. 21, 23); however, that of *Mauroli-cus* is unique with its large ethmoid cornu and elongate palatine bone. All three genera have the parietal in contact with the sphenotic. No other sternoptychid, gonostomatid, or photich-thyid appears to have these bones in contact. In *Maurolicus* the parietal-sphenotic joint is hidden by the frontal. It is visible in *Danaphos* and *Valenciennellus* (compare figs. 22, 24, 25). It is difficult to be certain but it seems that because this is only one of a very few details in which

Maurolicus really seems to approach *Danaphos* and *Valenciennellus*, the character is convergent. All three genera lack palatine teeth, a relatively unimportant character as teeth are easily lost. Finally, only *Maurolicus*, *Danaphos*, *Valenciennellus*, and many species of *Polyipnus* have strongly angulate maxillary bones; however only *Polyipnus* and *Maurolicus* have broad maxillaries, those of the other two genera being quite narrow. The angularity of maxillary bones in sternoptychids does not in itself seem convincing evidence for close relationship, especially since it apparently varies within the genus *Polyipnus* (Baird, 1971).

None of the above characters common to *Maurolicus*, *Danaphos*, and *Valenciennellus* seem to me to be really convincing indicators of relationship. As is shown below, *Danaphos* and *Valenciennellus* share some characters with *Argyripnus* and *Sonoda*, which I think are valid indicators of relationship.

Few characters are shared exclusively by *Maurolicus*, *Argyripnus*, and *Sonoda*. All have lateral ethmoids of moderate size, not reduced as in several other sternoptychids. Moderate lateral ethmoids are probably primitive in sternoptychids, even though they are small in the relatively primitive genus *Thorophos*. Moderate-sized lateral ethmoids are found in gonostomatids and photichthyids. All three genera have the pubic plate well developed, but on the whole the pelvic girdle of *Maurolicus* resembles that of the relatively primitive *Thorophos* more than that of *Argyripnus* and *Sonoda*. None of these characters provide convincing evidence of close relationships among *Argyripnus*, *Sonoda*, and *Maurolicus*.

DANAPHOS, VALENCIENNELLUS, ARGYRIPNUS, SONODA, POLYIPNUS, ARGYROPELECUS, AND STERNOPTYX

These genera appear to form a group more closely related to each other than to any other sternoptychid. The number of advanced characters in common among them does not appear to be many, but at least one of these is so unique among fishes as to provide rather convincing evidence of relationship. It is to be expected that the highly advanced state of the hatchetfish genera, *Polyipnus*, *Argyropelecus*, and *Sternoptyx* on the one hand and of *Danaphos* and *Valenciennellus* on the other would mask many characters that at one time were probably advanced for all members of the ancestral group. The case of *Sternoptyx* and the pelvic fin radials described

below is an excellent example. One would expect to find few characters in this group remaining in common among these fishes when so many of the genera have almost all the character complexes available greatly modified. Unique advanced characters are as follows.

All seven genera have six pelvic radials, except *Sternoptyx* which has only one. All teleosts I have examined previously have three pelvic radials or occasionally fewer and sometimes none. It appears that at some point in the evolution of sternoptychid fishes the pelvic radials were doubled. As is shown below, *Sternoptyx* without a doubt belongs to a group also containing *Polyipnus* and *Argyropelecus*. *Sternoptyx* has a reduced pelvic girdle and fin and has almost certainly reduced the number of radials from six to one.

Another nearly unique advanced feature of this group is the alteration of the sagitta. *Thorophos* at least shows some alteration in a shortening of the rostrum but it must be remarked that the otolith illustrated (fig. 42A) has an eroded rostral surface, and the shape as figured here is not so long as that of the specimen examined *in situ*. The sagitta of *Araiophos* is unknown, and that of *Maurolicus* has a well-developed rostrum like that of the gonostomatids and most photichthyids. The height of the sagitta when divided into the length goes about 1.3 to 2.0 times in *Thorophos*, *Maurolicus*, the gonostomatids, and all photichthyids except *Ichthyococcus*. The height of the sagitta in the group of sternoptychids considered here goes 0.4 to 0.9 times in its length. These genera have a relatively deep otolith, often almost circular in profile with a relatively reduced rostrum except in some species of *Polyipnus*. In any event all seem to have very modified sagittae.

All genera of this group have a reduced supraethmoid. Even in *Polyipnus* where it has a peculiar modification for the support of an anterior piece of ethmoid cartilage, the supraethmoid is relatively small. More important perhaps is the reduction or loss of the proethmoid processes which are very small in *Danaphos* and *Valenciennellus* and absent in all the other genera of this group. These processes are well developed in all other sternoptychids and in the gonostomatids and photichthyids.

Probably also correlated with this is the absence or near absence of ethmoid cornua in this group. These are at least moderately or well

developed in all other sternoptychids. These cartilaginous processes are absent or only weakly developed in some gonostomatids and photichthyids. The moderate to highly developed state in relatively primitive sternoptychid genera may be an "early" sternoptychid character lost by the group here being considered.

As is shown below, other characters in common between some of the genera of this group tend to indicate a relationship between all these genera and it seems to me that the evidence in favor of these genera forming a monophyletic group is fairly good.

DANAPHOS AND VALENCIENNELLUS

Danaphos and *Valenciennellus* are two closely related sternoptychid genera with many exclusive advanced characters in common. They appear to have retained no primitive stomiatoid features not found in at least some other sternoptychids and have lost many primitive features retained by several other genera.

One unique complex of characters associated with large eyes and a resulting narrow frontal-interorbital-ethmoid region occurs in both genera. Each has the posterior end of the supra-ethmoid dorsal to the anterior end of the frontal (rather than having the ethmoid bone or complex ventral to the frontals as in most teleosts). The anterior ends of the frontals are fused to each other, and the longitudinal frontal fossae are very deep, the lateral borders of the frontals being joined together but not fused, or at least approaching each other dorsally over the external surface of the frontal bones, forming a tube or deep channel. Frontal crests are absent anteriorly. *Danaphos* is the most advanced in this region, having the anterior part of the fused frontals rolled into a narrow tube, apparently for added strength between the orbits. Ethmoid cornua are absent. All these characters are advanced with the possible exception of the missing ethmoid cornua which are absent or weakly developed in gonostomatids and photichthyids, but as they are present in primitive sternoptychids they may represent a primitive feature for the family. At least weakly developed and often prominent ethmoid cornua are present in all other sternoptychids except the extremely modified *Sternoptyx*, where they are absent. The absence of these structures in *Danaphos* and *Valenciennellus* is probably a secondary loss,

because of the narrowing of the ethmoid region in these two genera. The sagitta in these two genera is very similar in shape and distinct from that of any other stomiatoid genus examined (compare C and D in fig. 42). The frontals do not enter the borders of the posttemporal fossa, and the lateral parasphenoid wings are very reduced or absent. The ossification of the subopercle is incomplete, and the ossified portion is nearly the same shape in the two genera. The retroarticular ligament does not extend directly to the epihyal (except for a small slip in *Valenciennellus*) but to the dorsal border of the interopercle and then to the epihyal. The other sternoptychid genera as well as the gonostomatids and photichthyids have the retroarticular ligament extending between the retroarticular and the lateral fossa on the posterior part of the epihyal and have only a few or no fibers extending to the interopercle. Both genera have the first six or seven neural spines unfused, whereas all other sternoptychid genera except *Argyropelecus* (eight or nine) and *Sternoptyx* (six or seven) have at least 10 unfused neural spines and in one case 16 or 17 (*Araiophos*). Both *Danaphos* and *Valenciennellus* have a pubic process that is broad, strong, and without a pubic plate (this plate is also absent in *Araiophos*). They have a small, posterior ischial process and a unique, extremely large anterior ischial process. Finally, both genera have the same type of upper jaws, each with a sharply angled or bent, but slender, maxillary and, as in *Maurolicus* and *Polyipnus* (both with broad maxillary), the joint between the quadrate and angular lies on a vertical below or nearly below the anterior border of the eye, rather than between the middle or posterior part of the eye.

The significance of the following characters is uncertain. All sternoptychids except *Danaphos*, *Valenciennellus*, and *Thorophos* have ural centra all fused. In these three genera a joint remains between the ural centra one and two. This unfused condition is primitive for teleosts but appears sporadically in stomiatoids, seemingly uncorrelated with the primitive or advanced nature of the stomiatoid genus in which it occurs. In the same three genera the palatine is toothless and *Maurolicus* is the only other sternoptychid with a toothless palatine. Teeth are easily lost and the significance of this character is obscure.

The unique or nearly unique characters

shared by *Danaphos* and *Valenciennellus* are found in many parts of the body representing different character complexes, and must indicate close relationship. *Danaphos* and *Valenciennellus* are so similar that the validity of recognizing both genera may be questioned. However, there are several dissimilarities, indicating that recognition of both is probably meaningful. In some characters *Danaphos* is the more primitive and *Valenciennellus* more primitive in others. *Danaphos* is advanced relative to *Valenciennellus* in having the anterior part of the fused frontals rolled into a tube (open in *Valenciennellus*) and *Danaphos* has only the ectopterygoid in contact with the dorsal border of the quadrate (both the ectopterygoid and metapterygoid contact the quadrate in *Valenciennellus*). However, most of these characters show more similarities than differences between *Danaphos* and *Valenciennellus* when these two genera are compared with other sternoptychid genera (compare figs. 24 and 25 with 18, 20, 22, 27, 28, 30, 32, and 34).

Characters in which *Danaphos* is primitive are a large posterior myodome (small in *Valenciennellus*), a small lateral ethmoid present (absent in *Valenciennellus*), and no part of the sphenotic entering the border of the posttemporal fossa in *Danaphos* (small part enters it in *Valenciennellus*). Further, *Danaphos* retains more vertebrae, 38 or 39, whereas *Valenciennellus* has a reduced number, 32 or 33. *Danaphos* has a more primitive number of supraneurals, six, compared with one or two for *Valenciennellus*.

Grey (1964) separated these two genera on the basis of AC photophore groups. The AC row consists of largely separate organs evenly spaced in *Danaphos* with one or two groups in the AC row, each group with two to four organs. *Valenciennellus* has the organs in the AC row clumped and more advanced (compare figs. 6, 7). The photophores in the PV group of *Danaphos* are very large and apparently more advanced than those of *Valenciennellus*. Another external difference can be noted. *Danaphos* has an extremely long-based adipose fin, that of *Valenciennellus* is relatively short based and apparently more primitive for a sternoptychid.

All the above differences are relatively small but indicate that both genera have specialized in somewhat different directions. In my opinion the genera are worthy of recognition, even if not so distinct from each other as the other sternoptychid genera recognized here.

