

Morphology of *Luvarus imperialis*
(Luvaridae), with a
Phylogenetic Analysis of the
Acanthuroidei (Pisces)

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and
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FRONTISPIECE.—Cleared and stained larval specimens of *Luvarus imperialis*, upper (MCZ 55291, 10.5 mm SL), and *Zanclus cornutus*, lower (MCZ 62046, 9.5 mm SL).

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ABSTRACT

Tyler, James C., G. David Johnson, Izumi Nakamura, and Bruce B. Collette. Morphology of *Luvarus imperialis* (Luvaridae), with a Phylogenetic Analysis of the Acanthuroidei (Pisces). *Smithsonian Contributions to Zoology*, number 485, 78 pages, 50 figures, 1989.—The osteology of the rarely collected epipelagic fish *Luvarus imperialis* Rafinesque, the louvar, is redescribed, based for the first time on cleared and stained specimens of juveniles and young adults, as well as on dried skeletons of larger adults. Knowledge of the structure of fossil luvarids, from their first occurrence in the upper Paleocene to a very well-preserved specimen from the lower Eocene, is reviewed and their status re-evaluated. Earlier comparative anatomical studies are reviewed in historical perspective with regard to previously proposed relationships. It has been postulated most frequently that *Luvarus* is related to carangoid or scombroid fishes, the latter hypothesis having been the most widely accepted. With cladistic methodology and with much additional detailed information on the osteology and larval morphology of *Luvarus* and other groups, the carangoid and scombroid hypotheses are refuted. *Luvarus* is actually a highly specialized pelagic member of the typically reef-associated Acanthuroidei, the surgeon fishes and their allies. Scatophagids and ephippidids, respectively, are the first and second outgroups for the Acanthuroidei. Anatomical diagnoses of all acanthuroid genera are given. A cladistic analysis of the intra-relationships of the Acanthuroidei, based on 90 characters encompassing both larval and adult morphology, provides a highly corroborated hypothesis indicating the following phyletic sequence: Siganidae—Luvaridae—Zanclidae—Acanthuridae.

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Contents

	<i>Page</i>
Introduction	1
Brief History of This Study	3
Methods	4
Material Examined	5
Acknowledgments	5
Anatomical Descriptions	6
79.2 mm SL	6
Skull	6
Gill Arches	14
Pectoral Girdle	17
Pelvic Girdle	18
Vertebral Column	19
Caudal Skeleton	20
Dorsal and Anal Fins	21
Scales	22
Olfactory Rosette	22
301 mm SL	22
485 mm SL	27
980 mm SL	27
1100 mm SL	29
1140 mm SL	29
1720 mm SL	29
1780 mm SL	31
Relationships	31
Fossil Record	31
Parasites	32
Diagnosis of the Family Luvaridae	32
Previously Proposed Relationships	34
Acanthuroid Characters	37
Character Analysis	42
Summary of Character Analysis	73
Evolution and Adaptations	73
Note	75
Literature Cited	76

Dedication

This contribution is dedicated to the memory of Robert H. Gibbs, Jr., 30 July 1929 to 3 April 1988, our dear friend and esteemed colleague in the study of scombroid fishes.

Morphology of *Luvarus imperialis* (Luvaridae), with a Phylogenetic Analysis of the Acanthuroidei (Pisces)

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Introduction

The louvar, *Luvarus imperialis* Rafinesque, 1810 (Figure 1), is an infrequently collected epipelagic fish of world-wide distribution in tropical and temperate marine waters. The monotypic *Luvarus* undergoes a remarkable and prolonged metamorphosis, various stages of which have received larval appellations (*Hystricinella*, *Astrodermella*, *Luvarella*, Figure 2), as described in detail by Roule (1924) and Roule and Angel (1930). The most recent descriptions of larval *Luvarus* are by Leis and Richards (1984), Johnson and Washington (1987), and Nishikawa (1987). Juveniles begin to resemble the adult by about 100 to 200 mm SL. Adults reach a size of over 1800 mm SL and 140 kg (for records see Bolin, 1940; Whitley, 1940; Gotshall and Fitch, 1968).

Like many other strange and exotic epipelagic species such as the oar fish *Regalecus* and the giant ocean sunfish *Mola*, *Luvarus* has excited the imagination and moved the pen so frequently that it has spawned a subset of ichthyological literature devoted to records of its occurrence and to its external anatomy. Most of the early work was summarized by Roule (1924), Roule and Angel (1930), and Gregory and Conrad (1943). Recent regional papers include Gotshall and Fitch (1968) for the eastern Pacific, Buen (1957) for the north and south western Atlantic, Paulin et al. (1982) for New Zealand, and Blache (1964) and Ibañez (1981) for the eastern Atlantic.

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Review Chairman: Storrs L. Olson, Smithsonian Institution. Reviewers: Gareth Nelson, American Museum of Natural History; Richard Rosenblatt, Scripps Institution of Oceanography; Camm C. Swift, Natural History Museum of Los Angeles County.

Günther (1866) provided a brief page-and-a-half description and a sketch of the lateral view of an entire dried skeleton of unspecified size in the Senckenberg Museum of Frankfurt. He was impressed by “the feeble development of the whole osseous structure” and inferred that *Luvarus* “is a deep-sea fish” from “a zone at a depth of perhaps a hundred fathoms.” He commented on the small mouth, curved haemal spines and elongate anal fin basal pterygiophores, the presence of 7 ribs on the 3rd to 9th vertebrae, the total of 22 vertebrae, and dorsal fin pterygiophores “so much dilated above that their upper extremities appear to be united by one semiofified ligament, which extends from the parietal crest to the end of the dorsal.” He noted that the pterygiophores of the anal fin are similar to those of the dorsal fin, their united extremities “extending from the end of the anal to the pubic bones, and forming a complete but feeble ring round and supporting the abdominal cavity.” Günther’s specimen apparently was at least a large juvenile or young adult, for the pelvic fin was proportionally small, being “very short and coalesced, but slightly divergent behind, so as to leave a narrow opening for the vent, which can be entirely closed by the rudimentary...ventral fins.”

Günther (1866) did not consider the classification or possible relationships of *Luvarus*, but in his “Catalogue” (1860) he placed *Luvarus* (as *Ausonia*), without significant explanation, in the Coryphaenina, as one of five subdivisions of his Scombridae. Shortly thereafter, Gill (1863), probably following Günther (1860), gave an equally vague allocation of *Luvarus* as an aside to his brief classification of the Scombroideae, stating that *Luvarus*, *Diana*, and *Lampris* represent distinct families related to *Coryphaena*, the latter of which Gill did not include among the scombrids.

Waite (1902) gave a more detailed description of the osteology of *Luvarus* based on a dried “skeleton, broken and incomplete” of a specimen of “about six feet two inches” in length. Like Günther (1866), Waite found that “a striking

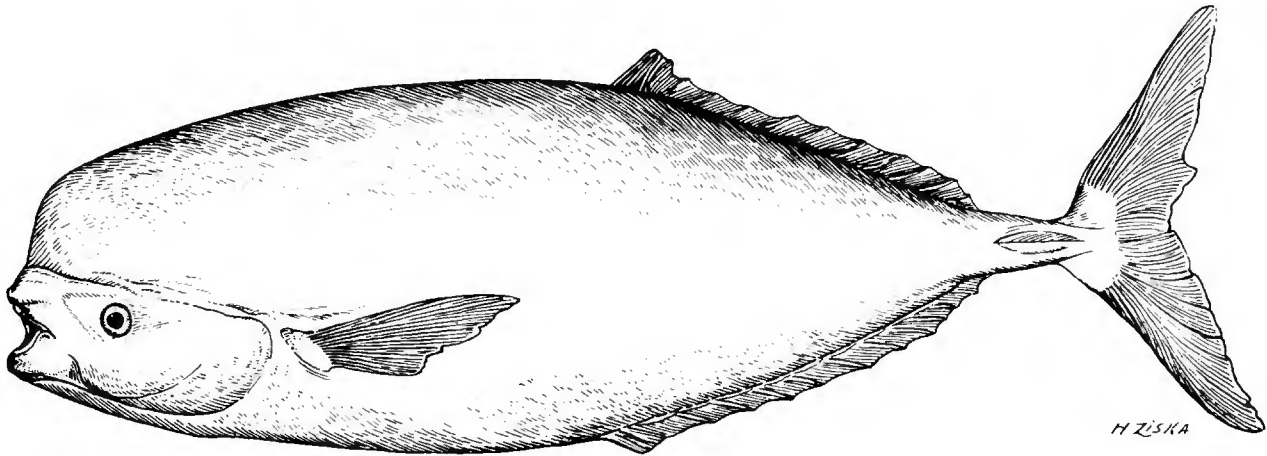


FIGURE 1.—*Luvarus imperialis*. Model based on cast made from 200 lb specimen caught at Cayo Costa, Florida. (From Gregory and Conrad, 1943, fig. 1).

feature of the skeleton is presented by the union of the interneural spines into a complete bony arch, which extends from the union of the ethmoid and parietal bones backwards to the eighteenth vertebrae; a similar arch is formed below. . . ." He presented a finely detailed description and illustration of the complex interlocking interdigitations of the distal ends of the pterygiophores of the dorsal and anal fins.

Even though he had difficulty in determining the limits of several cranial bones, Waite's descriptions and illustrations are mostly accurate and a great improvement over those of Günther (1866), except for the following misidentifications or misinterpretations: parietal = epiotic; epiotic = exoccipital; supraoccipital probably = mostly exoccipital. The nasals and lachrymals apparently were lost during skeletal preparation, and the short uppermost pectoral-fin ray apparently was counted as an actinost, giving an incorrect total of five.

In brief articles, Regan (1902, 1903) offered two surmises on the relationships of *Luvarus*. In the first, based on the older literature and no skeletal material, he associated *Luvarus* with the Acanthuridae. In the second, having studied both Waite's just-published paper and a skeleton of *Luvarus* (particularly the caudal skeleton), he rejected his 1902 hypothesis and proposed the subsequently commonly accepted view that *Luvarus* is in some poorly defined way related to the scombroid fishes.

Roule (1924) greatly supplemented and extended the earlier works describing various stages in the extensive ontogenetic metamorphosis of *Luvarus*, which he termed "hypermetamorphosis." Roule noted that in the earliest (5 mm) larvae ("*Hystricinella*") the hypurals are separate and the fin rays do not overlap them. These and other differences between larval *Luvarus* and adult scombroids led Roule to question whether *Luvarus* is closely related to scombroids. He elevated the series *Luvariformes* of Jordan (1923) to ordinal status and implied that *Luvarus* may have originated independently of the scombroids, apparent similarities between the two being the

result of convergence.

The most complete osteological description of *Luvarus* is that of Gregory and Conrad (1943), based on the dried skeleton of a 200 lb (91 kg) adult (Figure 1) of unspecified length (the skeleton at the American Museum is now so disarticulated that its length cannot be reasonably estimated, C.L. Smith, pers. comm.). This detailed description is remarkably accurate in most respects, especially considering that it was based on a single large specimen, dried and partly distorted by shrinkage of cartilaginous areas. Gregory (1933) illustrated the skull of this specimen, and placed *Luvarus* among the scombroids (*sensu lato*). Gregory and Conrad (1943) made extensive comparisons of the skeleton of *Luvarus* with that of a "typical" percoid, *Morone* (= *Roccus*), as well as with scombroids and carangoids, but did not settle on a preferred hypothesis concerning its affinities.

Monod (1968) described the caudal skeleton of *Luvarus*, based on a large dried skeleton at the Paris Museum and on the specimen studied by Gregory and Conrad (1943), concluding that the caudal skeleton is more or less similar to that of tunas.

A few other works have described certain aspects of the anatomy of *Luvarus* but reached no classificatory or phylogenetic conclusions: the intestines (Nardo, 1827, and Cuvier and Valenciennes, 1833); superficial description of the musculature, intestines, and brain (Haller, 1881); the eye (Berger, 1881); the pectoral girdle (Siebenrock, 1901); and certain bones and muscles of the head, branchial apparatus, and tail (Tominaga, 1964).

Given this lack of anatomical information, the primary purposes of this paper are to describe and illustrate completely the osteology of *Luvarus* and to assess its phylogenetic relationships. In so doing, we also present an analysis of the phylogenetic relationships of the suborder Acanthuroidei based on characters of larvae and adults. This work represents the first descriptive osteology of *Luvarus* from cleared and stained

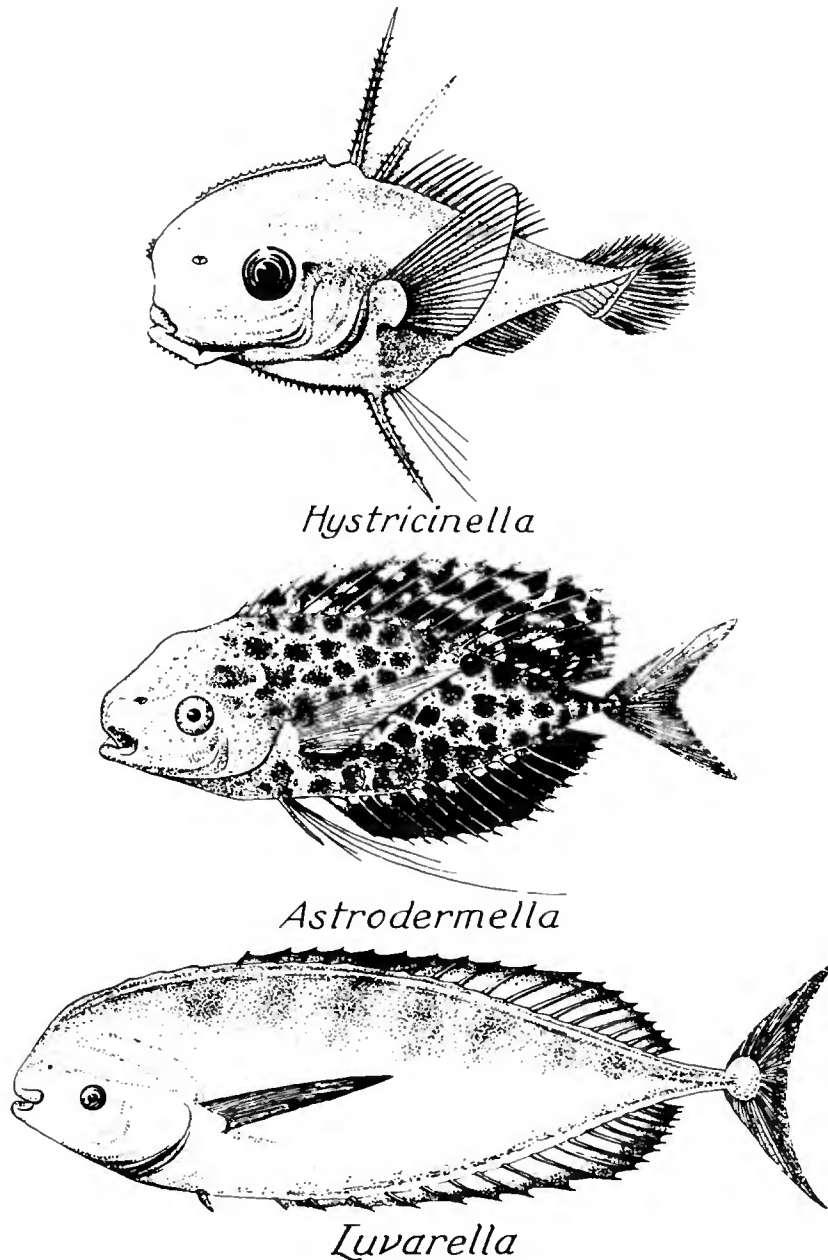


FIGURE 2.—Larval stages of *Luvarus*. (From Gregory and Conrad, 1943, fig. 37, based on Roule, 1924.)

juveniles and thus avoids previous difficulties in determining the limits of cranial and other bones of adults. The fossil record of luvarids also is reviewed.

Brief History of This Study

The organization of this paper is partially a reflection of its origin as a detailed osteological description of *Luvarus* based

on juvenile and adult specimens and its subsequent expansion into a wider-based study. The expansion involved two phases. First, a comparison of the anatomy of *Luvarus* with that of the scombroid and carangoid fishes to which *Luvarus* had been thought to be related; and second, a phylogenetic analysis of *Luvarus* based on larval as well as juvenile and adult characters. The latter clearly showed that *Luvarus* is neither a scombroid nor a carangoid but is related to the acanthuroid

fishes. Because the relationship of the acanthuroids themselves has been poorly known, and most recently misinterpreted cladistically, a major focus of this paper became a clarification of the relationships of the acanthuroids and the squamipinnes based on a phylogenetic analysis that eventually involved 90 characters. That analysis clarifies interrelationships among the four acanthuroid families (Siganidae, Luvaridae, Zanclidae, and Acanthuridae) and higher squamipinnes (Scatophagidae, Ehippididae, Chaetodontidae, Pomacanthidae, Drepanidae).

The initial impetus for this paper was a suggestion by Dr. Richard Rosenblatt in 1967 (pers. comm.) that *Luvarus* might not be a scombroid as commonly supposed, and that its osteology should be compared to that of several other large pelagic species, such as the giant ocean sunfish *Mola* on which one of us (Tyler) was then working. However, the few museum specimens of *Luvarus* then available, aside from larvae, were all large adults, either alcohol-preserved or dried skeletons much distorted by shriveling of relatively weakly ossified bones. It was not until the late 1970s that Dr. Rosenblatt obtained a relatively smaller 301 mm SL specimen from California that he could make available for clearing and staining. At about the same time, Dr. Luis Alberto Zavala-Camin obtained several juvenile *Luvarus* of less than 100 mm SL from off the coast of Brazil found in the stomachs of tunas he was studying. Some of these specimens of *Luvarus* from tuna stomachs were in nearly perfect condition, scarcely digested.

With the 301 mm SL California specimen and the smaller ones from Brazil in hand (including a fine 79 mm SL specimen that cleared and counter-stained especially well) the osteological study of these materials began in earnest in the Fish Division of the National Museum of Natural History, on a one-day-a-week basis while the first author was on release time from administrative duties at the National Science Foundation.

While the osteological descriptions and illustrations of these specimens of *Luvarus* were being prepared, Dr. Izumi Nakamura arrived from Japan to spend 1981 as a postdoctoral fellow at the Smithsonian Institution to work with Dr. Robert H. Gibbs, Jr., and Dr. Bruce B. Collette on the systematics and phylogeny of scombroids. Dr. Nakamura previously had prepared sketches and compiled data on alcohol-preserved and dried skeletons of *Luvarus* in Oriental, European, and U.S. museums as an aid in assessing the relationships of *Luvarus* and scombroids. Tyler and Nakamura joined forces to describe the osteology of *Luvarus* based on small cleared and stained specimens and larger dried skeletal material, while Collette contributed a section evaluating the evidence, pro and con, for the possible relationship of *Luvarus* with scombroids and carangoids.

By 1982 the osteological descriptions and illustrations were completed, as was Collette's analysis showing that *Luvarus* had no phylogenetic affinities with either scombroids or carangoids.

We then sought the advice of Dr. G. David Johnson on

perciform phylogeny as it might relate to *Luvarus*, and we soon together came to agree that *Luvarus* might have its closest affinities with acanthuroids, as first suggested by C. Tate Regan in a largely ignored 1902 publication. Our comparison of *Luvarus* with acanthuroids was made easier since one of us (Tyler) had a good many unpublished illustrations of acanthuroids prepared in conjunction with his studies of tetraodontiforms, while another (Johnson) had extensive knowledge of both perciform phylogeny and of the larval morphology of acanthuroids and squamipinne perciforms that were a natural complement to both his and our knowledge of the adult morphology of *Luvarus*, scombroids, and acanthuroids.

The paper thus evolved into a cladistic analysis of the acanthuroid fishes and their squamipinne relatives in relation to the proper phylogenetic placement of the unique epipelagic *Luvarus imperialis*. A substantial portion of the paper became devoted to an analysis of the larval characteristics of all of these acanthuroid and squamipinne-like fishes (Johnson) in comparison to the adults (Johnson, Collette, Tyler), as an adjunct to the anatomy of adult *Luvarus* (all of us). This paper thus has two goals—the description of the anatomy of *Luvarus* and the cladistic interpretation of the phylogeny of the acanthuroids and squamipinnes based on larval and adult synapomorphies.

With so many authors working on the project over such a long period of time, we realize that we have not been able to eliminate all traces of the composite nature of our efforts. For this we ask the indulgence of our readers.

Methods

Most of the osteological description in this paper is based on two cleared and counter-stained specimens, 79.2 and 301 mm SL. Sutures are much clearer on these specimens than on adults. The detailed description by Gregory and Conrad (1943) of a large dry skeleton eliminates the need for us to describe the osteology of adult *Luvarus* in detail. We hope that our descriptions and illustrations of the two small cleared and stained specimens are sufficiently detailed that they will not have to be repeated, regardless of the validity of our phylogenetic conclusions. Most specimens, larval and adult, were stained for both bone and cartilage.

The most detailed osteological description presented below is based on the 79.2 mm specimen, which produced a somewhat better cleared and stained preparation than the 301 mm specimen. This preparation also often shows the individual limits of bones more clearly than that of the 301 mm specimen, in which some bones already are becoming more fully sutured. Thus, study of the 79.2 mm specimen aids interpretation of the more consolidated structure found in the 301 mm specimen and especially in the larger dried skeletal specimens examined here and previously. Description of the 79.2 mm specimen is followed by progressively briefer comments on how each of the larger individuals studied differs from it.

A traditional and perhaps most widely understood nomencla-

ture for the bones is used here, although in cases where recent changes in names have been demonstrated to better express homologies, the more current terminology (such as in Weitzman, 1967 et seq.; Patterson, 1975; Parenti, 1981; Fink and Weitzman, 1982) is given in parentheses.

Institutional abbreviations follow the standard list of Leviton et al. (1985)

Material Examined

Luvuarus imperialis.—Cleared and Stained: MCZ 55287 (1, 5.8 mm SL). MCZ 55291 (1, 10.5 mm SL) W Atlantic, 42°24'N, 46°11'W, R/V *Atlantis II*, cruise 13, 9 Sep 1964, R.H. Backus 1021. MCZ 60721 (1, 19.2 mm SL) W Atlantic, 40°N, 61°W, TO-4. MCZ 59524 (1, 35.5 mm SL) W Atlantic, 32°53'S, 46°06'W, R/V *Atlantis II*, cruise 31, 1967. USNM 228612 (1, 79.2 mm SL) W Atlantic off SE Brazil, at about 25°00'S, from stomach of a tuna, Jan 1976, L.A. Zavala-Camin. USNM 231697 (2, ~84–119 mm SL) W Atlantic off SE Brazil (Santos), at about 23°00'S, from stomach of a tuna, Jan 1976, L.A. Zavala-Camin, smallest specimen badly digested and little more than a vertebral skeleton with posterior portion of head attached. SIO 79-281 (1, 301 mm SL) E Pacific S of Mexico in Guatemala Basin, 7°45'N, 98°04'W, M/V *Conquest*, tuna purse seine, 6 Feb 1975. ZMUT P1400 (1, 1720 mm SL) branchial apparatus only (see listing under alcohol-preserved specimens for data).

Dry Skeletons: USNM 230069 (1, ~980 mm SL, 1040 mm fork length = FL) NW Atlantic. CAS 13245 (1, ~485 mm SL) E Pacific off Santa Cruz, Calif., 10 Sep 1945, J. Strobeen (not recorded by Gotshall and Fitch, 1968, in their listing of E Pacific records of *Luvuarus*). LACM uncat. (1, ~1780 mm SL) no collection data. LACM 37052-1 (1, ~1140 mm SL) E Pacific off Newport Beach, Orange Co., Calif., Jul 1975, M. Birney. LACM 42597-1 (1, 1170 mm SL) E Pacific off Mexico, ~35 miles SW San Diego, Calif., 21 Sep 1981, A. West aboard the *Loretta Marie* (heart, gonads, branchial arches, one side of pectoral and pelvic fin alcohol preserved). USNM 296183 (1, 850 mm FL), Oregon, 3 mi N of Umpqua River Jetty, Dec 1987 (specimen received frozen).

Alcohol-Preserved Specimens: USNM 231696 (1, 63.6 mm SL) and IP uncat. (1, 115 mm SL) W Atlantic off SE Brazil (Santos), at about 23°00'S, from stomach of a tuna, 17 Mar 1976, L.A. Zavala-Camin. SIO 80-204 (1, 274 mm FL) E tropical Pacific, winter 1979. SIO 62-445 (1, 489 mm FL) E Pacific, 32°38'N, 117°57'W, 21 Aug 1962. SIO 59-351 (1, 1020 mm SL, 1075 mm FL) E Pacific off Ocean Beach, San Diego, Calif., 2 Sep 1959. FMNH 63116 (1, 121 mm SL) Mediterranean, Straits of Messina, 1960, G. Arena. LACM W 61/87-1 (1, 462 mm SL) E Pacific off east end of San Clemente Island, Calif., 1 Aug 1961, J. Califano. LACM W55/317-1 (1, 556 mm SL) E Pacific off Zuma Beach, Los Angeles, Calif., 12 Dec 1955, Y. Yoshioka. LACM 38416-1 (1, 610 mm SL) E Pacific. LACM 31754-1 (1, 240 mm SL) E Pacific, 70 mi off Point Telmo, Mexico, Feb 1971, purse seine by S. Giacalone aboard *Southern Queen*. LACM 36948-1 (1, 310 mm SL) E Pacific, 26 mi W of Cape Corrientes, Mexico, 16 May 1977, *Mawritania*. ZMUT P1400 (1, 1720 mm SL) Indian Ocean (~10°S, 70°E), Aug 1980. MCZ 55287 (1, 5.8 mm SL) W Atlantic, 41°31'N, 55°11'W, R/V *Atlantis II*, cruise 13, 5 Sep 1964, R.H. Backus 1010. MCZ 55288 (1, 13.6 mm SL) W Atlantic, 41°36'N, 52°21'W, R/V *Atlantis II*, cruise 13, 6 Sep 1964, R.H. Backus 1013. MCZ uncat. (1, 19.0 mm SL) W Atlantic, from Woods Hole Oceanographic Institution, "Berm. 86," no other data. MCZ 55291 (2, 18.5–20.2 mm SL) W Atlantic, 42°24'N, 46°11'W, R/V *Atlantis II*, cruise 13, 9 Sep 1964, R.H. Backus 1021. MCZ 59526 (1, 23.4 mm SL) W Atlantic, 36°39'S, 53°13'W, R/V *Atlantis II*, cruise 31, 19 Mar 1967, R.H. Backus 1442. MCZ 59525 (1, 29.1 mm SL) W Atlantic, 38°44'N, 71°53'W, R/V *Knorr*, cruise 58, sta 3, 31 Aug 1976, J.E. Craddock 76-33. MCZ 55003 (1, 158 mm SL) Mediterranean, Straits of Messina, Nov 1959, G. Arena.

Comparative Material, All Cleared and Stained (in mm SL)

ACANTHURIDAE.—*Acanthurus coeruleus*: USNM 240072 (1, 25.5); USNM 240075 (1, 18.0); USNM 240078 (1, 16.5). *Acanthurus trios-*

legus: USNM 218866 (1, 52.1); ANSP 109491 (7, 40.6–68.9). *Acanthurus xanthopterus*: USNM 196224 (2, 25.8–29.0). *Acanthurus* sp.: USNM 240072 (2, 8.7–10.2); MCZ uncat. (2, 5.1–7.5); MRRI 05821006, IKMT (1, 7.1). *Ctenochaetus* sp.: USNM 224345 (1, 40.0). *Naso fageni*: ANSP 103532 (1, 51.4). *Naso literatus*: ANSP 109497 (2, 111–209). *Naso thynnoides*: USNM 228361 (1, 128). *Naso unicornis*: USNM 259787 (1, 29.5); USNM uncat. (3, 53.0–55.0); ANSP 89114 (1, 267). *Naso* sp.: ANSP 108416 (1, 107); ANSP 108419 (1, 72.0); MCZ 63120 (6, 5.4–8.1); MCZ 63121 (5, 9.3–15.4). *Paracanthurus hepatus*: ANSP 108444 (1, 31.6); USNM 268913 (2, 79.1–83.0). *Prionurus laticlavus*: ANSP 81238 (3, 35.0–47.9). *Prionurus scalprum*: USNM 70753 (6, 24.5–42.8); ANSP 109770 (1, 44.3); ANSP 109553 (1, 110). *Zebrasoma flavescens*: USNM 109355 (1, 23.5); ANSP 109499 (1, 37.7). *Zebrasoma scopas*: USNM 245704 (1, 45.0). *Zebrasoma veliferum*: ANSP 109500 (1, 156).

CHAETODONTIDAE.—*Chaetodon lunulus*: no data (1, 31.4). *Chaetodon plebius*: no data (1, 42.2). *Chaetodon striatus*: ANSP 9118 (1, 44.6). *Chaetodon unimaculatus*: no data (1, 46.2). *Chelmon rostratus*: USNM 274681 (1, 77.0). Unidentified larvae: MRRI 6577284, 2N9 (1, 9.0); MRRI 05760339, 6B5 (3, 3.1–4.8).

CORACINIDAE.—*Coracinus multifasciatus*: USNM 274682 (1, 153).

DREPANIDAE.—*Drepane punctata*: USNM 143468 (1, 26.0); USNM 261421 (1, 48.8).

EPHIPPIDIDAE.—*Chaetodipterus faber*: USNM 196408 (1, 60.5); USNM uncat. (1, 29.2). *Ephippus orbis*: USNM 257868 (1, 93.1). *Parapsettus panamensis*: USNM uncat. (1, 102.0). *Platax pinnatus*: USNM uncat. (1, 59.1). *Platax orbicularis*: ANSP 56026 (1, 40.2). *Platax teira*: ANSP 109630 (1, 26.0). *Rhinoprenes pentanemus*: ANSP 134860 (1, 100). *Tripterodon orbicularis*: USNM 261384 (1, 45.0).

GIRELLIDAE.—*Girella elevaia*: USNM 269546 (1, 47.7). *Girella zebra*: USNM 269545 (1, 76.0). *Girella punctata*: USNM uncat. (2, 4.8–9.4).

KYPHOSIDAE.—*Kyphosus* sp.: USNM 218888 (1, 87.5); MRRI 0573088, 0753188, 0574220, 2N9 (18, 4.0–7.8).

MONODACTYLIDAE.—*Monodactylus argenteus*: USNM 258894 (3, 19.8–40.0); USNM uncat. (2, 2.9–4.0).

PENTACEROTIDAE.—*Pseudopentaceros richardsoni*: USNM uncat. (1, 142).

POMACANTHIDAE.—*Centropyge argi*: USNM uncat. (1, 14.5). *Centropyge lorculus*: USNM uncat. (1, 46.2). *Holacanthus ciliaris*: ANSP 91094 (1, 54.4). *Xiphopops* sp.: ANSP 108477 (1, 49.6). Unidentified larvae: MRRI 0573115, 2N9 (6, 3.2–4.8).

SCORPIDIDAE.—*Microcanthus strigatus*: SIO 61-146 (1, 80.8). *Scorpius chilensis*: USNM 218922 (1, 48.2).

SCATOPHAGIDAE.—*Scatophagus argus*: USNM 224393 (2, 54.4–55.0); AMS 1A.1811 (1, 9.7). *Selenotoca multifasciata*: USNM 245702 (1, 55.1).

SIGANIDAE.—*Lo vulpinus*: USNM uncat. (1, 79.0). *Siganus canaliculatus*: ANSP 77804 (1, 55.9). *Siganus corallinus*: ANSP 49224 (1, 139). *Siganus luridus*: USNM 218868 (2, 41.2–61.0). *Siganus* sp.: USNM 109355 (3, 16.0–31.5); MCZ 63119 (2, 7.7–9.7).

TOXOTIDAE.—*Toxotes jaculator*: USNM 270369 (1, 58.6).

ZANCLIDAE.—*Zanclus cornutus*: USNM 115008 (1, 66.4); USNM 274679 (1, 52.0); ANSP 109502 (2, 58.0–66.4); BPBM 9140 (1, 21.5); MCZ 62046 (1, 9.5).

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Anatomical Descriptions

79.2 mm SL

FIGURES 3-15

Skull

ORBITAL REGION.—*Frontal*: Wide posteriorly, tapering to a point anteriorly, where it overlies the large ethmoid cartilage (Figures 3-5); articulates through cartilage and fibrous tissue dorsally with the supraoccipital, whose posteroventral region it broadly overlies, and posteriorly with the epiotic; broadly separated from its opposite member on the dorsal surface of the skull by the supraoccipital and ethmoid cartilage; articulates posterolaterally through cartilage and slight interdigitation with the pterotic and sphcotic; articulates through cartilage ventromedially in the orbit with the pterosphenoid and lateral ethmoid; articulates anterolaterally by fibrous tissue with the medial surface of the posterior half of the nasal, which overlies it laterally.

Parietal: Absent in this and all larger specimens examined but present initially in larvae.

Lateral Ethmoid: Columnar, with the dorsal and ventral ends expanded and the middle moderately constricted (Figures 4-6); cartilage-filled at both ends and medially, with the thin perichondral ossification appearing as a U-shaped plate wrapped around the posterolateral columnar portion of the ethmoid cartilage anteriorly, laterally and posteriorly; this ossification makes no direct bony contact with other bones of the neurocranium.