ARGYRIPNUS, SONODA, POLYIPNUS, ARGYROPELECUS, AND STERNOPTYX

These genera are a sister group of *Danaphos* and *Valenciennellus* and may be distinguished from them by the peculiar advanced character of an anal fin hiatus in which the proximal radials near the midlength of the fin are separated or diverge from one another. The details of this separation are different in these included genera as described below, but the separation itself is found in no other sternoptychids and is probably an indication of ancestral relationship based on a common ancestor with divergent proximal radials. This group of sternoptychids is the only one to lack a proethmoid, although, as noted above, they are greatly reduced in *Danaphos* and *Valenciennellus*. Other advanced characters held in common by these five genera and absent in other sternoptychids appear not to exist, and any characters that did exist are probably masked or altered by further evolution in different directions in the hatchetfish genera. As noted below, in some advanced characteristics *Argyropelecus* and sometimes *Polyipnus* seem close to *Argyripnus* and *Sonoda*. For example *Argyropelecus*, *Argyripnus*, and *Sonoda* have the lateral and medial surfaces of the sagitta flat.

ARGYRIPNUS AND SONODA

Similarities of *Argyripnus* and *Sonoda* are many and the two genera undoubtedly are closely related. They are relatively advanced sternoptychids, having almost no primitive characters in common with *Thorophos*, gonostomatids, or photichthyids. They do retain epimerals, common in gonostomatids and photichthyids and apparently found in no other sternoptychid genera.

Of the several characters unique to these genera, probably the structural peculiarities of their anal fin hiatus are of the most significance. Both genera have the middle radial between the two anal fin segments developed into an elongate ligament. The similar type of hiatus in the anal fin of the hatchetfish genera, *Polyipnus*, *Argyropelecus*, and *Sternoptyx* have the pterygiophores at the hiatus with the proximal radials abutting or contacting each other through the middle radials, which remain cartilaginous or bony and are never excessively long and ligamentous. Other unique, advanced characters

in *Argyripnus* and *Sonoda* are as follows. The parasphenoids have the lateral wings in a very posterior position and form, with the posterior part of the parasphenoid, a cap ventral to the ventral part of the posterior myodome. A posterior parasphenoid cap is also present in *Polyipnus* but this is associated with the greatly enlarged otic region and appears to be an independently derived character which is different in osteological detail. Each palatine is modified into a cartilaginous bar (without obvious heads) and bears a ventral tooth plate in both genera. Other sternoptychid genera have well-developed anterior and posterior palatine heads, except *Araiophos* whose palatine appears arrested in development, or a club-shaped palatine (hatchetfish genera). In median view *Argyripnus* and *Sonoda* have the dorsal border of the quadrate in contact with the mesopterygoid. This is also true only in *Araiophos* and *Polyipnus*, where I presume the small size of the posterior process of the ectopterygoid and the resulting joint between the quadrate and mesopterygoid is convergent. Both *Argyripnus* and *Sonoda* have a crossed but no uncrossed premaxillary-proethmoid ligament. All other sternoptychids except *Polyipnus* and *Maurolicus* have uncrossed premaxillary-proethmoid ligaments. Again the similarities among these may be convergent for the snout ligaments of both *Polyipnus* and *Maurolicus* are highly modified in unique ways. *Argyripnus* and *Sonoda* have the anterior neural arches one through 10 or 11, 12 or 13 not fused to their respective centra below. In all other sternoptychid genera (except the neotenic *Araiphos* which has them all free) all neural arches are fused to their centra. *Argyripnus* and *Sonoda* have the anteroventral part of the cleithrum in the form of an expanded plate. This is also true for *Maurolicus* and *Polyipnus*, but the form of the plate is different (compare figs. 99, 101, 102). Finally, both genera have lost the anterior portion of the ischial process of the pelvic bone and are unique in this feature.

In some characters in which these genera differ, both seem specialized away from the primitive stomiatoid condition. The shape of the opercle in *Argyripnus* is roughly quadrangular with a relatively straight dorsal border. *Sonoda* has a strong, acutely angled dorsal border in the opercle and the bone is dorsoventrally elongate. The dorsal portion of the interopercle of

Argyripnus is a relatively slender, elongate projection, considerably more constricted relative to the ventral part of the bone. *Sonoda* has an elongate sickle-shaped interopercle with the dorsal limb only slightly more constricted than the ventral portion. From the above characters it seems that on the whole *Argyripnus* is somewhat more primitive than *Sonoda*.

Grey (1964, pp. 86, 87) noted that *Sonoda* has no adipose fin, whereas *Argyripnus* has. All Grey's specimens of *Sonoda* appear heavily damaged, and in my view the presence or absence of an adipose fin cannot be determined. Grey (1964) noted 40 vertebrae in *Sonoda*, 47 in *Argyripnus*. I find that specimens of *Argyripnus* sp. have 44 to 46 vertebrae. The count in *Sonoda* remains at 40, but few specimens are known. Grey's most important differences, those of the photophore pattern (see Grey, 1964, pp. 206, 211–212) remain the most valid differences between these two genera.

POLYIPNUS, ARGYROPELECUS, AND STERNOPTYX

The most recent studies of *Polyipnus*, *Argyropelecus*, and *Sternoptyx* (Schultz, 1964; Baird, 1971; Baird and Eckardt, 1972) have considered these genera the sole members of the Sternoptychidae. Baird (1971) was the first to provide an adequate definition of the group. Not all his morphological observations agree with those made here, he did not examine the characteristics of all known "maurolicid" genera, and a few of his family characters were not specializations in common among the three hatchetfish genera. Thus only three of his 14 family characters stand without modification. The three "successful" characters are a vertically oriented pelvic girdle in close association with the heavy posterior pleural ribs; the presence of a preopercular spine, and of a well-developed abdominal keel-like structure. The remainder need modification, and those not confined to all three genera under consideration are eliminated. There are, however, additional specialized characters which distinguish *Polyipnus*, *Argyropelecus*, and *Sternoptyx* from all other sternoptychids, and these three easily could be defined as a family, subfamily, or some other suprageneric category. In my opinion, this is not warranted, for if *Polyipnus*, *Argyropelecus*, and *Sternoptyx* as a group are more closely related to *Argyripnus*, *Sonoda*, *Danaphos*, and *Valenciennellus* than the latter four genera are to *Maur-*

olicus and especially to *Thorophos* and *Araiophos*, as the data presented here seem to indicate, then it would make better phylogenetic sense to separate *Thorophos* and *Araiophos*, or *Thorophos*, *Araiophos*, and *Maurolicus* as a separate, easily definable family. In fact, on the basis of morphological divergence or consideration of "grade" differences used by Baird (1971), three or even more families might be considered appropriate for the fishes all considered here as sternoptychids. I prefer to retain all former maurolicid and sternoptychid genera in one family because they appear to be a clearly definable, interrelated, evolutionary line of stomiatoids, despite their great morphological divergence and distinctness.

Polyipnus, *Argyropelecus*, and *Sternoptyx* are each morphologically unique and very advanced. Each has its own set of characteristic specializations. Despite this, all three are more closely related to one another than to any other sternoptychid. There appear to be no primitive sternoptychid characters present in common among these three genera that are not present in at least some other sternoptychid genus. They do have several advanced characters in common that distinguish them from all other stomiatoids as well as other sternoptychids. Characters separating them from all other stomiatoids are as follows. A deep body, greatest depth in standard length is 0.8 to 2.0 versus 3.7 to 7.7 in the remaining sternoptychid genera. Some stomiatoids are much more elongate than any sternoptychid (especially the Stomiatoidea) but none are short and deep bodied like the hatchetfishes. Correlated with a deep body is a deep head and a host of attendant advanced characters. Preopercular spines are present and apparently absent in all other stomiatoids. Iliac spines of the pelvic girdle (equal to the postabdominal spines of Schultz, 1964, and basipterygial spines of Baird, 1971) are present. These are absent in all other stomiatoids.

An abdominal keel of stiff bony scales and deeper-lying connective tissue is present in *Argyropelecus* and *Polyipnus*, and a ridge or strong membranous keel of nonbony connective tissue is found in *Sternoptyx*. The keel in *Sternoptyx* is the same as that in the other two genera, but does not have strong supporting scales. This keel is unique for these three genera, but in *Argyripnus* there is a strong band of connective tissue between the abdominal photophores where it does not form a ridge or keel. *Polyipnus*, *Argyropelecus*, and *Sternoptyx* have an epiphyal length more than one-half the ceratohyal length, and the posterior end of the ceratohyal is larger than the anterior end. In the remaining sternoptychid genera the epihyal length is less than one-half the ceratohyal length, and the anterior end of the ceratohyal is the largest. The Gonostomatidae, Photichthyidae, and most of the Stomiatoidea have the apparently more primitive condition. The pelvic girdles have a face (the dorsal surface in all other stomiatoids) turned medially and pressed against its fellow of the opposite side (fused in at least one species of *Argyropelecus*). The pelvic girdle is vertically oriented and is closely bound by ligaments to one, two, or three of the posterior enlarged pleural ribs of the abdominal cage. A well-developed bony ridge or crest on the parietal is continuous with the similar ridge of the frontal bones. Enlarged heavy pleural ribs are present on vertebrae three through eight, four through 10, or six through 10. There are five, six, or seven enlarged ribs. Baird (1971) gave six or seven, apparently counting the modified anterior rib in *Sternoptyx*, which supports the pectoral girdle rather than extending to the area of the abdominal keel. No other stomiatoid has a greatly enlarged rib cage. A club-shaped symplectic is present. All other stomiatoids have a slender bar of bone as a symplectic. The exoccipital pedicles are very much enlarged in *Polyipnus*, *Argyropelecus*, and *Sternoptyx*. No other stomiatoid has the same type of modification.

A few other advanced characters tend to unite *Polyipnus*, *Argyropelecus*, and *Sternoptyx*, even though these characters may not be unique. All have lost the supraorbital, and, perhaps more distinct, have lost the antorbital, a bone rarely if ever lost in other stomiatoids. The antorbital may be lost in *Sonoda*, but all specimens examined were damaged in the nasal area, and the presence or absence of this bone could not be determined in this genus. The sphenotic is relatively large in *Polyipnus*, *Argyropelecus*, and *Sternoptyx* and small in the remaining sternoptychids, gonostomatids, and photichthyids. The palatomaxillary ligament is of moderate length in *Polyipnus*, *Argyropelecus*, and *Sternoptyx* and relatively long in the remaining sternoptychids. *Polyipnus*, *Argyropelecus*, and *Sternoptyx* have two

anterior infraorbitals, never an almost complete ring as in several of the other sternoptychid genera. *Araiophos* and *Danaphos* also have two anterior infraorbitals, the others being absent. *Sonoda* may also have only two infraorbitals but damage to the specimens available precludes positive information.

Certain of the seemingly important characters used by Baird (1971) to define the Sternoptychidae (hatchetfish genera only) meet with difficulties when investigated in detail. The flattening of the neural spine of the penultimate vertebra (Baird's first) is also found in the relatively primitive *Thorophos*. This flattening seems to be a specialization, possibly due to the fusion of the spine with a radial element just dorsal and anterior to it. It appears to be one of the few specialized characters relative to primitive stomiatoids possessed by *Thorophos*. Elsewhere it is found only in the three deep-bodied genera under discussion. I suspect the character is convergent between these two otherwise divergent groups of sternoptychids. *Thorophos* also has the neural spine of the antepenultimate vertebra in contact with that of the penultimate. This contact is distal and minimal in *Thorophos*, not extensive as it is in the hatchetfishes. Again, the character is probably convergent.

Baird's second character, a broadening and flattening of the haemal and neural spines of the posterior caudal region seems certainly homologous only in *Polyipnus* and *Argyropelecus*. Except for possibly one or two very posterior neural spines, the flattening and expansion of the spines in *Sternoptyx* is a relatively small amount of broadening in the anterior posterior plane of the entire spine, not a formation of an extensive blade of part of the spine only as in the former two genera. Many genera of stomiatoids exhibit the type of broadening found in *Sternoptyx* but it is almost invariably confined to the terminal two or three caudal vertebrae. Compare the radiographs in Baird (1971, figs. 9, 10, 11) with the illustration of the axial skeleton in the present paper (figs. 80, 82, 84, 89–96).

The so-called dorsal blade, spine, or pterygiophore system in *Sternoptyx*, *Argyropelecus*, and *Polyipnus* was used by Baird (1971) to characterize his Sternoptychidae. The bones of the "blade" (figs. 85–87) appear certainly homologous in *Sternoptyx* and *Argyropelecus*, being formed of supraneurals independent of the dorsal fin pterygiophore structure. The "blade" in *Poly-*

ipnus is a special problem involving the homology of supraneurals and pterygiophores. The specialized anterior pterygiophore of *Polyipnus* (see fig. 83) may have a typical "blade," i.e. protruding supraneural, fused with it, or it may be simply a specialized anterior pterygiophore with a specialized emergent anterior process. The adult morphology does not give a positive answer, but I suspect that Baird is correct in assuming the dorsal "blades" of these three genera to be homologous and therefore indicative of a common specialized character possessed by the hatchetfishes.

Baird (1971) attempted to use characters of the posttemporal as characteristic of the family, citing fusion to the supracleithrum in *Polyipnus* and *Argyropelecus*, plus the fact that it is a heavy bone, and has developed a dorsal, superficial spine. These characters, however are not found in *Sternoptyx*. About the only thing in common for these three genera is that the posttemporal, in keeping with the deep body and well-developed pectoral girdle, is elongate, strong, and well ossified.

Baird (1971) also noted that there is a "progressive migration forward of the suspensorium" in *Polyipnus*, *Argyropelecus*, and *Sternoptyx*. Assessment of the relative anterior or posterior position of the quadrate-angular (dentary) joint requires rather careful alignment with the longitudinal axis of the body (snout tip to mid-posterior termination of the hypural fan) or with the axis of the vertebral column (these are not the same in these deep-bodied fishes) and the lower-upper jaw joint position. An index of the anterior migration of the suspensorium, relative to the orbit seems as good a measure as any of the two axis measurements mentioned above. The joint position relative to the orbit is not greatly different in any of the several sternoptychid genera but is most anterior in *Polyipnus* (compare figs. 18, 20, 22, 24, 25, 27, 28, 30, 32, and 34). The greatly increased depth and relative shortening of the head in *Polyipnus*, *Argyropelecus*, and *Sternoptyx* makes it seem that the position of the suspensorium is rather far forward, when in fact the relative anterior-posterior position of the suspensorium to other parts of the head is not greatly changed from that in other sternoptychids. The important change here is a deepening of the head, correlated with the deepening of the body. The snout of hatchetfishes is ventral to the axis of the

vertebral column compared with its position in other sternoptychids. The ventral deepening of the suspensorium is correlated with a relative increase in the length of the hyomandibular bone rather than with a relative lengthening of the quadrate and symplectic.

Baird (1971) in part defined his restricted family Sternoptychidae by a "reduction in the bony extension of the urohyal." On page 13 he made it clear that this is a reduction in the platelike posterior extension of the urohyal. The urohyal and its "platelike" extension varies considerably in stomiatoids and varies widely in sternoptychids (compare figs. 67–74). *Thorophos* (fig. 67) has a "reduced" plate much like that found in many relatively primitive stomiatoids. *Maurolicus, Polyipnus,* and *Argyripnus* have greatly expanded plates. It appears that an expanded plate is probably a specialized condition, possibly independently derived in these three genera (see discussion of this character under *Thorophos* and *Araiophos* above). The "reduced" plate is probably primitive for stomiatoids and therefore cannot be used to define the hatchetfishes.

Baird (1971) stated that a unifying character for the group is that the epiotics of each side in hatchetfishes contact each other, or tend to approach each other ventral to the supraoccipital. The bones actually meet in *Polyipnus* and in some species of *Argyropelecus.* They only approach each other in other species of *Argyropelecus* and in all specimens of *Sternoptyx* examined. They also tend to approach each other in *Argyripnus* in a state physically intermediate between that illustrated here for *Maurolicus* (fig. 36) and *Sternoptyx* (fig. 39). Thus the trend for these bones to meet is not exclusive among the three hatchetfishes nor do the bones meet in all of them. The character seems to be a trend within the family Sternoptychidae, which is more or less culminated in the three hatchetfish genera.

Again, Baird (1971) described the "circular gap" in the anal fin pterygiophore series as an exclusive characteristic for the hatchetfishes. This gap or hiatus varies in form in these genera from a circular structure associated with a photophore cluster and rather highly modified anal fin pterygiophores (see fig. 84 of *Argyropelecus aculeatus* and the radiogram of *Argyropelecus olfersi* in Baird, 1971, fig. 11) to a simple hiatus with only radial cartilages joining the separated but not highly modified pterygiophores (see Baird, 1971, figs. 9, 10, 15). A simi-

lar type of noncircular, relatively unmodified hiatus is present in *Argyripnus* and *Sonoda* (see fig. 82) except that the cartilages spanning the gap are elongate ligaments. The structure appears to be essentially the same in the two groups of genera and indicative of relationships.

Finally, Baird (1971) recorded that the three hatchetfish genera are characterized by a marked similarity in photophore pattern and number. This is true, and in general there is a reduction and further clustering of photophores in the three genera compared with other sternoptychid genera, especially *Sonoda* and *Argyripnus* as detailed comparison of figures 2 through 13 shows. Again, it appears that the photophore pattern in the hatchetfish genera is simply the extreme development of the clustering trend within the entire Sternoptychidae. No clustering tendencies are found in the Gonostomatidae or Photichthyidae. As a matter of fact, the details of photophore pattern of all sternoptychids and indeed all stomiatoids is so similar that it is difficult to see why the hatchetfishes should have a completely separate photophore terminology, and a synonymy of the terms for photophores in the deep-bodied genera as used by Schultz (1964) and Baird (1971) with those for other stomiatoids as defined and used by Morrow (1964b), Grey (1964), and Gibbs (1964) is presented in table 1. In those cases where a series is an exact equivalent, for example, IP equals I or PV equals AB, there would seem little excuse for a separate terminology for hatchetfishes. In those cases where a group of photophores such as the AC series form two distinct groups, AN and SC in the hatchetfishes, there is good, practical reason to retain the special terminology.

INTERRELATIONSHIPS OF *Polyipnus, Argyropelecus,* AND *Sternoptyx*

Baird (1971) and especially Baird and Eckardt (1972) utilized a considerable body of morphological evidence to determine the phylogenetic relationships among the three hatchetfish genera. Baird (1971) remarked: "The question of a monophyletic origin of the hatchetfish is unanswerable. The three genera show a great deal of divergence and independent evolution within genera." He nevertheless believed that, "The genus *Sternoptyx* seems to have evolved quite early from the line or lines

TABLE 1

A SYNONYMY OF STOMIATOID PHOTOPHORE ABBREVIATIONS BASED ON USAGE BY GREY (1964),
SCHULTZ (1964), AND MORROW (1964b)

Other Stomiatoids	*Polyipnus, Argyropelecus,* *Sternoptyx*
ORB–orbital photophores ———suborbital——— =	PO–preorbital
———postorbital——— =	PTO–postorbital
SO–mental or symphyseal photophores——————— =	(absent)
OP–opercular photophores———————————— =<	PRO–preopercular SO–subopercular
BR–branchiostegal photophores——————————— =	BR (same)
IC–all photophores of ventral series { IV–prepelvics < IP–ventral series, isthmus to pectoral insertion } =	I–isthmus
PV–ventral series, pectoral–pelvic insertion } =	AB–abdominal
VAV–ventral series, pelvic insertion to anal origin if row is continuous with AC or to end if AC row is separate } =	PAN–preanal
AC–from above anal fin to end of row if distinct from VAV, or from anal origin to end of row if continuous with VAV } =<	AN–anal SC–subcaudal
OA–photophores of lateral series { OV–lateral series behind operculum to above pelvic insertion } =<	SAB–supra-abdominal SP–suprapectoral
VAL–lateral series above pelvic insertion to end of row, above anal fin } =<	L–lateral (=anterior VAL) SAN–supra-anal (may= posterior part of VAL or displaced post part of VAV or anterior part of AC)

leading to *Polyipnus* and *Argyropelecus*. It then continued to evolve independently, resulting in the present highly specialized form." He further stated that, "Evolution from a premaurolicid ancestor can be traced somewhat more directly in the case of *Polyipnus* and *Argyropelecus*." He noted that these two genera share several character complexes not shared with *Sternoptyx*. He concluded, "The family consists of three divergent independently specialized genera. *Polyipnus* appears the most primitive, *Sternoptyx* the most highly specialized and the most difficult to place, while *Argyropelecus* falls somewhere in between." Baird and Eckardt (1972) stated that, "Baird (1971) proposed a common evolutionary grade (*sensu* Huxley, 1958) for the genera of Sternoptychidae [hatchetfishes only].

This grade was distinct from the closely related maurolicid-gonostomatids and formed the basis for maintaining the Sternoptychidae at the family rank. He was unable, however, to arrive at any definitive conclusions concerning phylogenetic relationships among the sternoptychid genera." In order to attain a more "objective methodology in studies of evolutionary relationships," Baird and Eckardt (1972) utilized some of the methods of numerical taxonomy to "illustrate some of the methods of quantitative phyletics in order to estimate the phylogenetic relationships of deepsea hatchetfishes at the generic and species group levels." For their numerical treatment they subjectively evaluated 41 phenotypic characters. Some were evaluated in terms of their "relative degree of

modification from what appears to be the primitive condition of that character found in the gonostomatid genera *Maurolicus*, *Valenciennellus*, and *Vinciguerria*." They then submitted their subjectively chosen and interpreted data to numerical taxonomic analysis. However, it should be clear that regardless of the objectivity of the numerical method used, the resultant hypothesis of relationships will be no more objective than the original subjective choice of characters or the subjective evaluation of these characters regarding their primitive or advanced nature. All studies of evolutionary relationships suffer from this problem. Additional data usually alter older hypotheses. Numerical taxonomic methods do not necessarily lead to more objective hypotheses, rather only to more consistent treatment of data once taken and evaluated. In fact, reliance on a numerical taxonomic method of processing data may lead an author to assume that the method will relieve him of the necessity of studying his data in relation to the various morphological adaptations that the organisms in question possess. They may prevent him from mentally considering as a whole the organisms being studied. Poor evaluation of character states lead to poor hypotheses despite consistent treatment by numerical taxonomic methods.