Parasphenoid: A thin, dorsoventrally flattened shaft throughout most of its length, with a low vertical crest on its dorsal surface in the anterior region of the orbit (Figures 4-7). The parasphenoid articulates anteriorly with the ventral surface of the flattened posterior end of the vomer, and the ventral surface of the ethmoid cartilage, both of which overlie it. At the rear of the orbit it is laterally expanded and lateral wings extend to either side of the midline to interdigitate with the prootics. The posterior end is bifurcate where it articulates through cartilage and slight interdigitation with the basioccipital, forming the floor of the shallow posterior myodome.

Pterosphenoid: A large plate of bone, rounded dorsally, cartilage-filled along all of its edges except medially. The pterosphenoid articulates through cartilage anteromedially with its opposite member and laterally with the frontal; it articulates through cartilage and slight interdigitation posterolaterally with the sphenotic and posteriorly with the prootic.

Infraorbitals: Each infraorbital series consists only of the large lachrymal and a tiny, horizontally oriented plate-like ossification that lies directly below the eye. The latter bears no pores or canals, but its location and orientation suggest that it

represents a vestige of the subocular shelf borne on the third infraorbital of many perciforms, including some acanthuroids.

The lachrymal is a thin, vertically oriented, plate-like bone, rounded anteroventrally, where it partially covers the maxilla (Figure 4), and prolonged posteriorly into a long slender process that almost reaches the anteroventral border of the orbit. The lachrymal lies free in the skin, well forward of the lateral ethmoid, with which it does not articulate. A short, extremely slender prong extends posteroventrally between the major rounded anterior region of the bone and its posterior elongation. There is a small sensory pore just anterior to the base of this short prong. A horizontally oriented, serrate ridge extends anteriorly along the lateral surface from a point just above the sensory pore two-thirds of the distance to the anterior margin of the bone.

Ethmoid (= Mesethmoid): An enormous, rectangular ethmoid cartilage (not illustrated) forms the major mass of the neurocranium anterior to the orbit. The regions between the anterior half of the supraoccipital and the frontals, and the long space between the ethmoid and lateral ethmoid ossifications, with the nasals above, and the vomer and anterior end of the parasphenoid below, are occupied by ethmoid cartilage. The ethmoid ossification is present only as a thin, vertically oriented perichondral saddle that wraps around the anterior margin of the ethmoid cartilage between the lower half of the ventral processes of the nasals and the dorsal and anterior ends of, respectively, the maxilla and palatine.

Vomer: A thin, flat, horizontally oriented plate of bone lying along the anterior portion of the ventral margin of the ethmoid cartilage, somewhat laterally expanded and rounded anteriorly, and tapering posteriorly to a narrow shaft. The vomer articulates posteriorly with fibrous tissue with the parasphenoid, which it overlies.

Nasal: Each nasal is a thin, laterally compressed, L-shaped bone, with the shorter anterior process vertical. The nasal overlies and arches around the anterodorsal corner of the anteriorly truncate ethmoid cartilage and articulates syndesmotically at its posterior end with the anterior end of the frontal. On its lateral surface, throughout its length, the nasal bears a distinct open channel (laterosensory canal) formed by two parallel serrate ridges, the more lateral of these being continuous posteriorly with a similar serrate ridge on the frontal. Pores are present in the bone.

The double, elliptical nostrils (anterior larger than posterior) are located below the posterior end of the posterior process of the nasal bone, and the spacious nasal cavity contains a well-developed elongate olfactory rosette (see subsequent description).

OTIC REGION.—*Pterotic:* Thickened and flange-like laterally, expanded and more massive medially; cartilage-filled along all of its edges of synchondral articulation with the other cranial bones. The pterotic articulates anteriorly through cartilage and slight interdigitation with the frontal, whose posteroventral end it slightly overlies; articulates anterolater-

ally through cartilage and interdigitation with the sphenotic; articulates dorsally through cartilage and fibrous tissue with the ventral portion of the epiotic, which it broadly overlies; articulates ventrally through cartilage and interdigitation anteriorly with the prootic and posteriorly with the exoccipital; articulates posteromedially through extensive interdigitation with the anterior end of the intercalar. Along most of its ventral surface the pterotic bears a depression (hyomandibular fossa) that forms the main articular facet for the dorsal head of the hyomandibula (diarthrodic, or at least slightly movable). The anterior end of this depression lies in the cartilaginous area in the region of synchondral articulation between the prootic and sphenotic.

Sphenotic: Cartilage filled medially along all of its edges of synchondral articulation with the other cranial bones. The sphenotic articulates anterolaterally through cartilage and fibrous tissue with the posterolateral end of the frontal, which overlies it; articulates through cartilage and interdigitation posteriorly with the pterotic, while posterolaterally the sphenotic articulates by fibrous tissue with the anterolateral portion of the pterotic, which broadly overlies it; articulates broadly through cartilage ventromedially with the prootic; articulates broadly through cartilage and slight interdigitation anteromedially on its ventral surface with the posterolateral region of the pterosphenoid; articulates through cartilage dorsally with the epiotic, but this articulation is obscured from lateral view by the anterolateral extension of the pterotic, which broadly overlies the sphenotic in this region. Ventrally, the posteromedial edge of the sphenotic articulates through cartilage with the anterolateral region of the dorsal head of the hyomandibula (forms part of hyomandibular fossa).

Epiotic (= Epioccipital): Cartilage filled medially along all of its edges of articulation with the other cranial bones. The epiotic articulates through cartilage dorsomedially with the supraoccipital and through cartilage and fibrous tissue dorso-laterally with the posterodorsal end of the frontal, which broadly overlies it; articulates through cartilage, fibrous tissue and slight interdigitation ventrolaterally with the dorsal region of the pterotic, which broadly overlies it; articulates through cartilage and interdigitation ventromedially on its posterior face with the exoccipital; articulates through cartilage and slight interdigitation medially on its dorsal and posterior faces with its opposite member in the midline; just medial to a longitudinal upright flange it articulates by fibrous tissue on its dorsal face with the dorsal (anteriormost) process of the posttemporal.

Prootic: Cartilage filled along all of its edges of articulation with the other cranial bones. The prootic articulates through cartilage and interdigitation anterodorsally with the pterosphenoid; articulates through cartilage and slight interdigitation anterolaterally with the sphenotic; articulates through cartilage and extensive interdigitation laterally with the pterotic, posteriorly with the exoccipital, posteromedially with the basioccipital, and ventromedially with its contralateral

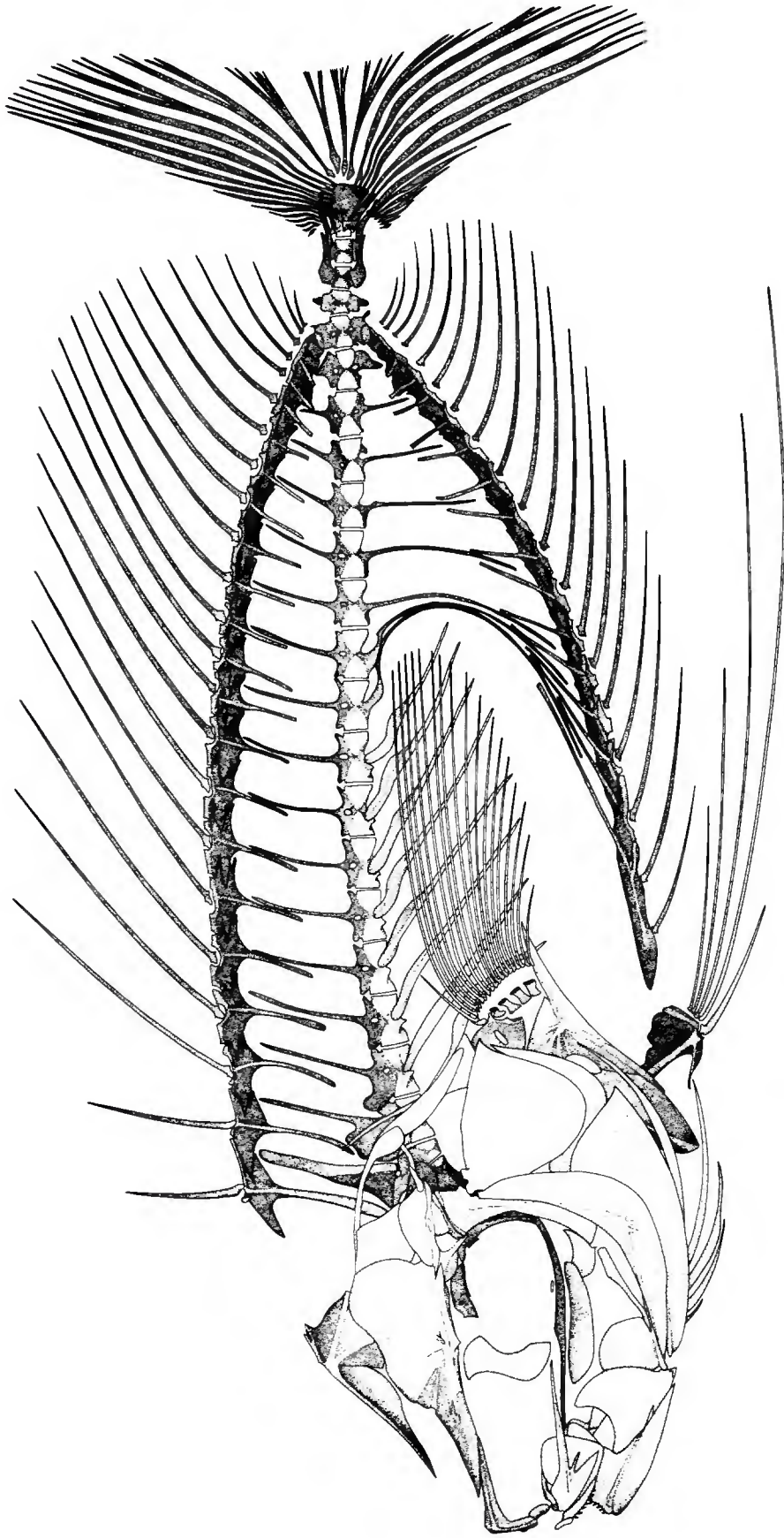


FIGURE 3.—*Luvarus imperialis*, USNM 228612, 79.2 mm SL, lateral view of entire skeleton.

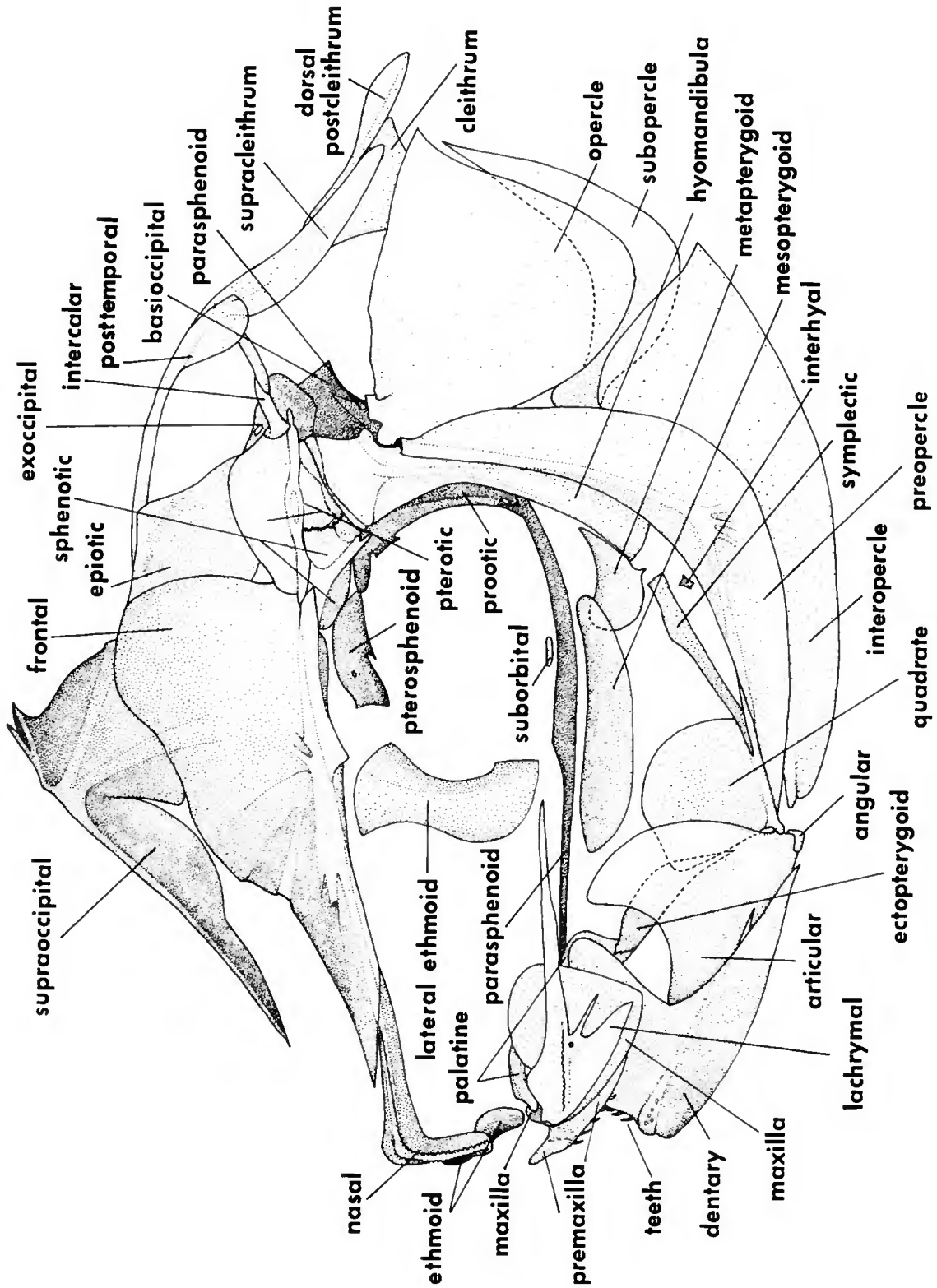


FIGURE 4.—*Luxilus imperialis*, USNM 228612, 79.2 mm SL, lateral view of skull (the two scale bones not shown).

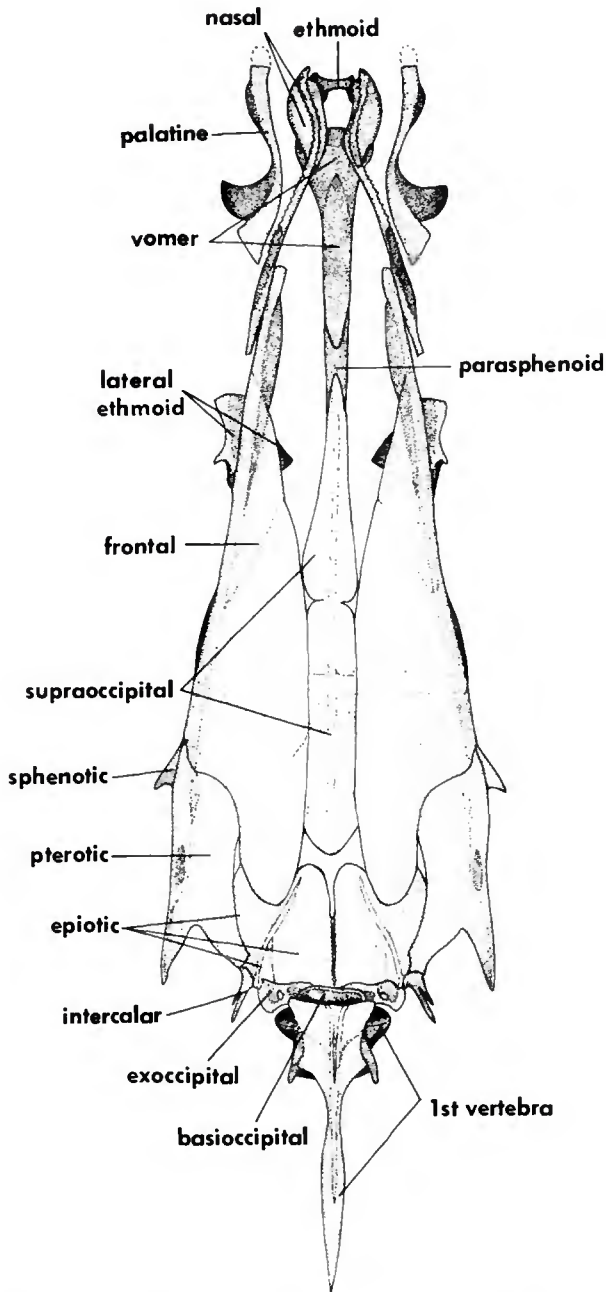


FIGURE 5.—*Luvarus imperialis*, USNM 228612, 79.2 mm SL, dorsal view of skull.

member, as well as to either side of the midline by broad interdigitation with the bifurcate dorsal flange of the parasphenoid at the rear base of the orbit. A shallow but complete posterior myodome is present in the posteroventral corner of the orbit, surrounded mostly by the prootic. The dorsal roof of

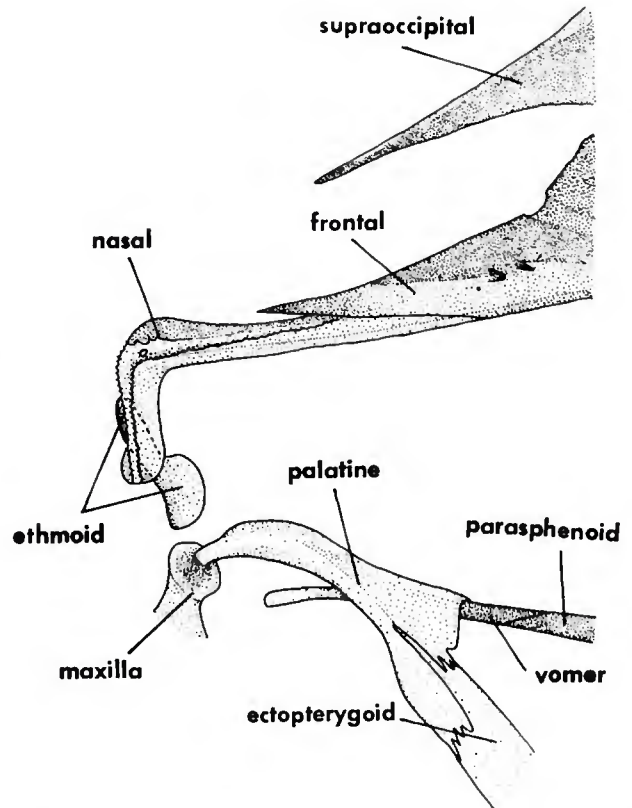


FIGURE 6.—*Luvarus imperialis*, USNM 228612, 79.2 mm SL, lateral view of ethmoid region, with lachrymal, premaxilla, and all but dorsal articular head of maxilla removed; dashed line on nasal represents course of ethmoid behind it.

the myodome is formed by medially projecting shelves of the prootics which interdigitate in the midline; the lateral walls of the myodome are formed by the ventromedial regions of the prootics; the floor of the myodome is formed by the parasphenoid from the region of its dorsal flanges, which interdigitate with the prootics at the posteroventral corner of the orbit, posteriorly to the bifurcate end of the parasphenoid, which surrounds the anterior prong of the basioccipital.

OCCIPITAL REGION.—*Basioccipital*: A short column with dorsolaterally projecting wings and an anteroventrally directed prong; cartilage-filled along its anterior margin. The basioccipital articulates by interdigitation dorsolaterally with the exoccipitals (Figure 7), anterolaterally through cartilage and slight interdigitation with the prootics, and anteriorly along the anteroventral prong through cartilage and some interdigitation with the slightly bifurcate posterior end of the parasphenoid. The rim of the round concave posterior end of the basioccipital articulates syndesmotically with the rim of the concave anterior face of the first vertebra. The area of articulation with the posterior end of the parasphenoid forms the extreme posteroventral wall of the shallow posterior myodome, but there is no distinctive channel apparent in the

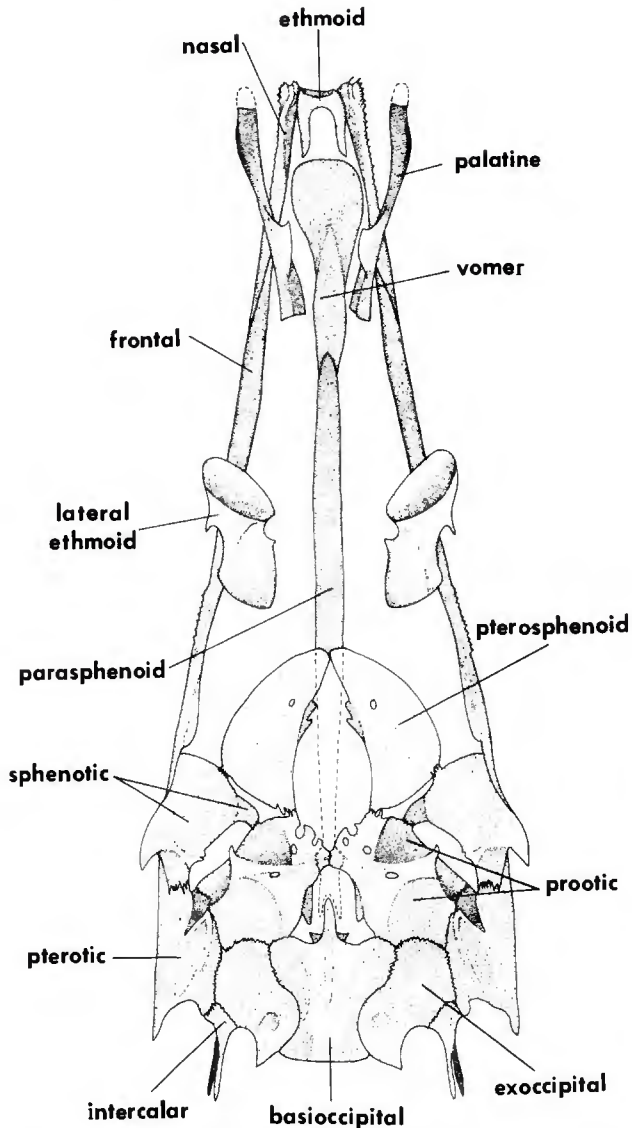


FIGURE 7.—*Luvarus imperialis*, USNM 228612, 79.2 mm SL, ventral view of skull, with posterior half of parasphenoid removed (indicated by dashed lines) to show the medial regions of pterosphenoids in posterodorsal wall of orbit and of prootics and anterior end of basioccipital on ventral surface of rear of skull.

region of the syndesmotic articulation between the basioccipital and parasphenoid that would form an opening into the posterior end of the myodome from the ventral surface of the skull. The anterior two-thirds of the ventral surface of the basioccipital bears a thin medial flange.

Exoccipital: Cartilage filled along most of its synchondral articulations with other bones; articulates by interdigitation (and cartilage internally) ventromedially with the basioccipital, anteroventrally with the prootic, dorso- and ventrolaterally with the pterotics, dorsally with the epiotics and posterolaterally entirely by interdigitation with the intercalar. Posteromedially

the exoccipitals are concave and form all of the walls of the foramen magnum. The exoccipitals bear medial extensions just above the posterodorsal surface of the basioccipital, which interdigitate with one another to form the floor of the posterior edge of the foramen; the concave posteromedial edges of the exoccipitals form the lateral walls of the foramen, above which medial projections from the exoccipitals meet their contralateral members to interdigitate and form the dorsal roof of the foramen. The extreme posteromedial region of the exoccipital has a short posterior prolongation forming a concave condyle for syndesmotic articulation with the similarly formed concave face of the anterolateral process of the first vertebra just above the region of the centrum. The posterior midline of the neurocranium has an elongate concavity above the foramen magnum in the region of articulation of the exoccipitals and epiotics with their opposite members; the anterior process of the neural arch and base of the neural spine is held firmly to this concave region by fibrous tissue.

Supraoccipital: A broad dome posteriorly that gradually narrows anteriorly into a long process with a thickened dorsomedial ridge (Figure 5); a thin sheet of bone extends ventrolaterally from the median ridge to overlie the ethmoid cartilage dorsolaterally; cartilage-filled along all of its ventral edges. The supraoccipital articulates through cartilage ventrally with the frontals, whose thin, sheet-like, dorsal extensions overlie it posteriorly, and posteromedially through a wide plate of exposed cartilage with the epiotics. Posterodorsally the supraoccipital is flattened into a thin medial flange only slightly thickened dorsally along the profile. The supraoccipital extends well forward anteriorly, with the anterior end reaching to about the level of one-third the distance between the tip of the snout and the orbit, or to the region where the anterior end of the frontal overlies the nasal.

SUSPENSORIUM (Figure 4).—Hyomandibula: Broad dorsally, tapering abruptly to a stout shaft which then gradually expands anteroventrally. The hyomandibula articulates at the cartilaginous dorsal end diarthrodially in the hyomandibular fossa formed by the sphenotic anterolaterally, the prootic anteromedially, and the pterotic posteriorly (about two-thirds of the articulation is with the pterotic). The posterior margin of the broad dorsal portion of the hyomandibula is expanded into a cartilage-tipped, rounded condyle that articulates diarthrodially with a concave facet on the anterodorsal margin of the opercle. The posterior edge of the anteroventral shaft articulates syndesmotically with the anterior margin of the preopercle; the ventral half of the anterior margin of this shaft is embraced syndesmotically by the bifurcate posterior margin of the metapterygoid; the ventral tip of this shaft articulates synchondrally with the symplectic and diarthrodially with the interhyal and metapterygoid.

Quadrate: Approximately square with a well-developed articular facet for the articular at its anteroventral corner. It articulates syndesmotically at the anterodorsal corner with the ectopterygoid and synchondrally along its posterodorsal mar-

gin through cartilage with the mesopterygoid. At its anterior end the symplectic is bound syndesmotically to the medial side of the quadrate along its ventral border (the anterior end of the symplectic behind the quadrate cannot be seen in Figure 4).

Metapterygoid: A relatively small thin plate, rounded anteriorly; cartilage-filled along its anterior and ventral edges. The metapterygoid articulates through cartilage anteriorly with the mesopterygoid, which slightly overlies it, ventrally with the symplectic and posteriorly with the hyomandibula, where it is also held syndesmotically by fibrous tissue along a non-cartilage-filled edge of the metapterygoid.

Symplectic: A long rod, somewhat stouter posteriorly (where it articulates through cartilage with the metapterygoid, hyomandibula and preopercle) than anteriorly (where it is held by fibrous tissue to the indentation on the posteroventral region of the quadrate); cartilage-filled at its anterior and posterior ends. The symplectic articulates dorsally with the sheet of cartilage between the quadrate, mesopterygoid, and metapterygoid.

PALATO-PTERYGOID REGION.—*Palatine:* The anterior portion a curved rod with a cartilaginous tip, the posterior portion expanded and longitudinally bifurcate (Figure 6); cartilage filled at its anterior and posterodorsal rami. The palatine articulates diarthrodially by fibrous tissue anteriorly with the cartilage-filled concave dorsal facet of the maxilla, medially syndesmotically with the rounded anterior region of the vomer, and the narrower posterior shaft of the latter, and through cartilage and fibrous tissue posterodorsally with the mesopterygoid. Posteroventrally the palatine overlies the anterodorsal end of the ectopterygoid, to which it is held syndesmotically by fibrous tissue and slight interdigitation.

Ectopterygoid: A thin plate, rounded posteriorly but nearly straight anteriorly. The ectopterygoid articulates by fibrous tissue and slight interdigitation anterodorsally with the posteroventral ramus of the palatine, which overlies it (see Figure 6 for details of palatine-ectopterygoid articulation), by fibrous tissue posteroventrally with the anterodorsal end of the quadrate, which it overlies, and through cartilage and fibrous tissue posteriorly with the mesopterygoid; all articulations are syndesmotical.

Mesopterygoid: An elongate plate, cartilage-filled along all of its ventral edge. The mesopterygoid articulates through cartilage anteriorly with the palatine and ectopterygoid, anteroventrally with the quadrate, ventrally with the symplectic, and posteroventrally with the metapterygoid, which it slightly overlies; all articulations are synchondral.

OPERCULAR REGION (Figure 4).—*Opercle:* A thin plate except anterodorsally, where it is expanded into a flange for muscle attachment and a knob-like condyle for diarthrodic articulation with the articular facet on the posterodorsal region of the hyomandibula. The opercle articulates by fibrous tissue ventrally with the subopercle, which it broadly overlies, and the dorsal edge of the interopercle.

Subopercle: A thin crescent-shaped (anterior edge con-

cave) plate, articulating with, and partially overlain by, the opercle dorsally, the preopercle anteriorly and the interopercle anteroventrally.

Interopercle: A large, thin, oblong plate, broad posteriorly, tapering gradually to a point anteriorly. The interopercle articulates by fibrous tissue posterodorsally with the subopercle, which it overlies, and the opercle; it is broadly held dorsally along most of its length by fibrous tissue to the preopercle, which overlies it. At a point just posterior to its midlength, a broad articular facet is borne on the medial side of the dorsal margin; the posterior end of the epiphyal articulates with this facet.

Preopercle: Crescent-shaped, with a slightly thickened ridge, enclosing the preoperculomandibular cephalic sensory canal along most of its length. Along the anterior half of its dorsal limb, the preopercle articulates by fibrous tissue with the hyomandibula; along the posterior half of its dorsal limb it overlies the opercle and subopercle. Ventrally, the preopercle overlies the dorsal edge of the interopercle along about three-quarters of the length of the former. Anteriorly, the dorsal margin of the preopercle articulates by fibrous tissue with the ventral margin of the quadrate.

UPPER JAW.—*Premaxilla:* A thin, gently curved, sickle-shaped bone, with a flange-like expansion at its anterodorsal end, representing the ascending articular process. The latter is bound by fibrous tissue to the ethmoid in a non-protrusible articulation and across the midline of the snout to its opposite member. The primary ramus is overlain along most of its length by the maxilla, and articulates diarthrodially by a somewhat consolidated band of fibrous tissue from its extreme ventromedial surface with the dorsolateral surface of the dentary. About eight or nine delicate, slightly curved, tiny conical teeth are present in a single row along the anteroventral edge of each premaxilla, with those toward the symphysis being the largest and most closely spaced.

Maxilla: A large flat plate, except anterodorsally where it is constricted into a cup-like diarthrodic articular facet that embraces the articular head of the premaxilla anteriorly and is attached posteriorly by fibrous tissue to the anterior end of the palatine, around which it rotates when the mouth opens. The maxilla articulates by fibrous tissue dorsomedially with the plate-like medial flange of the head of its opposite member, and anterodorsally with the posterior margin of the articular head of the premaxilla. Anteromedially it articulates by fibrous tissue with the posterolateral surface of the primary ramus of the premaxilla, which it overlies; laterally it articulates by fibrous tissue with the medial surface of most of the body of the lachrymal (except for the posterior two-thirds of its posterior prolongation), which broadly overlies it; ventromedially it articulates by a somewhat consolidated band of fibrous tissue with the dorsolateral surface of the dentary, with this same band continuing anteriorly between the premaxilla and dentary.

LOWER JAW.—*Dentary:* A large, flat, relatively thin plate, except anteroventrally where it is expanded medially into a

vertical flange for syndesmotic articulation with the similarly strengthened flange of its opposite member, and laterally along its surface where it bears a ridge of increasing height and strength anteriorly, that encloses the preoperculomandibular sensory canal. The posterior plate-like region is expanded posterodorsally and posteroventrally to form a broadly concave region on part of whose medial surface the anterior end of the articular is syndesmotically held by fibrous tissue, with the dentary only slightly overlying the anteroventral surface of the articular. The dorsolateral surface of the dentary connects by a somewhat consolidated band of fibrous tissue with the lower ventromedial surfaces of the premaxilla and maxilla. About six to eight delicate, slightly curved, tiny conical teeth similar to those of the premaxilla are present in a single row along the anterodorsal edge of each dentary, with those toward the symphysis being the largest and most closely spaced. Dorsolaterally along the toothed edge of the dentary, in the region where the teeth are most widely spaced and less regularly placed, the edge of the dentary is irregularly rugose or pitted, suggesting the former presence of small teeth.

Articular (= Anguloarticular): A thin flat plate thickened posteroventrally into a facet for diarthrodic articulation with the head of the quadrate and ventrally for syndesmotic articulation with the medial surface of the posterior arm of the dentary; cartilage-filled along a limited portion of its anterior edge and at the extreme posteroventral edge; articulates through cartilage and fibrous tissue at its extreme posteroventral end with the angular. The sesamoid articular is a small ossification held by fibrous tissue to the middle of the medial surface of the articular and connected posteriorly by a ligament to the quadrate region.

Angular (= Retroarticular): A small block of bone bound anterodorsally by fibrous tissue and slight interdigitation to the posteroventral corner of the articular and connected posteriorly by a ligament to the anterior end of the interopercle.