Their choice of *Vinciguerria*, *Valenciennellus*, and *Maurolicus* as a primitive base for comparison of the primitive versus advanced state of characters in the hatchetfishes does not appear to have been the best one. Better genera for such purposes would be *Thorophos* and *Diplophos*. Even so, their evaluations with regard to what characters are advanced or primitive in the hatchetfishes are often close to those developed here.

A subsequent reexamination of a group for characters usually shows that earlier authors missed a few important characters or even character complexes; such is the case here. For example, Baird and Eckardt (1972) completely missed the highly advanced nature of the jaws and ethmoid regions of *Polyipnus*. They also missed most of the significance in regard to advanced conditions in the otic region. These character complexes tend to show a somewhat different picture with regard to the relative advanced states in the hatchetfish genera. This omission has influenced the evaluation of some of the characters they utilized. For example, the presence or absence of an ascending process of

the premaxillary in the hatchetfishes was evaluated by the authors as primitive when present, advanced when absent. They weighted equally the presence of the premaxillary process in *Argyropelecus* and *Polyipnus*. It is true that a relatively short ascending process apparently is primitive for stomiatoids. The absence of one in *Sternoptyx* may be considered advanced because it is directly associated with the decreased mobility of the jaws and accompanying modifications in the ligaments of this genus. The long ascending process in *Polyipnus* must also be considered advanced relative to other stomiatoids and even just within the Sternoptychidae. This process is associated with a host of modifications that are correlated with a greatly increased mobility of the upper jaw in *Polyipnus*. As a matter of fact, even the relatively short premaxillary process of *Argyropelecus* is advanced in its own direction away from that of all other sternoptychid genera and cannot be evaluated on a simple presence versus absence alternative as Baird and Eckardt (1972) have done. This is true for many of the "presence or absence" characters (their numbers 1–13) treated by these authors. These characters when evaluated without regard to the associated character complexes can be very misleading. The next 12 (14–25) characters subjectively analyzed by Baird and Eckardt for primitive versus advanced states are subject to a variety of interpretations depending upon the adequacy of the comparison with character states in other sternoptychids and stomiatoids. For example, they utilize the relative size of the largest otolith (sagitta) as an indication of the advanced versus primitive nature of its bearer, giving *Sternoptyx* and *Argyropelecus* a low (primitive) value and *Polyipnus* a high (advanced) value. In point of fact, the otoliths of all three genera are highly advanced when one takes into account the relative size of the sagitta compared with that of the primitive stomiatoids *Thorophos*, *Diplophos*, or *Polymetme*. Comparison of the altered shape of the otolith also indicates the highly advanced nature of the otolith in the hatchetfish genera. Again, the otoliths are advanced in their own directions in these three genera, and it is difficult to say that one is more highly advanced than another. Certainly *Polyipnus* with its huge, deep-bodied sagitta with a long, slender rostrum is differently modified than that of the rounded, very small sagitta of

Argyropelecus and the extremely small sagitta in *Sternoptyx*. The general size and shape of the sagitta in the last two genera indicates a possible relationship between them, but their otoliths are in no way primitive with regard to the stomiatoids as a group or with sternoptychids as a group.

Without further criticism of Baird and Eckardt (1972) it seems best to provide my own subjective analysis of the interrelationships of the hatchetfish genera.

POLYIPNUS

Polyipnus has a large number of unique advanced characters, many associated with the rather protractile or protrusible mouth. These characters are as follows. The centrum-like facet of the basioccipital is reduced to a shallow fossa between the greatly enlarged otic bullae. In *Argyropelecus* this facet is of moderate size, somewhat reduced but essentially like that of most sternoptychids, gonostomatids, and photichthyids. That of *Sternoptyx* is small and fused with the exoccipital pedicels and appears specialized in a different direction from that of *Polyipnus*.

The epiotic process of *Polyipnus* is a prominent, dorsoposteriorly extending bone, whereas it is small in almost all other sternoptychids, and in all gonostomatids and photichthyids. *Sternoptyx* has a slender, spinelike epiotic process entirely different from the heavy, prominent process found in *Polyipnus*.

The sagitta of *Polyipnus* is very large, much deeper than long. The otolith, however, is not remarkably long relative to the head length when compared with most other sternoptychids. The sagitta length goes into the cranial length about five to six times in gonostomatids, most photichthyids, and sternoptychids, and about 5.5 times in *Polyipnus*. *Argyropelecus* and *Sternoptyx* have the length of the sagitta greatly reduced when compared with the length of the head. The otolith length varies depending upon the species. In *Argyropelecus* the otolith goes into the cranial length about 20 to 50 times, that of *Sternoptyx* 15 to 20 times. The great depth and highly modified, slender rostrum and sculptured surfaces of the sagitta in *Polyipnus* are advanced. Also the structure has a relatively flat, medial face and a strongly convex lateral face. Most sternoptychids have the sagitta with a relatively flat medial surface and a moderately convex

lateral face. There is a trend in some sternoptychids, especially *Argyripnus*, *Sonoda*, and *Argyropelecus*, to have both lateral and medial faces flat.

Polyipnus is the only sternoptychid with a club-shaped cartilaginous and bony palatine. Most sternoptychids, the gonostomatids, and photichthyids have a double-headed palatine with anterior and posterior cartilaginous articular surfaces. The palatine of *Sternoptyx*, *Argyropelecus*, *Sonoda*, and *Argyripnus* as well as *Polyipnus* is modified away from the double-headed type, that of *Argyripnus* and *Sonoda* being a cartilaginous bar with a ventral tooth-bearing bone, that of *Argyropelecus* being more or less quadrangular, and that of *Sternoptyx* being conical with a posterior apex. That of *Sternoptyx* most closely approaches that of *Polyipnus* but the teeth on the palatine of *Sternoptyx* are on a special dental process found in no other genus.

The long, rather loose upper jaw ligaments of *Polyipnus* are like those of no other stomiatoid and coupled with the exceptionally elongate ascending premaxillary process these modified ligaments allow a certain amount of protractibility to the upper jaw.

Associated with protractibility is the highly modified arrangement of the supraethmoid, lateral ethmoids, and vomer which support the anterior ethmoid plate. This arrangement is found in no other stomiatoid genus and may be considered a highly advanced support for the movable premaxillary bones.

The maxillary bone is both angulate and expanded in at least several species of *Polyipnus*, and although this may not be considered a character for the genus, it at least constitutes an advanced trend within the genus.

The mandible is short, with a deep midportion at least four to five times the depth of the anterior portion of the dentary bone. In most other sternoptychids the greatest depth of the mandible is three to four times the anterior depth of the dentary. In *Sternoptyx* the anterior and posterior depths of the mandible are equal and therefore advanced in a different direction than *Polyipnus*. *Argyropelecus* has a triangular mandible with the posterior part about three times the depth of the anterior part. This form seems closer to that of other sternoptychids except for the absence of a "coronoid shelf." In gonostomatids and photichthyids the posterior part of the mandible is usually elongate

with the posterior depth about two to three times the depth of the anterior portion. It appears that the general trend in the Sternoptychidae is for a shorter mandible with a deeper posterior part. This trend is most highly developed in *Polyipnus* and least developed in *Sternoptyx*.

Polyipnus has a peculiar, relatively short ceratohyal with a wing or blade dorsal to the constricted midlength. Most gonostomatids and photichthyids have an elongate, moderately constricted ceratohyal without a blade. This is also true of *Thorophos*, *Araiophos*, and *Argyripnus* except that the midlength is more constricted. The remainder of the sternoptychid genera have a moderately long, usually greatly constricted ceratohyal but no wing or blade. *Argyropelecus* differs in having a small ventral wing or blade at the constriction, whereas the moderately-long ceratohyal of *Sternoptyx* is not much constricted. Thus the short ceratohyal with a dorsal wing in *Polyipnus* seems to be advanced, and carries to the extreme the moderate shortening of this bone found in all the Sternoptychidae compared with the Gonostomatidae and Photichthyidae.

Finally, the urohyal of *Polyipnus* is very large and expanded, more so than in any other stomiatoid and therefore presumably advanced.

Polyipnus also has a large number of characters that are peculiar for the hatchetfish genera. The following appear primitive for the group and are held in common with other non-hatchetfish sternoptychids. The external surface of the frontal and parietal bones is smooth, not pitted as in *Sternoptyx* and *Argyropelecus*. The smooth condition is undoubtedly primitive for the group, for these bones are smooth in all other sternoptychids, gonostomatids, and photichthyids.

The triangular mesopterygoid of *Polyipnus* is relatively long, about three-fourths of the combined length of the mesopterygoid and metapterygoid. *Sternoptyx* and *Argyropelecus* have a relatively short mesopterygoid, one-half the combined mesopterygoid-metapterygoid length in *Sternoptyx* and one-half to about two-thirds in *Argyropelecus*. In gonostomatids and photichthyids the mesopterygoid length is relatively short, usually one-half to two-thirds the combined length. However, in most sternoptychids including the more primitive members such as *Thorophos* and *Araiophos* the mesopterygoid is usually relatively long, three-fourths (*Thorophos*)

to seven-eighths (*Sonoda*) the combined length. Clearly there is a tendency for an enlarged mesopterygoid in the Sternoptychidae. Its relative shortness in *Sternoptyx* and *Argyropelecus* undoubtedly has more to do with the deep heads of these genera than a "return" to the relatively short, primitive state of the mesopterygoid found in gonostomatids and photichthyids. Thus a short mesopterygoid in these two genera is probably an advanced feature.

The ectopterygoid bone is triangular in *Polyipnus* and in most sternoptychids (almost quadrangular in *Maurolicus*), never slender and elongate as in *Argyropelecus* and *Sternoptyx*.

The coronoid "platform" of the lower jaw is present in *Polyipnus* and absent in *Argyropelecus* and *Sternoptyx*. The presence of this toothed "platform" is found in some form in all other sternoptychids although it may not be toothed as in *Maurolicus*. The presence of the platform is probably primitive for stomiatoids as well as sternoptychids, because it is found in other teleosts (see Patterson [1970] for discussion of this structure).

The interopercle of *Polyipnus* is primitive for hatchetfishes, being somewhat elongate and sickle-shaped, much like that of *Argyripnus*, *Sonoda*, *Danaphos*, and *Valenciennellus*. The bone is triangular but dorsoventrally elongate in *Argyropelecus* and dorsoventrally long and slender in *Sternoptyx*. In *Sternoptyx* and *Argyropelecus* the length of the interopercle about equals that of the subopercle. In *Polyipnus* the bone is about half again as long as the subopercle. The interopercle is one and two-thirds to about twice the length of the interopercle in *Danaphos* (where it is one and two-thirds), *Valenciennellus*, and *Sonoda*. *Argyripnus* has the two bones about equal in relative length. In most of its characteristics the interopercle of *Polyipnus* is more like that of the nonhatchetfish sternoptychids than that of *Argyropelecus* and *Sternoptyx*.

A posterior supraethmoid process is present in *Polyipnus*, and absent in *Argyropelecus*. The supraethmoid is absent in *Sternoptyx*. In most gonostomatids and photichthyids, *Thorophos*, *Araiophos*, and *Maurolicus*, the supraethmoid process is long, slender, and pointed, extending ventral to the frontal bone. In the remaining sternoptychid genera the process varies and is often specialized in peculiar ways. For example, it is extremely short and dorsal to the frontal bone in *Danaphos* and *Valenciennellus*. The process

is very short in *Argyripnus*, and the supraethmoid is absent in *Sonoda*. The presence of a blunt posterior process in an otherwise highly modified supraethmoid in *Polyipnus* appears to be a primitive character of this bone.