HYOID APPARATUS (Figure 8).—Basihyal: A large block of glossohyal cartilage forms the core of a prominent tongue protruding from the floor of the mouth, with a cone-shaped (narrow end posterior) perichondral ossification around its posterior end. The basihyal ossification articulates posteriorly through cartilage and fibrous tissue with the anterior end of the

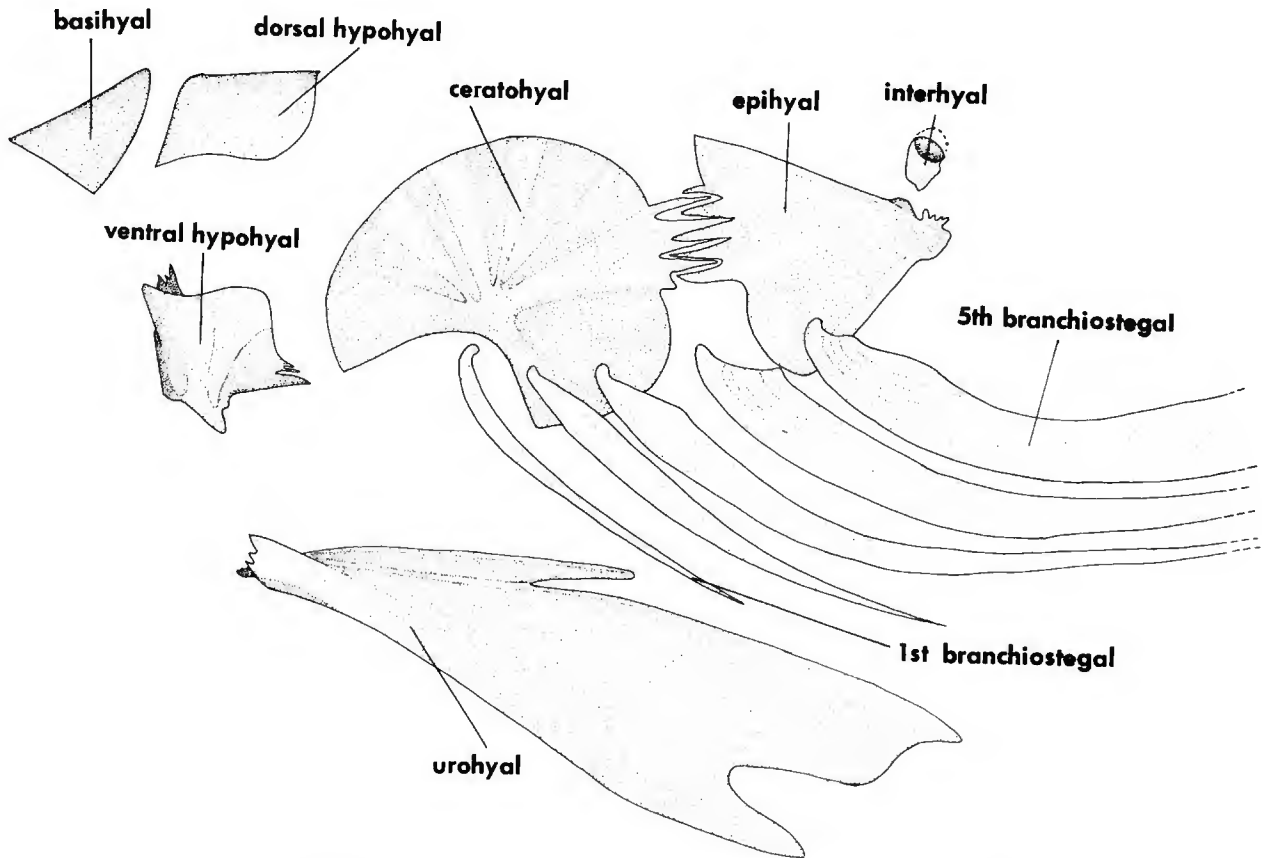


FIGURE 8.—*Luvarus imperialis*, USNM 228612, 79.2 mm SL, lateral view of hyoid arch and urohyal (full length of more posterior branchiostegal rays not shown).

first basibranchial, and posterolaterally by fibrous tissue with the medial region of the posterodorsal edge of the dorsal hypohyal.

Hypohyals: Dorsal hypohyal cartilage-filled at its ventral and posterior edges; ventral hypohyal cartilage-filled at its dorsal and posterior edges. The dorsal and ventral hypohyals articulate synchondrally with one another and with the anterior end of the ceratohyal; anteromedially, they articulate by fibrous tissue with their opposite members. The dorsomedial region of the dorsal hypohyal articulates with the region of articulation between the basihyal and first basibranchial; the dorsomedial and posteroventral edges of the ventral hypohyal bear irregular projections that foreshadow sutures with the dorsal hypohyal and the ceratohyal, found in adult specimens. Along the anterior region of its ventral edge, the ventral hypohyal bears a thickened region to which attaches a short ligament from the anterior end of the urohyal.

Ceratohyal (= Anterior Ceratohyal): A large rounded plate, convex dorsally and concave anteroventrally; cartilage-filled along all of its edges except in the concave anteroventral margin. The ceratohyal articulates anteriorly through cartilage with the dorsal and ventral hypohyals, posteriorly through cartilage and strong interdigitation with the epihyal, and along the middle of the ventral edge of its concave anteroventral margin by fibrous tissue with the head of the first branchiostegal ray. The anterior ends of the second and third branchiostegal rays are borne along the posterolateral surface of the ceratohyal. A fenestra or ceratohyal window (beryciform foramen) is lacking.

Epihyal (= Posterior Ceratohyal): A large triangular plate (apex posteriorly), thickened posterodorsally and posteroventrally; cartilage-filled at its anterior and extreme anteroventral edges, as well as at the extreme posterior end of the dorsal edge where it is laterally expanded into a cup-shaped (concave dorsally), cartilage-filled facet for diarthrodic articulation through cartilage and fibrous tissue with the interhyal. The epihyal articulates anteriorly through cartilage and strong interdigitation with the middle of the posterior end of the ceratohyal. The fifth branchiostegal ray is borne laterally on the ventral margin of the epihyal.

Interhyal: Short, columnar; cartilage-filled at its concave dorsal and ventral tips. The interhyal articulates diarthrodially through cartilage and fibrous tissue ventrally with the facet on the posterodorsal edge of the epihyal, and attaches dorsally by fibrous tissue to the cartilaginous plate and fibrous tissue sheet between the symplectic, metapterygoid, hyomandibula, and proopercle.

Branchiostegal Rays: Five rays, increasing in length and breadth posteriorly in the series; all relatively flattened blades. The branchiostegals articulate by fibrous tissue to the ceratohyal (first ray to ventral edge of anteroventral concavity, second and third rays to posterolateral surface) and epihyal (fifth ray to anterolateral surface) or to the cartilaginous plate between the posteroventral end of the ceratohyal and the

anteroventral end of the epihyal (fourth ray).

Urohyal: A large flat, vertically oriented plate; thickened along its dorsal edge and at its anterior end, where it bifurcates slightly into two prongs, from which arise the ligaments attaching the urohyal to the medial surfaces of the posteroventral processes of the ventral hypohyals. The urohyal is connected along its dorsal edge by fibrous tissue to the ventral surface of the basibranchial region.

Gill Arches

FIGURES 9, 10

All the elements are cartilage-filled at their articular tips and the synchondral articulations usually are diarthrodic. There are three median basibranchials, three pairs of hypobranchials, five pairs of ceratobranchials, four pairs of epibranchials, and four pairs of pharyngobranchials (infrapharyngobranchials, the first a toothless suspensory element and the other three toothed). Gill filaments are borne on the first four arches. The pseudobranch is well-developed, with about 22 lamellae.

First Arch: Basi-, hypo-, cerato-, epi-, and pharyngobranchial elements present. First basibranchial short and somewhat laterally compressed, its anterior end bent so that ventrally it lies below and articulates with the posterior tip of the basihyal; a deep groove bordered by a low ridge on either side of the midline extends anteriorly and posteriorly from the region of ventral flexion, more laterally expanded and cone-shaped posteriorly. Posteriorly, the first basibranchial articulates with the anterior end of the second basibranchial and the anteroventral ends of the first hypobranchials.

First hypobranchial the largest of the hypobranchial elements, which decrease in size posteriorly in the series; rod-like with a posteromedially directed flange extending along about the anterior half of its length; articulates mainly with the anterolateral edge of the second basibranchial and the cartilaginous region between the first and second basibranchials.

First ceratobranchial subequal in length to second through fourth ceratobranchials; a rounded shaft throughout its length, slightly constricted in the region about one-third along its length posterodorsally, where there is a low flange.

First epibranchial a stout rod ventrally, bifurcating dorsally into a longer anterior ramus and a shorter posterodorsal arm, or uncinat process, with thin laminae between the three major cylindrical arms; cartilaginous anterior arm tip connected by a band of fibrous tissue to the cartilaginous ventral tip of the first pharyngobranchial. A rod-like interarcual cartilage (Figure 10) extends between the cartilaginous tip of the uncinat process and the anterodorsal cartilaginous tip of the second pharyngobranchial.

First pharyngobranchial (suspensory pharyngeal) a narrow, cylindrical rod, slightly expanded ventrally, where it articulates through cartilage and fibrous tissue with the anterior arm of the first epibranchial; distally (dorsomedially) it is held by fibrous

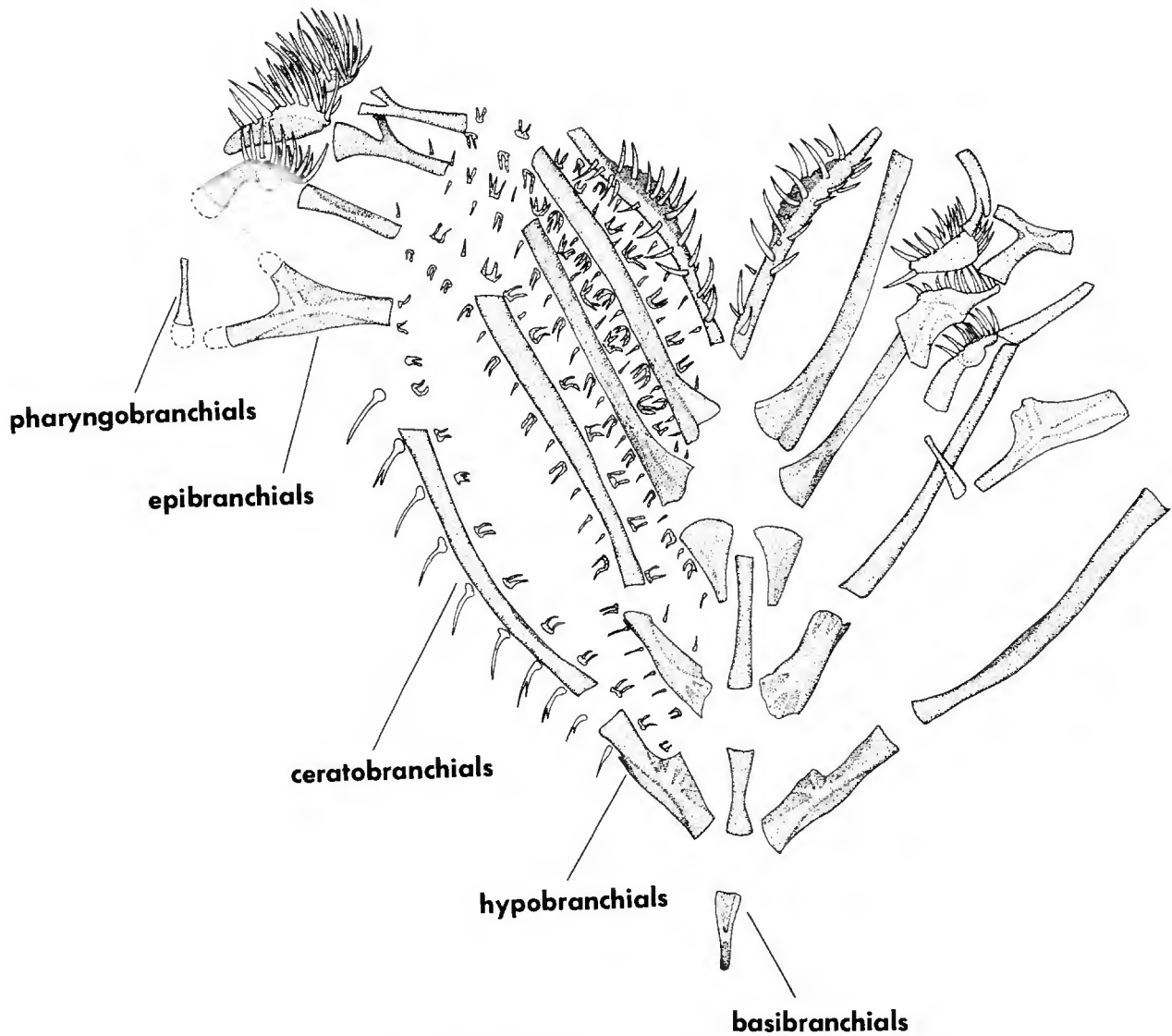


FIGURE 9.—*Luvarus imperialis*, USNM 228612, 79.2 mm SL, dorsal view of branchial arch bones (extended on right side; interarcual, basihyal, and glossohyal cartilages not shown).

tissue to the neurocranium in the region of articulation between the dorsolateral wings of the parasphenoid and the prootic.

Gill rakers present along the anterior and posterior edges of the first arch, about three times longer along the anterior edge than posteriorly; about ten rakers along the anterior edge, becoming slightly shorter anteroventrally; most of the rakers with one or two elongate, conical teeth, syndesmotically articulated to a conical basal plate; uppermost raker of anterior series placed at the angle of the arch, about half way between the epibranchial and ceratobranchial, and the lowermost anterior raker placed at the upper (lateral) region of the first

hypobranchial; uppermost raker of posterior series placed at base of first epibranchial and lowermost raker placed at middle of posterior edge of first hypobranchial.

Second Arch: Basi-, hypo-, cerato-, epi-, and pharyngobranchial elements present. Second basibranchial a short stout rod, slightly longer than the first but shorter than the third, slightly constricted in the middle but otherwise relatively simple; articulates anteriorly with the first basibranchial, anterolaterally with the first hypobranchials, posteriorly with the third basibranchial and posterolaterally with the second hypobranchials.

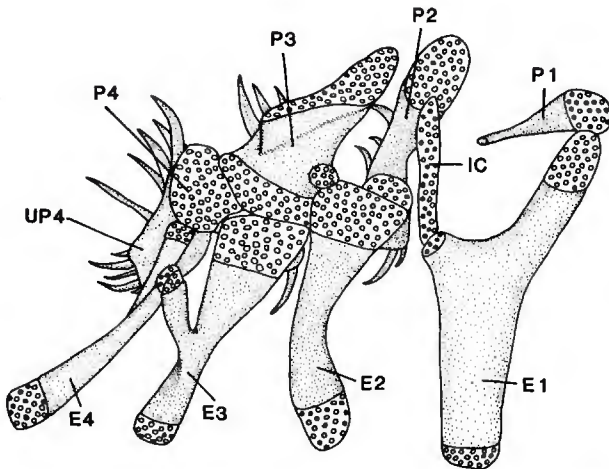


FIGURE 10.—*Luvarus imperialis*, USNM 228612, 79.2 mm SL, dorsal view of dorsal gill arch skeleton, right side. (E1-4 = epibranchials 1-4; IC = interarcual cartilage; P1-4 = pharyngobranchials 1-4; UP4 = upper pharyngeal tooth plate.)

Second hypobranchial with a central rod-like portion constricted near the middle, with flanges extending anteriorly and posteriorly from the rod; articulates anteriorly with the ventrolateral surface of the cartilaginous area of articulation between the second and third basibranchials; articulates posteriorly with the second ceratobranchial. The second ceratobranchial is rod-like throughout its length and articulates anteriorly with the second hypobranchial and posteriorly with the second epibranchial. The second epibranchial is a somewhat compressed, slightly bent rod with a small flange along its anterodorsal surface; its cartilaginous anterodorsal tip is expanded and articulates with a cartilage-tipped process on the dorsal surface of the second pharyngobranchial and a cartilaginous condyle on the dorsolateral margin of the third pharyngobranchial.

The second pharyngobranchial bears about eight elongate, conical, slightly curved, teeth, set in shallow sockets and articulated at their basal pedicles, in an anterior row, and about four slightly smaller but similar teeth behind them in a posterior row. The pharyngeal teeth are similar in form to those in the primary jaws, but approximately three or four times longer. The tooth-bearing surface and tooth rows are oriented approximately perpendicular to the longitudinal body axis. The tooth-bearing portion (tooth plate) of the second pharyngobranchial bears a cartilaginous condyle on its dorsal surface for articulation with the cartilaginous tip of the second epibranchial; a large, cartilage-filled columnar process extends anterodorsally from the anteromedial corner of the tooth plate; the expanded cartilaginous tip of this process is connected to the uncinat process of the first epibranchial via the interarcual cartilage

Gill rakers similar to those of the first arch are borne along

the anterior and posterior edges of the second arch; about equal in length along both edges.

Third Arch: Basi-, hypo-, cerato-, epi-, and pharyngobranchial elements present. Third basibranchial a long simple rod; articulates anteriorly with the second basibranchial, and anterolaterally with the second hypobranchial; posteriorly, it extends below the third hypobranchial, where its cartilaginous tip bends sharply downward and is connected by fibrous tissue to the ventral surface of the third hypobranchials and the dorsal surface of the urohyal. Third hypobranchial triangular, with the narrow apex directed anterovertrally, where its elongate cartilaginous tip is connected beneath the third basibranchial by fibrous tissue to its opposite member and the dorsal edge of the urohyal. Posteriorly, there is broad synchondral articulation with the opposite member and the anterior tip of the third ceratobranchial. Third ceratobranchial rod-like, expanded anteriorly; articulates anteriorly with the third hypobranchial and posteriorly with the third epibranchial. Third epibranchial Y-shaped, the simple rod-like posteroventral end bifurcating anterodorsally to form a slightly longer, stouter, and distally expanded anteromedial arm that articulates broadly with the cartilage-filled posterior margin of the third pharyngobranchial, and a shorter, narrower, medially directed arm that articulates with the short arm of the bifurcate anterodorsal end of the fourth epibranchial. Third pharyngobranchial a relatively large, cup-shaped (concave dorsally) element with a broad cartilage-filled posterior margin, a cartilage-filled condyle on the dorsomedial margin (for articulation with the second epibranchial) and a large cartilage-filled columnar process directed anteriorly from the anteromedial corner of its tooth-bearing surface; the latter process bears a vertically oriented flange along most of its length and extends along the medial side of a similar process on the second pharyngobranchial, with which its cartilaginous tip articulates. The ventral surface of the third pharyngobranchial bears a transversely oriented row of about 15 irregularly placed teeth, similar in size and form to those of the second and fourth pharyngobranchials.

Gill rakers, similar in form to those of the other arches, are borne along the anterior and posterior edges of the third arch, all being of about equal length.

Fourth Arch: Basi- (cartilaginous), cerato-, epi-, and pharyngobranchial elements present. The fourth basibranchial is a short, centrally constricted, unossified rod of cartilage, articulating anteriorly at the medial junction of the cartilaginous posterior ends of the third hypobranchials and posteriorly with the medial junction of the cartilaginous anterior ends of the fourth ceratobranchials. Like the third ceratobranchial, the fourth ceratobranchial is rod-like along most of its length, with a spatulate expansion anteriorly; the cartilaginous anterior tip articulates with its opposite member in the midline and with the fourth basibranchial just anterior to this; the posterior tip articulates with the fourth epibranchial. Fourth epibranchial a simple rod posteroventrally where it articulates with the fourth ceratobranchial, bifurcating anterodorsally into a slightly

longer and stouter anteromedial arm, which articulates with the fourth pharyngobranchial, and a smaller dorsally directed uncinuate process, which articulates with the short uncinuate process of the bifurcate dorsal end of the third epibranchial. Fourth pharyngobranchial the smallest of the three toothed upper pharyngeals, consisting of a tooth-bearing portion, and a large block-shaped cartilage on the dorsal surface of the tooth plate. The cartilage articulates anteriorly with the cartilage-filled posterior margin of the third pharyngobranchial and posterolaterally with the cartilaginous tip of the fourth epibranchial. The tooth plate bears about 22 teeth, similar in form to those of the other pharyngobranchials, in an irregular cluster.

Gill rakers present along the anterior and posterior edges of the fourth arch, similar in length, placement, and form along both sides.

Fifth Arch: Ceratobranchial (lower pharyngeal) element only. Fifth ceratobranchial a slender rod with a horizontal, medially directed, cancellous laminar expansion along approximately the middle half of its length. Its long, cartilaginous anterior tip articulates with that of its opposite member medially and with the posteroventral surface of the cartilaginous tip of the fourth ceratobranchial anteriorly; its cartilaginous posterior tip articulates by a fibrous tissue band to the region between the cartilaginous ventral end of the fourth epibranchial and fourth ceratobranchial. It bears on its dorsal surface about 20 long, slender, sharp-pointed teeth (similar in size and form to those of the three toothed pharyngobranchials), about 8 of them more or less in an anterior row and the others less regularly clustered along the rear of the bone, especially on the medial flange. Gill rakers present only along the lateral edge of the bone; mostly simple, similar in form to those on the other arches.

Pectoral Girdle

FIGURE 11

Extrascapular Bones: Two, each bearing laterosensory canals. The medial extrascapula is a simple vertically oriented tube with an opening at each end; the lateral extrascapula, located directly below the medial, is Y-shaped, with an opening at each of its three ends (extrascapulas not shown in illustrations).

Posttemporal: A laminar plate, rounded ventrally and extending anterodorsally as a long, flattened ramus to articulate syndesmotically with the dorsal surface of the epiotic just medial to the dorsolateral ridge of that bone. A shorter anteroventral process extends from the medial surface of the laminar plate to articulate syndesmotically with the posterior end of the intercalar. The posteroventral border of the laminar plate overlies and is syndesmotically bound to the lateral surface of the dorsal end of the supracleithrum. There is no laterosensory canal in the posttemporal.

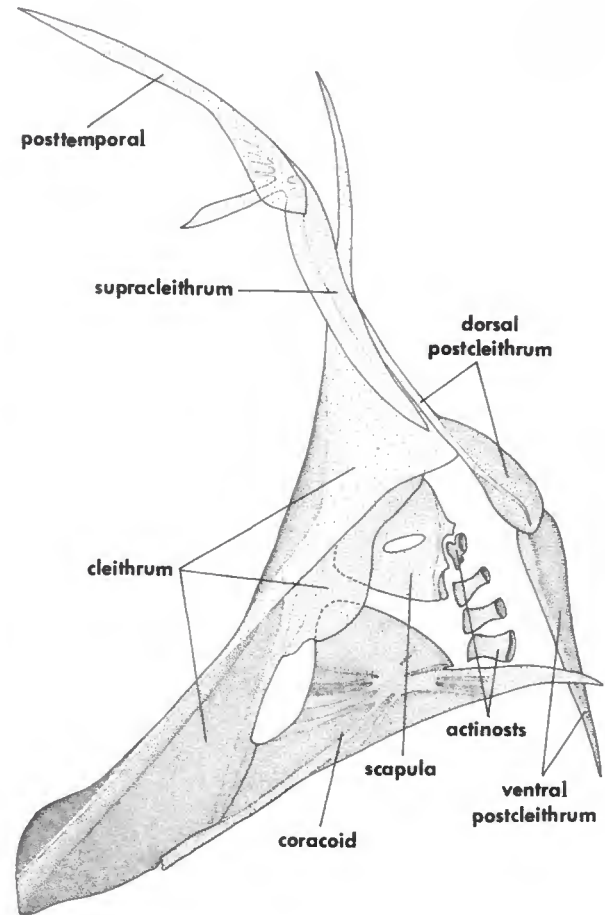


FIGURE 11.—*Luvarus imperialis*, USNM 228612, 79.2 mm SL, lateral view of pectoral girdle (dashed lines show portions of scapula and coracoid overlain by cleithrum).

Intercalar: A relatively short horizontal rod, tapered posteriorly where it articulates by fibrous tissue and slight interdigitation with the ventral process of the posttemporal, but expanded anteriorly where it articulates by interdigitation with the exoccipital medially and the pterotic laterally, in all cases syndesmotically.

Supracleithrum: A blade-like bone with a low keel-like ridge along most of the length of its medial surface, obliquely oriented with respect to the long axis of the body. Dorsally, it articulates with the posteroventral medial surface of the posttemporal, as described above. The entire length of the medial surface of the supracleithrum is syndesmotically bound to the lateral surface of the dorsal ramus of the cleithrum. The supracleithrum bears no laterosensory canal.

Cleithrum: The blade-like dorsal ramus tapers to a point at its dorsal tip and is bound to the medial surface of the supracleithrum along its entire length. The midportion is

broadly expanded; its medial surface articulates syndesmotically with the anterior third of the scapula, which it broadly overlies, and with the anterodorsal end of the coracoid. The posterior margin of the expanded midportion turns laterally as it continues ventrally to form the laterally directed wing of the ventral ramus; a broad, posteriorly directed wing extends from the medial edge of this lateral wing. The posterior margin of the posterior wing articulates syndesmotically with the ventral ramus of the coracoid. Ventrally, the posterior wing of the ventral ramus is broadly attached by connective tissue to its opposite member.

Postcleithra: Two elements, together forming a moderately developed strut extending from the posterodorsal region of the main body of the cleithrum along the abdominal wall musculature to a point just ventral to the posterodorsal ramus of the coracoid. The dorsal postcleithrum is expanded into a thin rounded plate ventrally where it overlies and is held by fibrous tissue to the similarly expanded and slightly rounded dorsal region of the ventral postcleithrum. The main shaft of the dorsal postcleithrum is bound by fibrous tissue along the posterodorsal edge of the cleithrum.

Coracoid: Reminiscent of the hyomandibula in shape, but with a long, laminar, posteriorly tapering process extending from its posterodorsal corner to a point just posterior to the bases of the ventralmost pectoral fin rays. The rod-like anteroventral ramus is expanded dorsally and articulates along its anterior margin with the cleithrum; its ventral end cartilage-tipped. The coracoid is cartilage-filled dorsally, where it articulates synchondrally with the scapula. The cartilaginous posterodorsal margin of the coracoid articulates with the cartilaginous proximal ends of the three ventralmost actinosts.

Scapula: A laterally compressed plate, thickened along its posterior edge where it bears a short process below which is a concave articular facet for the first actinost; below this is another concavity that receives the dorsal portion of the cartilaginous base of the second actinost. Dorsal to the short process there is an articular facet for the first pectoral fin ray. A central, oval scapular foramen is completely surrounded by bone. The anterior portion of the scapula is overlain by and articulates syndesmotically with the cleithrum. The cartilage-filled ventral portion of the scapula articulates synchondrally with the coracoid.

Actinosts (= Proximal Radials): Four, increasing in size from the first (dorsalmost) to the fourth. The first is cartilage-filled distally but not proximally, where it articulates diarthrodistally with the scapula. The remaining three actinosts are cartilage-filled at the proximal and distal tips and are hour-glass shaped. Proximally, these three actinosts articulate with the posterior margin of the coracoscapular cartilage. The dorsal portion of the proximal base of the second actinost also articulates with the ventral corner of the scapula. Distally, the actinosts articulate with the distal radials of all the pectoral fin rays, except the first.

Fin Rays: Eighteen on each side, all bilaterally divided,

unbranched, and unsegmented. The first (dorsalmost) is much shorter than the others and the base of its medial half is greatly enlarged and extends laterally to form a condyle that articulates with an articular facet on the scapula. The bases of each of the remaining pectoral-fin rays each embrace a cartilaginous distal radial; the distal radials articulate proximally with the cartilaginous distal tips of the four actinosts. The bases of the lateral and medial halves of each ray are expanded for muscle attachment; the expansions on the medial halves (not shown in Figure 18) are several times longer than those on the lateral halves. The lateral halves of all but the first and last ray bear serrae along the proximal one-third or less of their length (not shown in Figure 18).

Pelvic Girdle

FIGURE 12

Pelvis: Approximately triangular, comprising two vertically oriented, laterally compressed plates along the anteroventral margin of which two stout shafts extend anterodorsally between the cleithra, so they lie at an angle of about 45° to the long axis of the body. Each shaft is bound by connective tissue to the medial surface of the cleithrum lateral to it and terminates anteriorly in a cartilaginous tip that contacts that of its opposite member. The flat plates are bound together medially by connective tissue but do not make bony contact. Each shaft terminates posteriorly at the ventral corner of the plate where there is a large facet for diarthrodic articulation of the pelvic spine. A slender, horizontally oriented process, apparently representing the subpelvic keel, extends anteriorly from this point; its length is about one-third of the primary ramus (stout shaft). The ventral half of the posterior margin of the flat plate is cartilaginous and articulates with the bases of the four soft pelvic-fin rays.

Pelvic Spine: Relatively short and slender; approximately X-shaped in cross-section, with the lateralmost ridge bearing well-developed serrations along the proximal two-thirds of its length; the dorsalmost and ventralmost ridges bear a few serrations near the base (serrate ridges not shown in illustrations). The base of the spine expands to form an articular surface for diarthrodic articulation with the facet at the ventral corner of the pelvic girdle.

Fin Rays: There are four long, thin, soft rays, each bilaterally divided, unbranched and unsegmented. The first ray is the longest, extending posteriorly past the base of the last anal fin ray; the other rays are progressively shorter, the fourth (innermost) ray extending posteriorly to about the level of the base of the third anal-fin ray. The bases of all four rays are slightly expanded for muscle attachment and articulate with the cartilaginous vertically oriented border of the pelvic girdle. There are no distal radials. The lateral halves of all four rays are weakly spinulose proximally (not shown in illustrations).

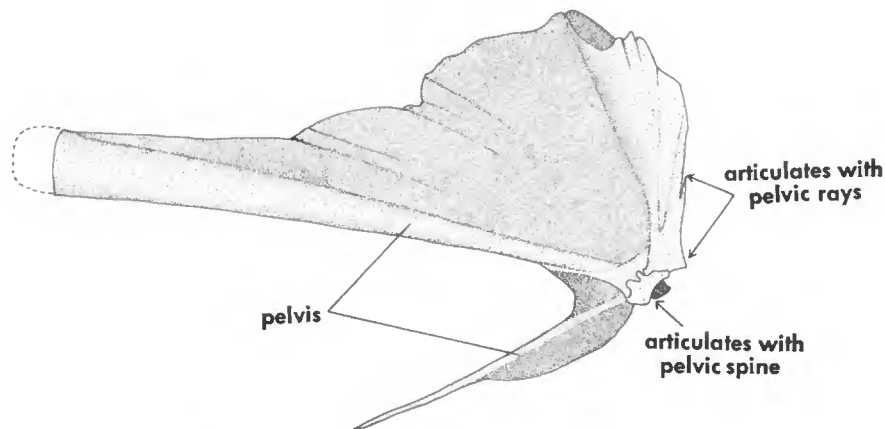


FIGURE 12.—*Luvarus imperialis*, USNM 228612, 79.2 mm SL, lateral view of pelvis.

Vertebral Column

FIGURE 3

There are 22 vertebrae, 9 precaudal and 13 caudal. With the exception of the terminal urostylar centrum, all centra are amphicoelous. All except the urostylar and second preural vertebrae have a bony roof over the neural canal and a median, undivided neural spine. All centra are bound to one another by fibrous connective tissue.

The centrum of the first vertebra is about half the length of the centra of the succeeding vertebrae. Anteriorly the first vertebra bears three articular facets, that of the centrum proper, which articulates with the centrum-like posterior end of the basioccipital, and a pair of larger cartilage-filled facets dorsolaterally that articulate with the exoccipital condyles. Posteriorly, the first centrum articulates with the rounded rim of the anterior end of the second centrum. The neural spine of the first vertebra is greatly expanded anteroposteriorly. Ventrally, it is fused with the closed neural arches, which in turn are fused narrowly with the centrum anteriorly at the dorsomedial edges of the facets that articulate with the exoccipital condyles. The neural arches are expanded anteriorly and slanted obliquely forward, and so they, and the main body of the neural spine, actually lie anterior to the centrum. The anterior margin of the first neural spine is bound by a connective-tissue sheet to the posterior midline of the neurocranium. The first neural spine reaches dorsally to the interlocking processes of the first and second dorsal pterygiophores.

The neural spines of the remaining precaudal vertebrae are slightly shorter and very slender. The neural arch of the second vertebra is greatly expanded anterodorsally, like that of the first. There is a well-developed prezygapophysis extending forward well beyond the level of the anterior edge of the centrum, where it is bound by fibrous connective tissue to the posterior margins of the neural spine and neural postzygapophysis of the first vertebra. The neural postzygapophysis of the

second vertebra is better developed than that of the first or third vertebrae, making broad contact with the neural prezygapophysis of the third vertebra, which overlies it posterodorsally. The neural pre- and postzygapophyses of the fourth and subsequent vertebrae are notably smaller. Haemal pre- and postzygapophyses, arches, and spines are lacking on all of the precaudal vertebrae.

Long, relatively stout, pleural ribs with a laminar expansion along the dorsal half of their length are present on the third to ninth precaudal vertebrae. They become progressively shorter posteriorly. The proximal tip of each rib inserts into a lateral pit in each centrum in a diarthrodic articulation. A thin, triangular flange extends anteroventrally from each pit, providing an oblique shelf on which the expanded head of each rib rests and to which it is bound by fibrous connective tissue. The distal tips of the pleural ribs are cartilaginous. There are no epipleural ribs.