In comparing figures 101–104 of the cleithrum of, respectively, *Argyripnus*, *Polyipnus*, *Argyropelecus*, and *Sternoptyx* it can be seen that this bone in *Polyipnus* is most like that of *Argyripnus* and possibly like that in the most primitive of the hatchetfish genera. In *Argyropelecus* a deep notch is present in the ventral lateral wing, leaving a large hiatus through which the coracoid may be seen in lateral view. *Polyipnus* and *Argyripnus* do not have this notch. The area of the ventral lateral plate in *Argyropelecus* is divided into two processes, one anterior to the notch, one posterior. *Sternoptyx* lacks the posterior process, otherwise its cleithrum is similar to that of *Argyropelecus*. In other sternoptychids the ventral lateral plate is not notched nor as large as it is in *Argyripnus* and *Polyipnus*. In fact the plate is so small and anterior in position as to look somewhat like the condition in *Sternoptyx*. However, *Sternoptyx* lacks any evidence of a plate in this region, having only an anterior spinous process.

The pectoral fin radials of *Polyipnus* are similar to those of most sternoptychids, the first or dorsal radial articulating with the scapula, the second with the scapula and coracoid, and the third and fourth with the coracoid only. In *Argyropelecus* the first and second radials articulate only with the scapula, the third with the scapula and coracoid, and the fourth with the coracoid only. In *Sternoptyx* the first, second, and third radials articulate only with the scapula, the fourth both with the scapula and coracoid. The arrangement found in *Polyipnus* and most other sternoptychids (*Araiophos* is an exception with the first radial articulating with the scapula and the coracoid, the second, third, and fourth with the coracoid only) is the same found in most gonostomatids and photichthyids and is therefore presumably the primitive arrangement.

The ischial process of the pelvic girdle points posteriorly in *Polyipnus* as it does in most other sternoptychids, the gonostomatids, and photichthyids. In *Argyropelecus* and *Sternoptyx* the process is directed dorsally or dorsoposteriorly.

The usual number of pelvic fin rays in sternoptychids is seven (reduced to six in *Sonoda*

and five in *Araiophos*). Seven is also the usual number in gonostomatids and photichthyids. *Polyipnus* has seven, *Argyropelecus* six, and *Sternoptyx* five. Of the hatchetfish genera *Polyipnus* seems to be the least derived in possessing this character.

Finally, the dorsal fin blade of *Polyipnus* (if it is a structure homologous with those of *Sternoptyx* and *Argyropelecus*) is less complex and protrudes beyond the dorsal body profile far less than in *Argyropelecus* and *Sternoptyx* and therefore is probably a primitive character, as the bone remains in the usual teleost condition in all other stomiatoids.

There are several characters in *Polyipnus* which, although unique among the hatchetfish genera, are difficult to interpret as advanced or primitive for the hatchetfish group. Some of these characters may be labile among sternoptychid genera and therefore insignificant for generic comparison, even though constant at the species level.

Such a character is that of the parietal bone contacting the sphenotic. This character is constant in at least the several examined species of *Polyipnus*, in which the two bones do contact each other, but it is variable in *Argyropelecus*, where sometimes the two bones are in contact, sometimes not, depending on the species. In *Sternoptyx* the two bones are always in contact. The bones are not in contact in *Thorophos* or *Araiophos*, *Argyripnus* or *Sonoda* but are in contact in *Maurolicus*, *Danaphos*, and *Valenciennellus*. They appear invariably to be in contact in at least the Gonostomatidae. The two bones in contact is presumably the primitive state, but the distribution of the character is mosaic within the Sternoptychidae and therefore difficult to interpret within that group.

A presumably primitive character of *Polyipnus* is the presence of one or two elongate, cylindrical epurals. All other sternoptychids have only one, forming a flat plate except in *Maurolicus*, which has one cylindrical, cartilaginous epural. The single, flat, cartilaginous plate of *Thorophos* is slightly constricted and looks as though it may be formed of two slender rods fused to a single element. The elongate, slender epurals (two or three) of the Gonostomatidae and Photichthyidae are typical of relatively primitive teleost epurals. The occurrence of such epurals in *Maurolicus* and *Polyipnus*, both rather advanced sternoptychid genera, is diffi-

cult to interpret but is probably a return to a primitive character rather than a retention of one.

An exclusive character in *Polyipnus* among sternoptychids is the presence of posterior terminal dorsal and anal fin rays divided to their bases. They appear to be undivided in all other sternoptychids. In gonostomatids and photichthyids the presence of posterior terminal divided rays is mosaic, sometimes present in the dorsal fin of a species, whereas the anal fin will have an undivided posterior ray. The character appears labile in stomiatoids and therefore difficult to interpret. The general trend in sternoptychids is for single posterior terminal rays but *Polyipnus* is an exception, presumably returning to a more primitive state.

Vertebrae and ribs are another problem difficult to interpret in the Sternoptychidae. There is a general trend in the sternoptychids for a reduced number of vertebrae and rib-bearing vertebrae. Although a primitive number of vertebrae for the suborder Stomiatoidea cannot be given with great confidence, most genera primitive on other grounds have about 40 to 45. In the Sternoptychidae, *Thorophos* and *Araiophos* have this number. The number is reduced to 31 to 34 in *Maurolicus*, 38 or 39 in *Danaphos*, 32 or 33 in *Valenciennellus*. *Argyripnus* has 42 to 46 and *Sonoda* 40 vertebrae. *Polyipnus* has 32 to 35, *Sternoptyx* 29 to 31, and *Argyropelecus* 34 to 40 vertebrae. Thus of the three hatchetfish genera, *Polyipnus* and *Sternoptyx* appear to be slightly more advanced by having reduced numbers of vertebrae. *Polyipnus* does not seem remarkably advanced in vertebral numbers but it also has a relatively reduced number of pleural ribs compared with most sternoptychid genera with ribs on vertebrae three through eight, nine, or 10. *Argyropelecus* and *Sternoptyx* have pleural ribs on vertebrae three through 10, 11, or 12 and *Argyripnus* and *Sonoda* on vertebrae three through 12 or 13. There are pleural ribs on vertebrae three through 11 in *Maurolicus*, two through nine in *Danaphos*, two through 10 in *Valenciennellus*, two or three through 13 to 15 in *Thorophos*, and two through 17 in *Araiopohos*. Thus in a trend toward reduction of pleural ribs, *Polyipnus* seems to have gone the farthest, having as few as six pleural ribs in some instances, and never more than eight. *Danaphos*, *Argyropelecus*, and *Sternoptyx* occasionally have as few as eight.

Another character rather difficult to assess but probably advanced, is a reduction in the number of large ribs in *Polyipnus*. Enlarged ribs unquestionably constitute an advanced character for the hatchetfish group as a whole, but interpretation of the number of such ribs in terms of a primitive or specialized condition is a problem. On vertebrae three through eight *Polyipnus* has a total of six enlarged ribs. *Argyropelecus* has seven, one on each of vertebrae four through 10. *Sternoptyx* has a total of five enlarged ribs on vertebrae six through 10. *Argyropelecus*, with the most enlarged ribs (seven) could be considered the most advanced in this character, *Polyipnus* with six somewhat less advanced, and *Sternoptyx* with five even less advanced. However, it seems likely that the loss of vertebrae and ribs would be an important evolutionary feature in sternoptychids and that this has modified the number of enlarged pleural ribs in *Polyipnus* and *Sternoptyx* more than in *Argyropelecus*. Thus a low number of enlarged ribs is an advanced character, not a relatively primitive state with regard to the three hatchetfish genera. Perhaps all the ancestors of these genera had the seven (or perhaps even more) enlarged ribs found in *Argyropelecus* but subsequently lost them in the reduction of vertebral numbers or just simply lost pleural ribs. The fact that *Polyipnus* has retained an enlarged rib on the third vertebra is undoubtedly primitive for the hatchetfish group. Its reduction in *Argyropelecus* and *Sternoptyx* is an advance. However, the size, numbers, and placement of large ribs in the hatchetfish genera is a complex problem not to be easily and confidently solved by simple assumptions concerning their past evolutionary history.

The small size of the second infraorbital bone in *Polyipnus* poses interpretive problems. First, there is some question as to the homology of the bones labeled first and second infraorbitals in the present report. Identification of these bones has been made by position only, shifting of position, change of size, and fusions may have confused their identification to the point where they are no longer useful in interpretation of phylogeny. All three hatchetfish genera have two anterior infraorbitals, the second of *Polyipnus* is very small, whereas it is very large and probably homologous in *Sternoptyx* and *Argyropelecus*. The other sternoptychid genera have from two to four infraorbitals. Most genera have the second somewhat reduced or nearly the size of

the first except *Thorophos*, in which it is exceptionally large. The second is usually small in gonostomatids and photichthyids. Presumably the enlarged second infraorbital of some sternoptychids is advanced, and the otherwise relatively primitive sternoptychid *Thorophos* is advanced in this character. However, the bone that is enlarged in *Thorophos*, *Argyropelecus*, and *Sternoptyx* may be the large third infraorbital of gonostomatids and photichthyids, or it may be the second and third infraorbitals fused and moved somewhat anteriorly. The very small second infraorbital of *Polyipnus* looks almost vestigial, rather than a functional part of the series as this small bone appears in the Gonostomatidae and Photichthyidae. A very small second infraorbital bone is probably advanced for sternoptychids or the hatchetfish genera. The enlarged second infraorbitals of *Argyropelecus* and *Sternoptyx* may be the advanced "end points" of a trend to enlarge the second infraorbital within some parts of the family but the other member with such an infraorbital, *Thorophos*, is not closely related to these two genera on other grounds. All interpretations of the infraorbitals appear doubtful in sternoptychids, and the bones are best considered labile and of relatively minor importance in determining relationships within the family Sternoptychidae.

In a comparison of the three hatchetfish genera there are many characters shared by *Polyipnus* and *Argyropelecus* that are not found in *Sternoptyx*. These characters are primitive for the hatchetfish group and are the relatively primitive expression of advanced characters in *Sternoptyx*. These will be treated below under that genus.

Advanced characters shared by *Polyipnus* and *Argyropelecus* and relatively primitive (or advanced in a different direction) in *Sternoptyx* are few and doubtful, but may include some of the following. The posterior myodome is vertical although not greatly enlarged, whereas it is horizontal in *Sternoptyx*, other sternoptychid genera, and the gonostomatids and photichthyids. Presumably a vertical posterior myodome is advanced and correlated with the deep head in *Polyipnus* and *Argyropelecus*. That the rather enlarged myodome of *Sternoptyx* remains horizontal as in nonhatchetfish sternoptychids is somewhat puzzling because the head in this genus is very deep, and the position of the

myodome relative to the eye and orbit appears about the same in *Argyropelecus* and *Sternoptyx*. In *Polyipnus* the myodome is very low or ventral in the posterior ventral region of the orbit because of the downward expansion of the skull that is correlated with the enlarged otic region. Thus in the position of the myodome *Argyropelecus* and *Sternoptyx* are alike, but in the vertical versus horizontal orientation and size *Polyipnus* and *Argyropelecus* are alike. Presumably the enlarged size of the myodome in *Sternoptyx* is advanced, as is the vertical orientation of this structure in *Polyipnus* and *Argyropelecus* but the size may be independently derived because of the influence of the greatly enlarged otic region in *Polyipnus*. Probably the horizontal position of the myodome in *Sternoptyx* is primitive.

Possibly more convincing evidence of a close relationship between *Polyipnus* and *Argyropelecus* can be adduced by comparing the expanded neural and haemal spines of the hatchetfish genera. As pointed out under the definition of the hatchetfish group, these spines in *Sternoptyx* are expanded in a different fashion than in *Polyipnus* and *Argyropelecus*. However, the character is not completely exclusive because *Sternoptyx* has a couple of *Polyipnus-Argyropelecus*-type neural spines just anterior to the termination of the vertebral column. The far greater development of these neural spines in *Argyropelecus* and *Polyipnus* than in *Sternoptyx* might be taken to indicate a relationship. Possibly the character was common to the unknown ancestor of the hatchetfish line and has been largely lost in *Sternoptyx*. If this is so, the character cannot be used to relate *Polyipnus* and *Argyropelecus* more closely to each other than either to *Sternoptyx*. On the other hand the ancestral character could have been something like that of *Sternoptyx*, with both *Polyipnus* and *Argyropelecus* developing the character to an extreme. I prefer the first hypothesis in view of the overall advanced nature of *Sternoptyx* and the relatively primitive nature of *Argyropelecus* and *Polyipnus* for hatchetfish genera.

One character that definitely seems advanced and common only to *Polyipnus* and *Argyropelecus* is the fusion between the posttemporal and supracleithrum. This feature appears nowhere else in the Gonostomata. It seems likely that these two genera share this feature because they had a common ancestor with such a condition and *Sternoptyx* did not share that immediate

common ancestor. However, similar functional requirements for the pectoral girdle in both genera could have led to this fusion independently. Because this character is not correlated with much other evidence of close relationship between these two genera, one must reserve judgment as to its significance. On the whole, evidence for a close relationship between *Polyipnus* and *Argyropelecus* is relatively weak.

Polyipnus shares a few characters with *Sternoptyx* not shared with *Argyropelecus*, but these all seem primitive for the hatchetfish genera, and since their advanced counterparts appear in *Argyropelecus*. they will be discussed under that genus.

ARGYROPELECUS

Argyropelecus retains a few primitive characters not found in other hatchetfish genera. For example a hyomandibular spine is absent in *Polyipnus* and *Sternoptyx* but present in *Argyropelecus*, *Thorophos*, *Araiophos*, *Maurolicus*, and *Argyripnus*. It is also present in most gonostomatids and photichthyids. In *Danaphos*, *Valenciennellus*, and *Sonoda* the loss of the spine presumably is independent of the same loss in *Polyipnus* and *Sternoptyx*.

The ethmoid complex is of simpler overall form in *Argyropelecus*, more like that of the nonhatchetfish genera of the Sternoptychidae. The ethmoid complex of bones is completely lacking in *Sternoptyx* and highly modified in *Polyipnus* as described above under that genus. The ethmoid bones of *Argyropelecus* are advanced somewhat in the direction of *Polyipnus*. For example, when compared with those in the nonhatchetfish genera of the Sternoptychidae the lateral ethmoids of *Argyropelecus* are thrust forward somewhat to help support a large ethmoid plate. The lateral ethmoids are not modified so far in this direction as they are in *Polyipnus* and are nearer to those of *Argyripnus* than *Polyipnus* in their general proportions and shape (compare figs. 59, 61, 63). The position, shape, and structural contribution of the supraethmoid of *Argyropelecus* to the support of the ethmoid plate also suggests a relationship with *Polyipnus* and *Argyripnus*. It may be that the ancestor of *Sternoptyx* at one time had similar structures, but with a changed function of the jaws lost the need of any bony ethmoid support.

The premaxillary bone of *Argyropelecus* has a moderately long ascending process, more so

than in the nonhatchetfish sternoptychids but not nearly so long as that in *Polyipnus*. The premaxillary process is absent in *Sternoptyx*. In their total aspect the premaxillary, maxillary, and bones of the ethmoid region of *Polyipnus* and *Argyropelecus* approach each other more than either approaches that of *Sternoptyx*. This area is most advanced in the direction of upper jaw mobility in *Polyipnus* and in the direction of rigidity (see below under *Sternoptyx*) in *Sternoptyx*. This region in *Argyropelecus* is more like that of the other nonhatchetfish sternoptychid genera and is presumably relatively primitive for the hatchetfish group. Its components could be considered as being in the ancestral condition for either *Polyipnus* or *Sternoptyx*, and because of this the region cannot be used to relate *Argyropelecus* more closely to either of the other hatchetfish genera.

Argyropelecus has a relatively strong interpremaxillary ligament. It is weak in both *Polyipnus* and *Sternoptyx* but strong in the remaining sternoptychids, most gonostomatids, and photichthyids. A strong interpremaxillary ligament is primitive for the hatchetfish genera. Both *Polyipnus* and *Argyropelecus* have a moderately long palatomaxillary ligament, whereas it is very short in *Sternoptyx*. It is long in other sternoptychids, and presumably a rather elongate ligament is primitive for the hatchetfish genera. The suspensory-palatine ligament is long in *Argyropelecus* and short in both *Polyipnus* and *Sternoptyx*. It is long in all other sternoptychids, gonostomatids, and photichthyids.

As discussed above under *Polyipnus*, the greater number of enlarged ribs in *Argyropelecus* may be primitive for the hatchetfish group, but as evidence taken by itself, is not very convincing.

The complex of characters associated with vertebral numbers suggests that, in at least this respect, *Argyropelecus* may be primitive for the three hatchetfish genera. For example, as noted under *Polyipnus*, about 40 to 45 vertebrae appear primitive for stomiatoids. Of the hatchetfish genera only *Argyropelecus* has members within this range (34 to 40). *Polyipnus* has 32 to 35 and *Sternoptyx* 29 to 31, these figures being reductions and therefore representing an advanced state. It has already been noted under *Polyipnus* that *Argyropelecus* and *Sternoptyx* have more total ribs (eight, nine, or 10) than *Polyipnus* (six to eight). *Polyipnus* and *Argyropelecus* have

epimerals, which are absent in *Sternoptyx* but present in almost all the Gonostomatidae, Photichthyidae, and other genera of the Sternoptychidae (apparently absent in *Danaphos*). There is a trend toward reduction of the supraneurals in the Sternoptychidae, but *Argyropelecus* retains more (eight) than the other hatchetfish genera (*Sternoptyx* has four and *Polyipnus* six).

As discussed above under several of the genera, the various characters in the caudal skeleton of sternoptychids are so variable that useful analysis for phylogenetic purposes seems excluded. *Argyropelecus* does have the parahypural free of all other elements, presumably a primitive feature. The bone is fused with the first ural centrum, the preural centrum, and the first and second hypural in *Sternoptyx*. *Polyipnus* has the parahypural free of the centra and fused to the base only of the first and second hypurals. Primitively the parahypural is autogenous in stomiatoids, but the bone is fused to some of its surrounding elements in various genera including the various sternoptychid genera. The distribution of these fusions is mosaic among the genera and defies conclusive interpretation.

Really exclusive advanced features in *Argyropelecus* relative to the other hatchetfish genera are few, and the genus is hard to define on a basis of advanced characters not found at least to a certain extent in *Polyipnus* and especially *Sternoptyx*. *Argyropelecus* apparently shares several primitive characters with *Polyipnus* and many more advanced characters with *Sternoptyx*. Derived characters shared with *Sternoptyx* are treated below under that genus.

One exclusive advanced feature of *Argyropelecus*, simply a failure of ossification rather than a loss, is the apparent absence of bone in the area of the basisphenoid. Connective tissue is present in the morphological form of a basisphenoid, but no bone is deposited in it. Ossification is present here in all other sternoptychids with the exception of *Danaphos* where the absence is presumably convergent with the condition in *Argyropelecus*. Another advanced character of *Argyropelecus* not found in other hatchetfish genera is the presence of more than one dorsal fin blade (modified supraneural) that is well exserted above the profile of the muscular part of the back. These two characters can be used to define the genus.

Sternoptyx and *Argyropelecus* share several advanced characters not found in *Polyipnus* and together form a sister group of *Polyipnus*.

The frontals, parietals, a few other externally exposed skull bones, and the cleithrum are heavily pitted. Some pitting of the cleithrum occurs in *Polyipnus* but never so much as in the former two genera. Both *Sternoptyx* and *Argyropelecus* have exceptionally small sagittae, being quite small relative to cranial length as described under *Polyipnus*. The sagittae of these two genera have a very reduced rostrum (prominent in *Polyipnus*), and the crista inferior absent (present in *Polyipnus*). The mesopterygoid is relatively short in *Sternoptyx* and *Argyropelecus*, and the ectopterygoid is elongate and slender, both highly advanced conditions relative to other sternoptychids. The coronoid platform or process of the dentary is absent in *Sternoptyx* and *Argyropelecus* and present in most other sternoptychids and gonostomatids. The dorsal limbs of the preopercles are elongate relative to all other Gonostomata as is the hyomandibular, the greatest relative length being attained in *Sternoptyx*.

Sternoptyx and *Argyropelecus* apparently share a few primitive characters not found in *Polyipnus*. Both have the dorsal border of the quadrate articulating with the metapterygoid. It articulates with the mesopterygoid in *Polyipnus*. Usually in sternoptychids and gonostomatids the dorsal border of the quadrate articulates with the metapterygoid or that bone and the ectopterygoid. In *Argyripnus* and *Sonoda* parts of the mesopterygoid also enter the joint. The ventral border of the parasphenoid is strongly convex and seemingly advanced, but this may be more correlated with the absence of the enlarged otic bullae found in *Polyipnus* than an advanced condition for the hatchetfish genera. The straight parasphenoid of *Polyipnus* under these circumstances would be more advanced. The maxillary is not sharply angulate in *Argyropelecus* and *Sternoptyx* as it is in most species of *Polyipnus* and *Maurolicus*. Most sternoptychids, gonostomatids, and photichthyids have no sharp angles in the maxillary. *Sternoptyx* and *Argyropelecus* have a slender maxillary, a feature common to most Gonostomata and the Photichthyidae, rather than the expanded and sharply angled maxillary found in most species of *Polyipnus*. *Sternoptyx* and *Argyropelecus* have more rib-bearing vertebrae, presumably a primitive feature. The urohyal of *Sternoptyx* and

Argyropelecus is deeply incised, not expanded as in *Polyipnus*, again a primitive feature for the two former genera.

STERNOPTYX

Relative to *Polyipnus* and *Argyropelecus*, *Sternoptyx* apparently has no exclusive primitive characters except possibly the horizontal myodome discussed above under *Polyipnus*. *Sternoptyx* is highly advanced and has many unique characters as follows.