The tenth (first caudal) vertebra bears the first haemal arch and spine. The wide base of the haemal arch originates on the anterior half of this centrum and is slanted strongly backward, and so it joins its opposite member medially below the posterior end of the centrum. At this point, an extremely long and slender haemal spine continues posteriorly below the eleventh centrum, contacting the haemal arches and spine of that centrum and gradually curving ventrally, then recurving anteriorly, to interdigitate between the slender proximal ends of the first and second anal pterygiophores.

The haemal arch and spine of the second caudal vertebra resemble those of the first caudal vertebra, but the spine is slightly shorter and bears a small anterodorsally directed process near its junction with the arch. The haemal arches of the third to seventh caudal vertebrae are narrower and not slanted posteriorly; the haemal spines are progressively shorter and less curved. The haemal arches and spines of the eighth and ninth caudal vertebrae are markedly shorter and broader than those anterior to them, and are specialized to support the last two anal

pterygiophores. The haemal arch of the eighth extends along the posterior half of the centrum, is closed ventrally, and bears a short haemal spine. The haemal arch of the ninth extends along the entire length of the centrum, and remains open ventrally, where it embraces the posterior half of the last anal pterygiophore; the latter forms a functional roof over the haemal canal. A short spine extends from the posteroventral corner of the haemal arch of the ninth vertebra but it does not contact its opposite member in the midline. The neural arches of the eighth and ninth caudal vertebrae are similar in configuration to the haemal arches, and that of the ninth embraces the last dorsal pterygiophore. The neural arches and spines of the anterior caudal vertebrae are similar to those of the posterior precaudal vertebrae. The spines become progressively shorter posteriorly in the series, and the neural arches bear well-developed pre- and postzygapophyses.

Caudal Skeleton

FIGURE 13

The caudal complex includes caudal vertebrae 10–13. The tenth caudal (preural 4) vertebra is shorter than those preceding it and appears to provide a pivot for the caudal peduncle; the closed neural and haemal arches are short and broad, each bearing a short rounded spine. The broad neural and haemal arches on each side of preural 3 (eleventh caudal) are directed somewhat laterally (away from the midline), so the arches are open widely along most of the length of the centrum; the arches

join in the midline only above the posterior end of the centrum, at which point stout, dorsoventrally compressed, neural and haemal spines continue posteriorly. These neural and haemal spines are almost horizontal and extend posteriorly beyond the anterior end of the urostylar centrum. They are almost identical in configuration, but the haemal spine (together with its arch), unlike the neural, is autogenous. The broad neural arch of preural 2 (twelfth caudal) is fully open and embraces the dorsoventrally compressed proximal end of the single epural; the haemal arch and associated spine are autogenous. Distally, the cartilaginous tips of the epural and the second preural haemal spine support most of the dorsal and ventral procurrent caudal rays, respectively.

There are no autogenous uroneurals. An elongate, posteriorly tapering, saddle-like structure on the dorsal surface of the urostylar centrum (PU1 + U1) represents the fused anterior uroneural. Posteriorly, the ventral surface of this fused uroneural embraces the dorsal margin of the well-developed fifth hypural, the proximal tip of which is fused to the uroneural-urostylar complex. A single triangular hypural plate, comprising hypurals 1–4 (based on its known ontogeny, even though Roule (1924) showed the development of the plate from about six hypurals) lies between the ventral border of hypural 5 and the dorsal margin of the parhypural, articulating at its anterior apex with the urostylar centrum, but not fused to it. The longitudinal midline of this plate is cleft posteriorly; its vertical posterior border is cartilaginous. An autogenous parhypural, similar in shape to the fused uroneural, articulates proximally with the ventral surface of the urostylar centrum; the parhypural

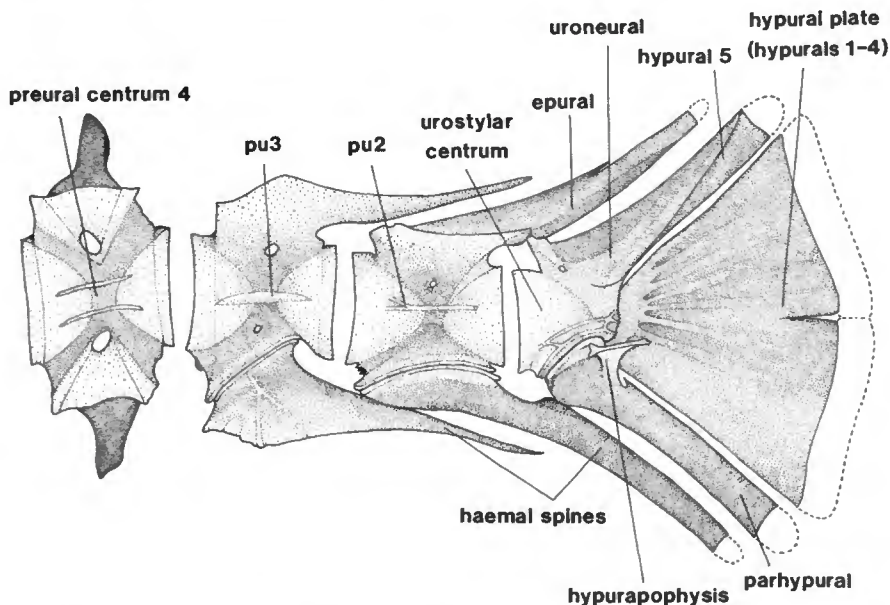


FIGURE 13.—*Luvarus imperialis*, USNM 228612, 79.2 mm SL, lateral view of caudal fin supporting structures (last four of 13 caudal vertebrae, to the last two of which procurrent and principal caudal-fin rays are most closely associated; see Figure 21 for relationship of caudal-fin rays to terminal vertebrae in 301 mm SL specimen).

bears a flattened, horizontally oriented hypurapophysis. The bases of all but the middle four principal caudal fin rays deeply embrace the distal regions of the hypurals, parhypural, uroneural, epural, and the neural and haemal spines of the third preural centrum, as described below.

There are 16 principal caudal fin rays (14 branched + 2 unbranched); all principal rays are divided bilaterally and all but the two dorsalmost and two ventralmost have at least some segmentation, the middle four being most extensively segmented and branched. There are eight procurrent caudal rays dorsally and seven ventrally, all bilaterally divided, none segmented or branched. There is a single row of comb-like, spiny serrations along most of the lateral side of each half of every caudal fin ray, except the anteriormost one or two procurrent rays. The serrations are borne along the posterior to ventral margins of the dorsal rays and the posterior to dorsal margins of the ventral rays (depending on the orientation of each ray), the individual spines also being pointed in these respective directions. These serrations (not shown in illustrations) are largest at the proximal ends of the more medial rays of the fin, where some are bifurcate distally. The bases of the medial four rays overlap only the cartilaginous border of the hypural plate. The remaining principal rays increasingly overlap the hypural plate anteriorly. The distal regions of the epural, autogenous haemal spine of the second preural vertebra, and the extreme distal ends of the neural spine and autogenous haemal spine of the third preural vertebra support the procurrent caudal fin rays above and below. The first (unbranched) principal caudal fin ray above and below have the greatest degree of overlap of the caudal skeleton.

Dorsal and Anal Fins

FIGURES 3, 14

There are 23 dorsal-fin rays (plus a tiny spine rudiment on the first pterygiophore). The first two of these are true spines; i.e., median, unsegmented, unbranched elements. The first spine is borne in supernumerary association with the first dorsal pterygiophore, on which it rests. A tiny, semicircular, flat nubbin of bone rests on the first pterygiophore just anterior to the base of the first spine, but does not protrude above the skin. In larval specimens (see Figure 46b), this element is relatively better developed and rotates about a rudimentary crescentic flange on the anterodorsal corner of the pterygiophore. The second spine is serially associated with the first pterygiophore, and rests on the second. The base of each spine is expanded, and its ventral surface bears an anteroposteriorly oriented concavity that articulates with a low vertical flange medially on the dorsal surface of the expanded distal end of the pterygiophore. The first spine bears a single series of serrations (not shown in illustrations) along the proximal half of the length of each posterolateral wing. The first pterygiophore is roughly T-shaped with a long robust ventral shaft; the posteroventral

margin of the shaft is attached by fibrous tissue to the anterior edge of the neural spine of the first vertebra and the ventral tip contacts the slightly concave region medially on the posterior face of the skull where the epiotics meet. Dorsally the first pterygiophore has a well-developed anterior flange and a deeply indented posterior flange with which the anterior flange of the dorsal end of the second dorsal pterygiophore interdigitates. The second pterygiophore is like the first, but less robust and with a shorter ventral shaft and a more complexly indented posterodorsal flange. The slender ventral shaft articulates posteroventrally with the anterodorsal edge of the neural arch of the second vertebra. The first and second dorsal pterygiophores lack separate middle radials and the first lacks a distal radial.

There are 20 dorsal-fin soft rays. The last ray is split to the base. There are 21 dorsal pterygiophores; except for the last three, each proximal radial is approximately T-shaped with a slender ventral shaft, and a dorsal region expanded into anteriorly and posteriorly directed plates that complexly suture with one another by elaborate emarginations and interdigitations (Figure 14). The dorsal surface of these plates is laterally expanded to form a concave laminar trough. The open bases of each soft ray embrace a spherical cartilaginous distal radial that rests in a bowl-shaped depression midway along each of the proximal-radial troughs; bilaterally paired, lens-shaped ossifications are present on the sides of each cartilaginous distal radial at the point where each ray base contacts the radial. All but the first two pterygiophores have separate middle radials. On all but the last few pterygiophores, each middle radial

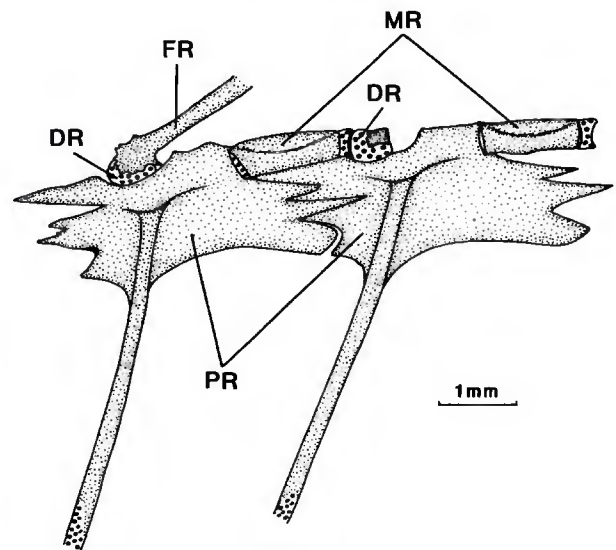


FIGURE 14.—*Luvarus imperialis*, USNM 228612, 79.2 mm SL, lateral view of dorsal pterygiophores 6 and 7, showing separate middle (MR) and distal (DR) radials and interdigitation of proximal (PR) radials; seventh fin ray (FR) removed.

ossification is a concave laminar trough similar in appearance to, and providing a continuation of, the trough-like dorsal surface of the serially corresponding proximal radial. These middle-radial troughs overlie each anterior expansion of succeeding proximal radials and essentially rest in or over the trough-like dorsal surface of that expansion. The base of each bilaterally paired ray is laterally expanded, and bears anteriorly and posteriorly directed processes for muscle attachment, these better developed posteriorly on each ray than anteriorly. All of the soft rays are unsegmented and unbranched. The first ray is much longer than either of the two preceding spines and slightly shorter than the succeeding rays, which gradually increase in length in the series posteriorly to about the middle of the fin and then decrease in length gradually to the last ray.

The anal fin comprises 18 soft rays and no spines; the last ray is split to the base. The first two rays are borne in supernumerary association on the elongate and thickened ventral plate of the proximal radial of the first pterygiophore; as in the dorsal fin, each of the remaining rays is borne on the proximal radial of the pterygiophore just posterior to the one with which it is serially associated. There are 17 anal pterygiophores. The proximal radials are similar to those of the soft dorsal fin, except that the first few are more anteroposteriorly elongate along the ventral edge of the body and have much longer and more posteriorly curved shafts. There are separate middle and distal radials associated with each anal pterygiophore, similar in configuration to those described for the dorsal fin. The posterodorsally extended shaft of the first anal proximal radial extends along the anterior edge of the distal portion of the slender, extremely elongate haemal spine of the first caudal vertebra; the posterodorsal shafts of the second, third and fourth proximal radials lie between the distal portions of the haemal spines of the first and second caudal vertebrae; the shaft of the fifth is between the haemal spines of the second and third caudal vertebra, and that of the sixth lies just posterior to the haemal spine of the third. The dorsal shafts of the proximal radials of the seventh and eighth converge dorsally, and so their tips lie on either side of the haemal spine of the fourth; those of the ninth and tenth, eleventh and twelfth, and thirteenth and fourteenth converge on the haemal spines of the fifth, six, and seventh caudal vertebrae respectively. The last three proximal radials of the anal fin lack elongate shafts. Fin rays, like those of the soft dorsal fin, are bilaterally split, unbranched and unsegmented, with expanded bases that embrace the spherical, cartilaginous distal radials.

Scales

FIGURE 15

Body covered with scattered and mostly non-overlapping round scale plates of variable sizes (smallest and most numerous about 0.1 mm diameter, larger ones typically about 1.0 mm, and largest ones, dorsally and ventrally along the bases

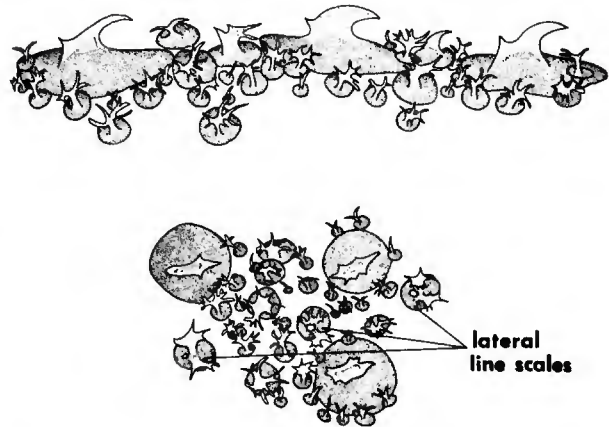


FIGURE 15.—*Luvarus imperialis*, USNM 228612, 79.2 mm SL: *above*, scales along rear base of soft dorsal fin; *below*, scales from anterior end of caudal peduncle, including three lateral line scales (bearing pores and with paired central spinules).

of the fins, about 2.0 mm diameter). Each basal plate typically bears a single stalk that is distally expanded into a stellate plate in a plane horizontal to the surface of the body. Scales along bases of dorsal and anal fins with more robust thorn-like processes, with a major posteriorly directed prong and a smaller anterodorsally oriented one. Lateral-line scales with a pore to each side of which are distally branched plates (Figure 13). (Lateral-line scales were described and illustrated in detail for a variety of specimen sizes by Roulé, 1924.)

Olfactory Rosette

The nasal rosette of the 79.2 mm specimen was not examined prior to clearing and staining, but it is similar to that in a 121 mm alcohol-preserved specimen (FMNH 63116), in which it is anteroposteriorly elongate, and bears about 15 lamellae on each side (above and below the central rachis), the lamellae largest anteriorly, decreasing in size to minute posteriorly.

301 mm SL

FIGURES 16-21

Cranium

OCCIPITAL REGION.—The basioccipital and exoccipital are more extensively sutured than in the 79.2 mm specimen, and the walls of the foramen magnum, entirely surrounded by the exoccipitals, are thicker and stronger, otherwise the configuration of these two bones is like that of the smaller specimen. The supraoccipital is larger, more extensively covering the dorsal surface of the ethmoid cartilage and extending anteriorly to almost contact the dorsal expansion of the ethmoid ossification.