Sternoptyx lacks all ethmoid bones and also the vomer. The premaxillaries are small, each without an ascending process, and they are firmly attached by a very short premaxillary-proethmoid ligament to the ethmoid cartilage. The upper jaw has very little mobility at its point of ligamentous attachment.

The parietals are only partially separated by the supraoccipital, whereas they are completely separated in all other sternoptychids. The parietal bones are in contact with the intercalar; no other stomiatoid appears to have this condition The posttemporal fossa is absent, the extremely large intercalar occupying its space. The intercalar covers parts of the epiotic, exoccipital, and pterotic. All other sternoptychids, gonostomatids, and photichthyids have a well-developed posttemporal fossa and a relatively small intercalar that usually covers parts of the exoccipital, prootic, and rarely a small part of the pterotic, but never the epiotic. *Sternoptyx* is the only member of the Gonostomata with the exoccipital plates not in contact dorsal to the foramen magnum.

The posterior myodome of *Sternoptyx* is exceptionally large for any stomiatoid and none, other than *Sternoptyx*, has a glossopharyngeal tunnel in the parasphenoid bone. The relative size of the sphenotic is larger in *Sternoptyx* than any other member of the Gonostomata. The palatine bone has a special tooth-bearing process found in no other stomiatoid. The maxillary bone has a concave toothed border, whereas it is convex in all other sternoptychids. Only a slender posterior supramaxillary bone is present, whereas *Argyropelecus* and *Polyipnus* retain both anterior and broad posterior supramaxillaries. Both are present in most species of the Gonostomatidae and the Photichthyidae, but the character is somewhat variable in the Sternoptychidae, the anterior being absent in *Danaphos*, *Valenciennellus*, *Argyripnus*, and *Sonoda*.

Because the hatchetfish genera seem related to these four genera, this might indicate that the three hatchetfish genera evolved from a common ancestor with two supramaxillaries and that as suggested above, the near relationship of the hatchetfishes with *Argyripnus* and *Sonoda* may be faulty. However, the anterior supramaxillaries of *Danaphos* and *Valenciennellus* on the one hand and of *Argyripnus* and *Sonoda* on the other could easily have been lost independently. Certainly the relationships suggested by the peculiar hiatus in the anal fin in *Argyripnus*, *Sonoda*, and the hatchetfishes is a more important indicator of relationships than the loss of the anterior supramaxillary. In any event, probably all seven genera evolved from a common ancestor with two supramaxillaries and six pelvic radials.

Both *Polyipnus* and *Argyropelecus* have a triangular subopercle, whereas it is dorsoventrally elongate in *Sternoptyx* (and also *Argyripnus* in which the bone differs greatly in shape from that in *Sternoptyx*). The bone is more or less rectangular to somewhat triangular in other sternoptychids, but rectangular in gonostomatids and photichthyids. A triangular interopercle is an advanced trend within the Sternoptychidae and appears correlated with a vertically narrow opercle. The opercle in *Polyipnus* and *Argyropelecus* is dorsoventrally long but retains a short, straight, horizontal ventral border. The posterior ventral corner of the subopercle is reduced or "rounded off," giving the bone a triangular shape. The opercle in *Sternoptyx*, however, is advanced in having a pointed ventral border for which the subopercle compensates by extending dorsally and becoming elongate along the posterior and anterior borders of the opercle. Thus it appears that the opercle and subopercle of *Sternoptyx* is more modified from the relatively primitive sternoptychid condition than that of *Polyipnus* and *Argyropelecus* and that the subopercular condition found in these two genera is not advanced for hatchetfishes but primitive relative to the condition found in *Sternoptyx*.

Sternoptyx has the ceratohyal less constricted along its midlength than any other sternoptychid or gonostomatid. It also has fewer branchiostegal rays (six versus 10 in all other sternoptychids).

Sternoptyx has fewer vertebrae, 29 to 31, than any other sternoptychid genus and is the only

member of the family without epimerals, with the possible exception of *Danaphos*. *Sternoptyx* has four free supraneurals, whereas other sternoptychids have at least six (except *Valenciennellus* with one or two) and usually more (up to 19 in *Thorophos*). *Sternoptyx* has the posterior supraneural modified as a blade, and the modification of it is more extreme than the blades in *Argyropelecus*; however, the latter genus has seven of its eight supraneurals modified, whereas *Sternoptyx* has only one modified. *Sternoptyx* has all the caudal hypural and vertebral elements fused. This is more fusion than any other genus of the Sternoptychidae. In addition, the hypural fan and posterior caudal vertebrae are bent dorsally, a condition found in no other member of the Gonostomata or in the Photichthyidae.

The pectoral girdle is very advanced in *Sternoptyx*, with a peculiar slender cleithrum without a notch for the pectoral fin or a ventral lateral plate. The scapular foramen is absent. The pectoral fin radials have a unique attachment, all four articulating with the scapular and only the fourth on the coracoid bone (compared above under *Polyipnus*).

The pelvic girdle of *Sternoptyx* is the most advanced of all the three hatchetfish genera, with only one instead of six radials. Most sternopty-chid genera have seven pelvic fin rays (except *Araiophos* which has five, presumably correlated with its small size and neotenic nature). *Sonoda* and *Argyropelecus* have six and *Sternoptyx* has five. Thus in *Sternoptyx* the pelvic fin rays are reduced farther than any of the other hatchetfish genera. *Sternoptyx* seems to have redeveloped a strong anterior ischial process, or perhaps it has been lost in the other two hatchetfish genera. The process is also absent in *Sonoda* and *Argyripnus*, but is prominent in *Thorophos* and very large in *Danaphos* and *Valenciennellus*. It is small in *Maurolicus* and almost absent in the neotenic *Araiophos*.

Sternoptyx has the anterior anal fin pterygiophore highly modified with protuberant spines, structures found nowhere else in the stomiatoids. The peculiar absence of muscle fibers immediately dorsal to the joints between the fin rays and radial elements of the anal fin is exclusive to *Sternoptyx* and is apparently associated with the photophore mass above as well as with the anal fin hiatus. Muscles are present for the fins but are far removed from the fins, and long tendons extend from the muscles, along the proximal radials to the fin rays. The skin is very thin over this area giving a "window" effect in lateral view.

CONCLUSIONS

ON THE BASIS of the present studies the suborder Stomiatoidei is divided into two new infraorders (see fig. 1). The first, Gonostomata, has members with four pectoral fin radials (unless independently reduced as in *Cyclothone*) and either type Alpha or type Beta photophores. The second, Photichthya, has members with the advanced characters of three pectoral fin radials (farther reduced in some genera with extremely small pectoral fins) and apparently relatively advanced type Gamma photophores.

The Photichthya was analyzed primarily on the basis of the literature and determined to include two new superfamilies, the Photichthyoidea and the Stomiatoidea. The Photichthyoidea are tentatively defined as Photichthya with serial photophores having a lumen and duct, an advanced character. This group retains primitive characters such as well-developed gill rakers in adults and usually two supramaxillaries (these last are fused with the maxillary in *Ichthyococcus*). There is one family, the Photichthyidae, herein named as new, its characters are those of the superfamily. The Photichthyidae was determined to include seven former gonostomatid genera, *Polymetme*, *Yarrella*, *Photichthys*, *Pollichthys*, *Vinciguerria*, *Woodsia*, and *Ichthyococcus*. The interrelationships of these genera were not studied fully but the first six above appear relatively primitive, the last very advanced.

The Stomiatoidea are defined as Photichthya with no gill rakers in adults and one or no supramaxillaries, both advanced characters. This group has been found to have photophores without ducts or lumen, presumably a primitive feature, however, extensive analysis of photophore structure remains to be done. Species in this group often have other advanced characters such as large, fanglike teeth in the jaws, scales reduced or absent, and a single median barbel beneath the head. The superfamily Stomiatoidea currently includes six families, but the family groupings in this superfamily were found to be in need of reorganization. They were discussed briefly here but not regrouped.

The Gonostomata is divided into two families, the Gonostomatidae and the Sternoptychidae.

The Gonostomatidae includes six genera, *Diplophos*, *Triplophos*, *Bonapartia*, *Margrethia*, *Gonostoma*, and *Cyclothone*. The interrelationships of these genera were not treated here, and the family remains a "catch basket" of relatively primitive and advanced stomiatoid genera. Advanced characters for stomiatoids were not found that could be used to define the group. The family may tentatively be defined as Gonostomata having 12 to 16 branchiostegal rays with four, five, or six such rays on the epihyal, eight to 16 branchiostegal photophores and type Beta A-photocytes. All these characters are considered relatively primitive when compared with their homologues in the Sternoptychidae.

The Sternoptychidae as proposed here consists of 10 genera, *Thorophos*, *Araiophos*, *Maurolicus*, *Danaphos*, *Valenciennellus*, *Argyripnus*, *Sonoda*, *Polyipnus*, *Argyropelecus*, and *Sternoptyx*. With regard to the suborder Stomiatoidea as a whole, sternoptychids are a line of evolution in which some members are relatively primitive and some are extremely advanced. As is to be expected in any group whose members display wide morphological divergence, it is difficult to find characters universally present that are advanced for the group as a whole. Most such characters are altered beyond recognition by subsequent evolution in the more divergent members. In the Sternoptychidae a few characters present in all genera and apparently species seem to fit this category and thus are convenient for a definition of the group. There are 10 or fewer (six) branchiostegal rays and invariably three such rays on the epihyal. There are six branchiostegal photophores in most genera (rarely seven in *Sonoda*). *Sternoptyx* has three. Two and often more of the longitudinal body photophores are clumped into specialized photophore organs and apparently all photophores are of the Alpha type.

Some advanced characters within the Sternoptychidae have been so modified within the group that they cannot be used for a simple definition, nevertheless these characters do indicate interrelationships among the member genera when they are properly compared. For example, the usually long palatomaxillary ligament, a basic advanced character for the family,

is shortened in some very modified genera; the parietal bones are separated from each other by the supraoccipital bone (not separated in the highly advanced *Sternoptyx*); the epurals are almost always flattened and platelike (*Polyipnus* occasionally retains or redevelops rodlike epurals).

Other advanced characters typical of sternoptychids appear independently derived in a few other stomiatoids. The adipose fin, when present, is long based in almost all sternoptychids, but it is also long based in *Ichthyococcus*, a photichthyid; the extrascapular bones are absent but are possibly absent in several genera of the Photichthya (where the apparent loss may not be natural but due to damage); the basihyal is absent but is also absent in *Cyclothone*, a gonostomatid; six or fewer branchiostegal photophores are found in the Sternoptychidae but occasional specimens of *Sonoda* will have seven and only an occasional specimen of the photichthyid *Vinciguerria* will have fewer than eight, i.e. seven; the melanostomiatid *Bathophilus* has fewer than seven branchiostegal photophores; the basibranchial is toothless in sternoptychids (this bone becomes toothless independently in a few other stomiatoid genera, for example *Ichthyococcus*, in which all gill teeth are reduced); no lateral line canal is present in the cleithrum or posttemporal (the distribution of this loss in other stomiatoid genera is not completely certain, but where it does occur, it appears to be independently acquired).

Certain advanced trends appear to be present in sternoptychids, for example, there is a tendency to deepen the head, snout region, and sometimes the entire body, to reduce the number of orbital bones, never to have the terminal dorsal or anal fin rays divided to their bases, and to lose the mesopterygoid teeth and teeth on the infrapharyngobranchials of the second gill arch.

All sternoptychids retain one primitive character, the pseudobranch, which is lost or tends to be lost in other stomiatoid groups.

The phylogenetic interrelationships of the sternoptychid genera were investigated and a hypothesis concerning their ancestral relationship was proposed (see fig. 113).

Thorophos is the most primitive genus and its sister group is *Araiophos*, a neotenic and more advanced genus. *Thorophos* and *Araiophos* retain many relatively primitive stomiatoid characters

not found in any other sternoptychid and share additional primitive characters with a few sternoptychid genera. Advanced characters shared exclusively by *Thorophos* and *Araiophos* are few (for example exoccipitals not entering the borders of the posttemporal fossa), and whether these characters are primitive or advanced is doubtful. However, in many fine details the skull bones of these two genera are remarkably similar and not like those of any other stomiatoid genus. *Araiophos* is characterized by a neotenic pectoral girdle and fin, reduced ossification of skull bones, and modifications of the opercular apparatus. An exclusive and possibly advanced character in *Thorophos* is the presence of median teeth on the vomer. The posterior supramaxillary of *Thorophos* is reduced and narrow and is probably advanced relative to that in *Araiophos*.

The sister group of the group formed by *Thorophos* and *Araiophos* includes all the remaining sternoptychid genera. As these genera have advanced in a variety of very different directions and have undergone a great amount of morphological change, advanced characters common to all are largely masked. The few advanced characters common to all may include a deep longitudinal frontal fossa or modification of such a fossa, a mesopterygoid with a triangular profile, and the adductor pocket of the lower jaw nearer the middle or anterior part of the mandible than to the posterior one-third or one-fourth of the mandible.

Within the group defined above, *Maurolicus* appears to stand alone, retaining some primitive stomiatoid characters but as a whole being highly advanced in its own peculiar way. The cranium and jaws are especially characteristic and advanced in having, among other things, the capsular ethmoids fused to each other below the independent supraethmoid, a long, slender palatine bone with a very modified posterior head, an exceptionally large ectopterygoid, a broad, flat, sharply angled maxillary bone, and an exceedingly deep mandible.

Again the remaining sternoptychid genera, *Danaphos*, *Valenciennellus*, *Argyripnus*, *Sonoda*, *Polyipnus*, *Argyropelecus*, and *Sternoptyx*, form a monophyletic group and are characterized by at least one very peculiar advanced character, a doubling of the pelvic radial elements, there being six instead of three as in all other stern-

optychids as well as stomiatoids or for that matter most relatively primitive teleosts. *Sternoptyx*, a member of this group, has these six small radials reduced to one large radial and can be seen as related to this group because it is re-related to *Argyropelecus*. All members of this group have modified sagittae, which have a reduced rostrum and a deep, rather than elongate, shape. All these genera have the supraethmoid reduced or even lacking. The proethmoid process where present is reduced. The ethmoid cornua are very weakly developed or occasionally lost.

Two genera, *Danaphos* and *Valenciennellus*, are highly advanced, very closely related, and appear to form a sister group of the remaining five sternoptychid genera. The following advanced features especially distinguish *Danaphos* and *Valenciennellus*: narrow interorbit with the frontal bones fused anteriorly and the anterior tip of the common frontal bones lying below the supraethmoid; similar and very distinctive sagittae; and incomplete ossification of the subopercle. These are only a few of their common advanced and unique characters. Although the two genera are very closely related, *Danaphos* is more advanced in having the anterior portion of the fused frontal bones rolled into a nearly closed tube, only the ectopterygoid in contact with the dorsal border of the quadrate, an extremely long-based adipose fin, and an enlarged PV photophore group. *Valenciennellus* is advanced in having fewer vertebrae, 32 or 33 rather than 38 or 39 of *Danaphos*, a small posterior myodome, no lateral ethmoid, only two supraneurals (six in *Danaphos*), and clumped photophores in the AC row. The two genera are advanced in different directions but neither is remarkably more advanced than the other.

Argyripnus, *Sonoda*, *Polyipnus*, *Argyropelecus*, and *Sternoptyx* appear to form a sister group of *Danaphos* and *Valenciennellus*. They are the only sternoptychid genera with an anal fin hiatus and no proethmoid process. The anal fin hiatus is unique for stomiatoids and even though somewhat different seems similar enough not to be of independent origin in *Argyripnus* and *Sonoda* on the one hand and the three hatchetfish genera on the other. All five genera have a similar and peculiar "quadrangular" palatine. In addition, certain advanced characters in *Polyipnus* and *Argyropelecus* appear similar to those in *Argyripnus* and *Sonoda* but are so altered

in *Sternoptyx* that they cannot be recognized.

Argyripnus and *Sonoda* share several unique advanced characters such as very posterior parasphenoid wings united into a cap ventral to the posterior myodome, palatine mostly cartilaginous and without obvious heads, with the anterior 10 through 13 neural arches not fused to their respective centra, and without ischial process on the pelvic bone. Finally, both have the same type of anal fin hiatus that is apparently advanced in having a medial radial altered into a long ligament. The two genera differ in several unique advanced characters; for example *Argyripnus* has a quadrangular opercle in profile, a differently shaped interopercle, a deeper snout region and ethmoid cartilage, and 44 to 46 vertebrae (40 in *Sonoda*). *Sonoda* has a dorsoventrally elongate opercle with a peculiar dorsal border and an elongate, sickle-shaped interopercle, different from that of all other stomiatoids.

Polyipnus, *Argyropelecus*, and *Sternoptyx* (here called the hatchetfish genera) form a sister group of *Argyripnus* and *Sonoda*. They have many advanced characters shared only among themselves, such as vertically oriented pelvic bones, an abdominal keel-like structure, enlarged pleural ribs, a deep body 0.8 to 2.0 times in standard length (3.7 to 7.9 in other sternoptychids), preopercular spines, iliac spines on the pelvic girdle, an epihyal length more than half the ceratohyal length, the posterior end of the ceratohyal larger than the anterior end, a club-shaped symplectic, a bony ridge on the parietal continuous with one on the frontal bone, and a further clustering of photophores into supra-anal, suprapectoral, and supra-abdominal groups.

Polyipnus has a large number of unique advanced characters associated with movable upper jaw bones and hearing apparatus. Otherwise it retains a large number of characters primitive for the hatchetfish genera and not found in either *Argyropelecus* or *Sternoptyx*. It forms a sister group of the other two hatchetfish genera and is easily definable by its possession of movable premaxillaries each with a long ascending process, complicated and elongate upper jaw ligaments, and a greatly enlarged otic region containing a peculiar, extremely deep sagitta with a narrow, slender rostrum. Many detailed, unique characters can be associated with these two complexes. Other

characters restricted to *Polyipnus* are found in the hyoid apparatus, and the pectoral and pelvic girdles.

Advanced characters shared only by *Argyropelecus* and *Sternoptyx* are several. For example, they have the exposed portion of their skulls heavily pitted; both have very small sagittae, advanced in a very different direction from those in *Polyipnus*; both have extremely elongate preopercles relative to any other sternoptychid; both have characteristic and similar pterygoid bones; and both have a deeply incised urohyal with the notch being associated with photophores.

Argyropelecus, for a hatchetfish genus, shares a large number of primitive features with *Polyipnus*. These are the primitive expressions of the advanced features found in *Sternoptyx*. In addition, *Argyropelecus* has some primitive hatchetfish characters not found in the other two genera. Both *Polyipnus* and *Sternoptyx* have highly advanced mouth and ethmoid structures, each different in its own exclusive way. *Argyropelecus* is the most primitive hatchetfish genus in this respect. Exclusive advanced characters in *Argyropelecus* are relatively few, the absence of ossification in the basisphenoid being one and the tendency to have more than one highly

modified supraneural exerted above the muscular profile of the back being another.

Finally, *Sternoptyx* remains as an extremely advanced sternoptychid with many characters found nowhere else. It completely lacks all ethmoid bones and a vomer. The upper jaws are attached by very short, almost nonmovable ligaments to the ethmoid cartilage and there is almost no upper jaw mobility. The skull, among other modifications, is advanced by having an enlarged intercalar filling the space of the posttemporal fossa, a peculiar glossopharyngeal tunnel on the parasphenoid, and the maxillary with a concave tooth border. The opercular and hyoid apparatus is greatly elongated dorsoventrally, and most of the associated bones have a characteristic shape. The vertebrae and supraneurals are reduced in number, the hypural apparatus is completely fused with the terminal caudal vertebrae and "bent" dorsally, and the pectoral girdle is extremely elongate and has a unique fin-radial-girdle attachment. The pelvic girdle is very advanced with one instead of six radials, five fin rays, and a characteristic girdle shape. Finally, the "window" effect caused by the absence of muscle fibers near the base of the anterior anal fin rays is found only in *Sternoptyx*.

APPENDIX: THE STATUS OF *NEOPHOS*

Grey (1960a) reviewed the generic status of the monotypic *Neophos* Myers, 1932 (fig. 2), and noted its close relationship to the monotypic genus *Thorophos* Bruun (1931, fig. 3). She considered *Neophos* possibly synonymous with the latter genus. In 1964, she attempted to distinguish the two in her key to gonostomatid genera, noting that the teeth of the premaxillary were biserial in *Neophos nexilis* and uniserial in *Thorophos euryops*. She further stated that the lower jaw teeth were biserial in the anterior half in *Neophos* and that there was no adipose fin. She reported "lower jaw teeth uniserial?" in *Thorophos* and an adipose fin present.

At that time Grey had been able to examine only the holotype of *Neophos* and a badly damaged specimen of *Thorophos*. Since then, nine additional specimens of *Neophos* have been found in the USNM collections, all from the type locality and collected at the same time as the holotype. I have been able to examine two specimens of *Thorophos*, the battered specimen examined by Grey, and an excellent speci-

men from the type series cleared and stained for the present report.

Examination of these specimens shows the adipose fin present in *Neophos* and the premaxillary in both *Neophos* and *Thorophos* having two rows of teeth (see fig. 53 and discussion, page 381). The lower jaw of both nominal genera have three rows of teeth anteriorly and only one row posteriorly (see p. 394). This removes Grey's three most important characters for recognizing *Neophos* as distinct from *Thorophos*. The slight difference in dorsal fin position as noted by Grey (1964) in these two genera seems insufficient for recognition at the generic level. Differences noted by Grey in anal and dorsal fin ray counts and in photophore counts seem hardly distinctive enough for acceptance of two genera. Nothing in the osteology investigated here pointed to differences great enough for generic separation or even comparable with the differences in the other closely related sternoptychid genera such as *Danaphos* and *Valenciennellus* or *Argyripnus* and *Sonoda*. *Thorophos euryops* and *T. nexilis* appear to be distinct but closely related species of the same genus, *Thorophos*.

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