ORBITAL REGION.—The parasphenoid is stronger and more

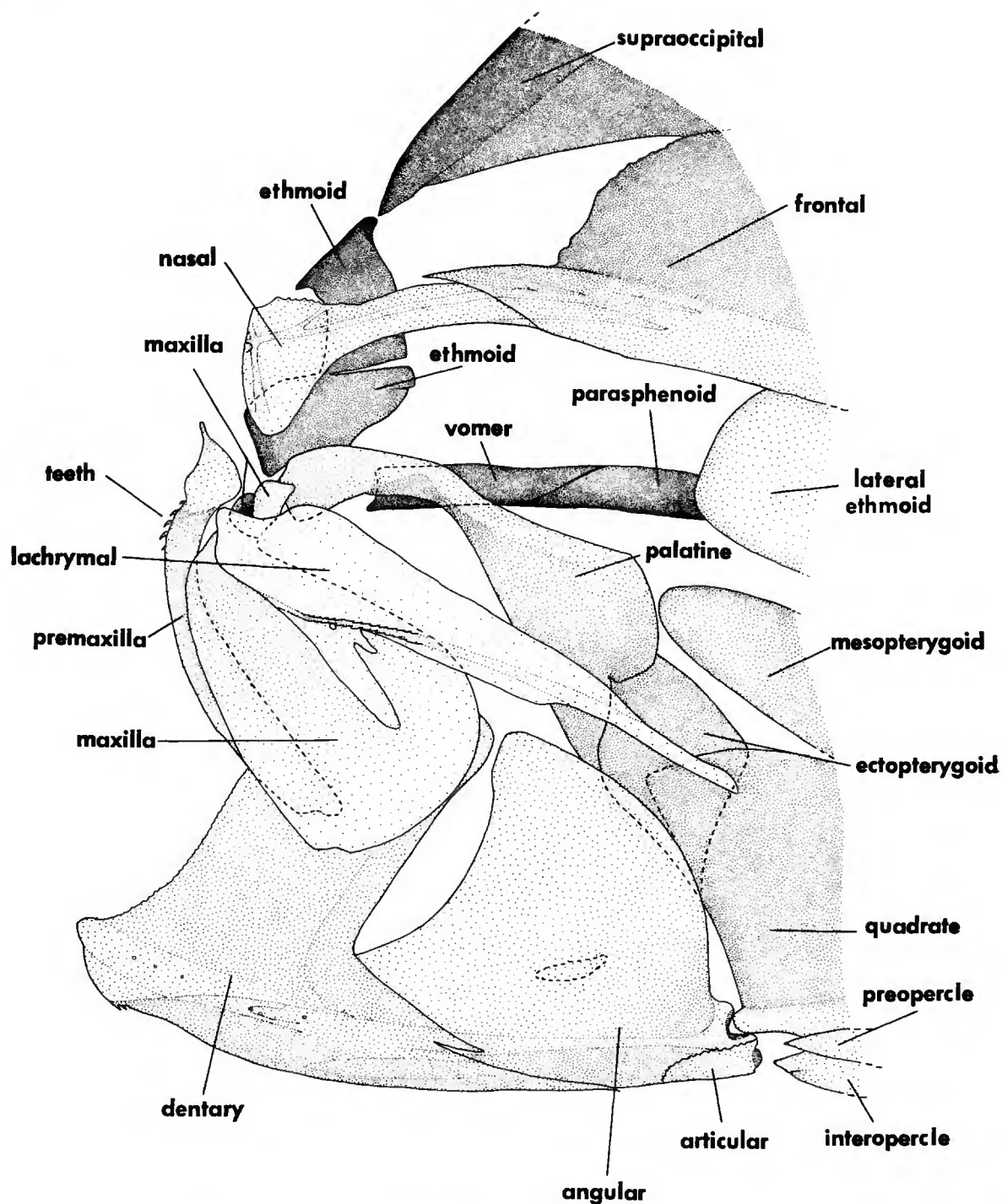


FIGURE 16.—*Luvarus imperialis*, SIO 79-281, 301 mm SL, lateral view of anterior end of skull, with dashed lines showing course of bones otherwise obscured from lateral view by overlying elements (dashes approximately from above to below being for ethmoid behind nasal, vomer behind palatine, ectopterygoid behind palatine and lachrymal, premaxilla behind maxilla, maxilla behind lachrymal, and sesamoid articular on medial surface of articular).

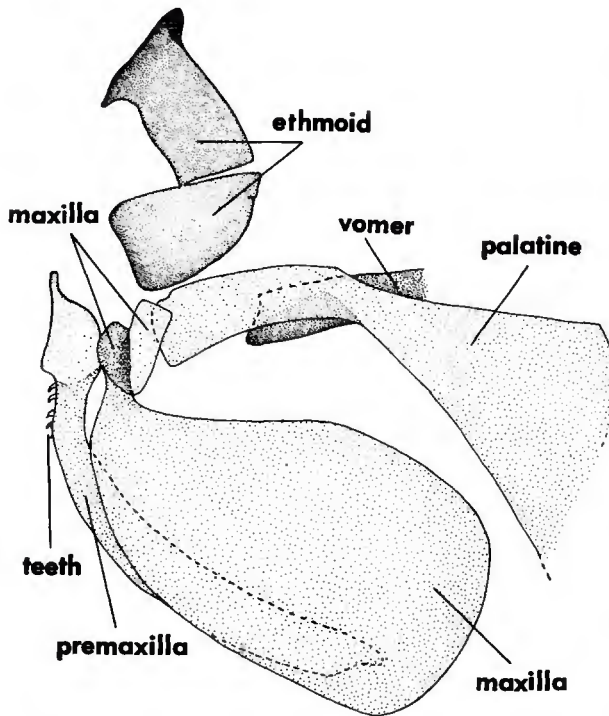


FIGURE 17.—*Luvarus imperialis*, SIO 79-281, 301 mm SL, lateral view of ethmoid region and upper jaw, with lachrymal and nasal removed; dashed lines show course of bones otherwise obscured from lateral view by overlying elements (those of vomer behind palatine and premaxilla behind maxilla).

expanded where it is sutured to the prootics and basioccipital. The pterosphenoids are more broadly and extensively interdigitated to one another anterodorsally in the midline of the dorsal roof of the orbit. The flattened (dorsoventrally) anterior end of the parasphenoid is more broadly overlain dorsally by the equally flattened posterior end of the vomer.

ETHMOID REGION (Figure 16).—The ethmoid cartilage, although not as severely truncate at the snout, still constitutes the major mass of the neurocranium anterior to the orbit. The ethmoid ossification is notably larger and more expanded dorsally but is still confined to a thin sheet of perichondral bone that wraps around the lateral and anterior surfaces of the anterior region of the ethmoid cartilage. The vomer and lateral ethmoid ossifications are larger, and the surfaces of the latter are extremely cancellous. The nasals are no longer L-shaped, being broader and more rounded anteriorly, without a distinct ventral process; the previously open sensory canals are bone-enclosed.

SUSPENSORIUM (Figure 16).—Not significantly different from smaller specimen.

PALATO-PTERYGOID REGION (Figures 16, 17).—Not significantly different from smaller specimen.

OPERCULAR REGION.—Not significantly different from smaller specimen.

UPPER JAW (Figures 16, 17).—The premaxilla is similar to that of the smaller specimen, but with a slightly larger and more dorsolaterally expanded anterior articular facet and with fewer and smaller teeth. There are four to six minute teeth confined to the dorsal end of each premaxillary shaft, not extending as far ventrolaterally along the anterior edge as in the smaller specimen. The maxilla differs only in having a relatively larger, more fully developed articular head.

LOWER JAW.—The dentary has a somewhat stouter, laterally thickened region along its length. It is essentially edentulous, with an irregular rugose area along most of its anterodorsal margin, which probably represents partially resorbed tooth sockets; the margin is especially deeply pitted near the symphysis of the lower jaw where there are short, blunt remnants of the bases of several teeth. The articular and angular are more extensively interdigitated with one another than in the smaller specimen, and the sesamoid articular is slightly larger.

HYOID APPARATUS (Figure 18).—Similar to that of the 79.2 mm specimen, except for more extensive interdigitation between some of the elements. The dorsal and ventral hypohyals interdigitate on their medial surfaces through a dorsal extension of the dorsomedial edge of the ventral hypohyal. The posterior end of the ceratohyal is more strongly sutured with the anterior end of the epihyal than in the smaller specimen. The urohyal is more rounded in lateral view, with a continuous posterior margin. The medial surface of the anterodorsal end of the dorsal hypohyal is slightly enlarged where it contacts the region of articulation between the posterior end of the basihyal and the anteroventrally directed end of the first basibranchial. The basihyal is slightly larger than in the smaller specimen. As in the smaller specimen, there are five branchiostegal rays.

Gill Arches

FIGURE 19

Similar in configuration to those of the 79.2 mm specimen, but most elements are more robust. Gill rakers, fifth ceratobranchials, and pharyngobranchials 2-4 are more extensively toothed.

Paired Fin Girdles

PECTORAL FIN.—In contrast to the 79.2 mm specimen, in which the scapula and coracoid are distinctly separated by cartilage, there is close apposition and extensive interdigitation between the ventral edge of the scapula and the anterodorsal edge of the coracoid, with cartilage remaining between them only posteriorly (Figure 20). The actinosts are similarly configured with cartilaginous proximal and distal tips, except for the dorsalmost, which is cartilage-filled only distally. The scapular foramen remains complete and about the same size as in the smaller specimen. The articulation between the coracoid and cleithrum is extensively interdigitated anterodorsally and

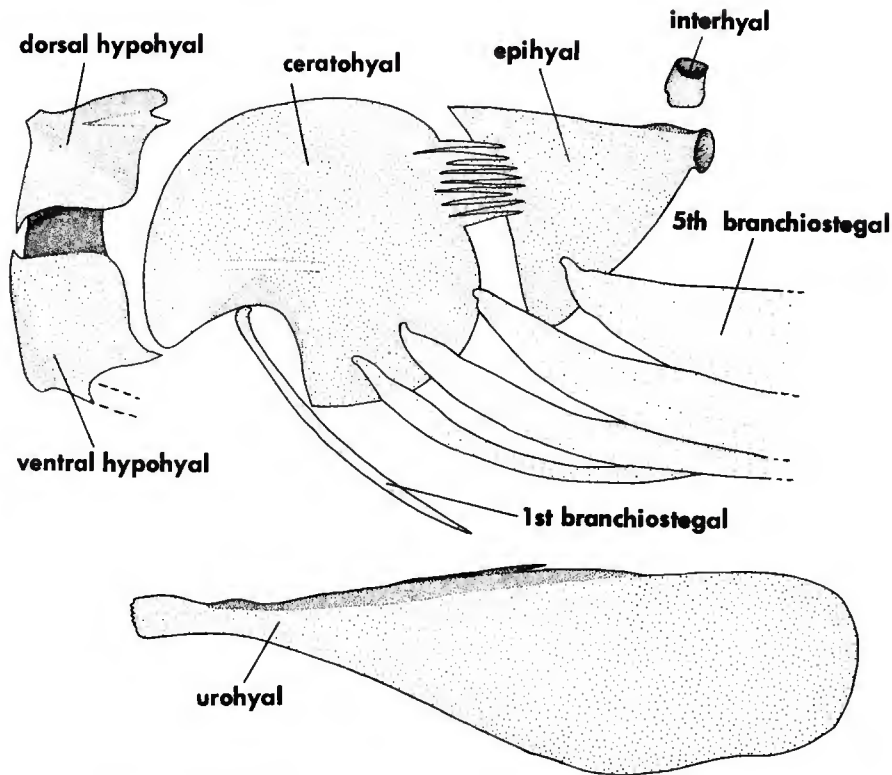


FIGURE 18.—*Luvarus imperialis*, SIO 79-281, 301 mm SL, lateral view of hyoid arch and urohyal (basihyal not shown; full length of more posterior branchiostegal rays not shown).

anteroventrally, but a large space between the two points of articulation remains. The dorsal and ventral postcleithra are tightly attached. There are 18 fin rays on the left side and 19 on the right, bilaterally separated throughout their lengths. The first (dorsalmost) ray is relatively shorter than in the smaller specimen; all but the first and second rays are branched once distally.

PELVIC FIN.—The pelvis consists of two separate halves throughout its length, as in the smaller specimen, but the two halves are in closer apposition, especially posteriorly. The pelvic fin is proportionally much smaller than in the smaller specimen, the spine is only about 11 mm long and the four soft rays decrease in length from the first to the fourth. The lateral or leading edge of the pelvic spine is more strongly serrate and rugose than in the smaller specimen. The soft rays are similar in configuration to those of the smaller specimen.

Vertebral Column

There are 22 vertebrae (9+13), including the hypural, with well-developed ribs on the third to ninth. The vertebrae are similar to those of the smaller specimen except that the neural spine of the first vertebra is stouter and the region of fusion of the neural arch to the first centrum is narrower. Of five

specimens from California, Gotschall and Fitch (1968) found one with 23 vertebrae.

Caudal Skeleton

FIGURE 21

The caudal skeleton is essentially like that of the smaller specimen. There are 16 principal caudal-fin rays and eight procurent rays dorsally and ventrally. More of the principal rays are branched and segmented than in the smaller specimen, and the bases of the rays overlap the hypural plate more extensively. Hypural 5 is more fully consolidated with the uroneural-urostyler complex and the posterior margin of the hypural plate is no longer cleft at the longitudinal midline.

Dorsal and Anal Fins

There are two spines (plus a tiny vestigial spine) and 20 soft rays in the dorsal fin, supported as in the smaller specimen. The spine remnant anterior to the first full spine is further reduced although still visible as a tiny crescentic plate of bone. In contrast to the smaller specimen, most of the dorsal-fin rays are branched distally (one bifurcation) but, like the smaller specimen, none of them are segmented. The interlocking

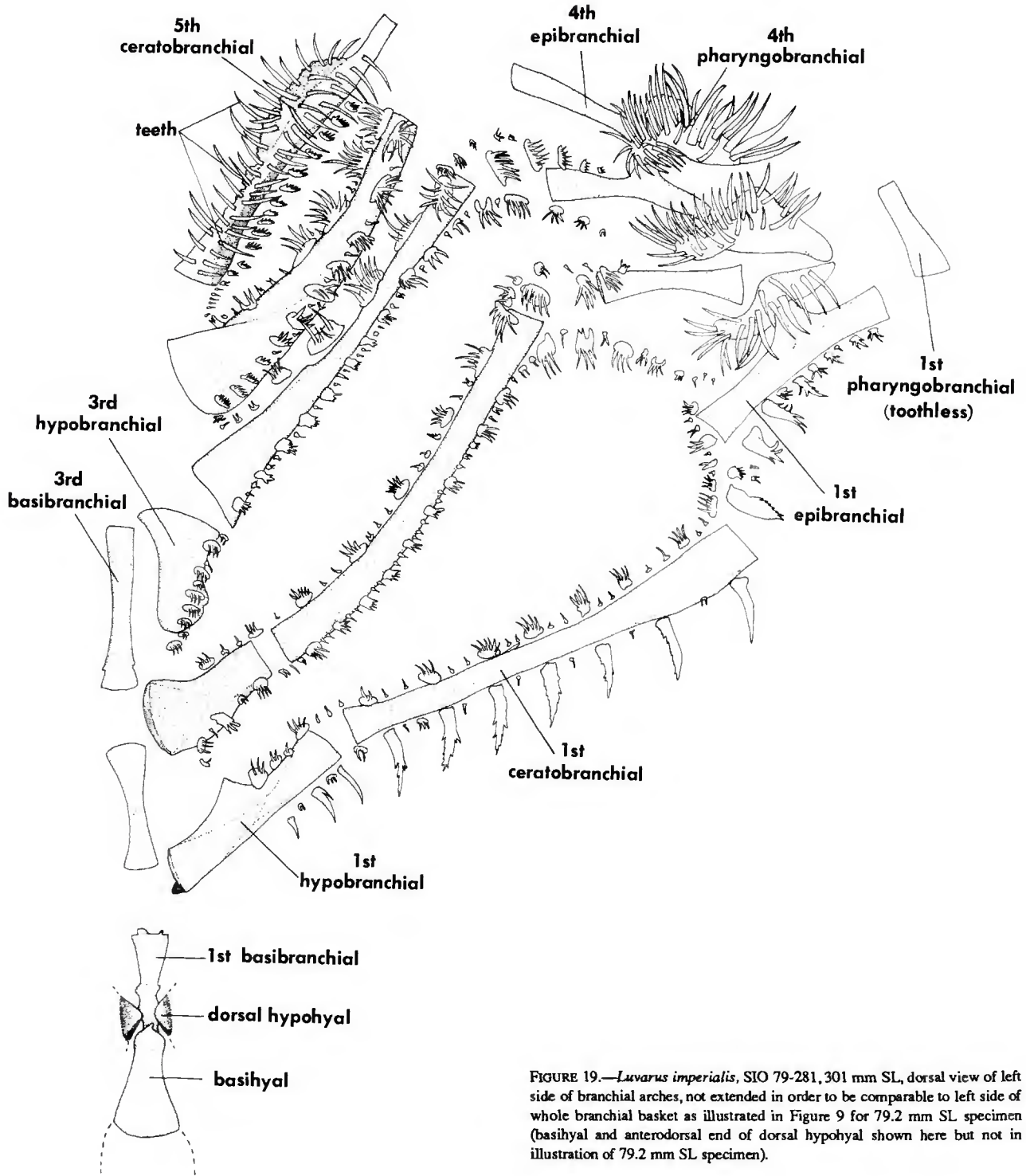


FIGURE 19.—*Luvarus imperialis*, SIO 79-281, 301 mm SL, dorsal view of left side of branchial arches, not extended in order to be comparable to left side of whole branchial basket as illustrated in Figure 9 for 79.2 mm SL specimen (basihyal and anterodorsal end of dorsal hypohyal shown here but not in illustration of 79.2 mm SL specimen).

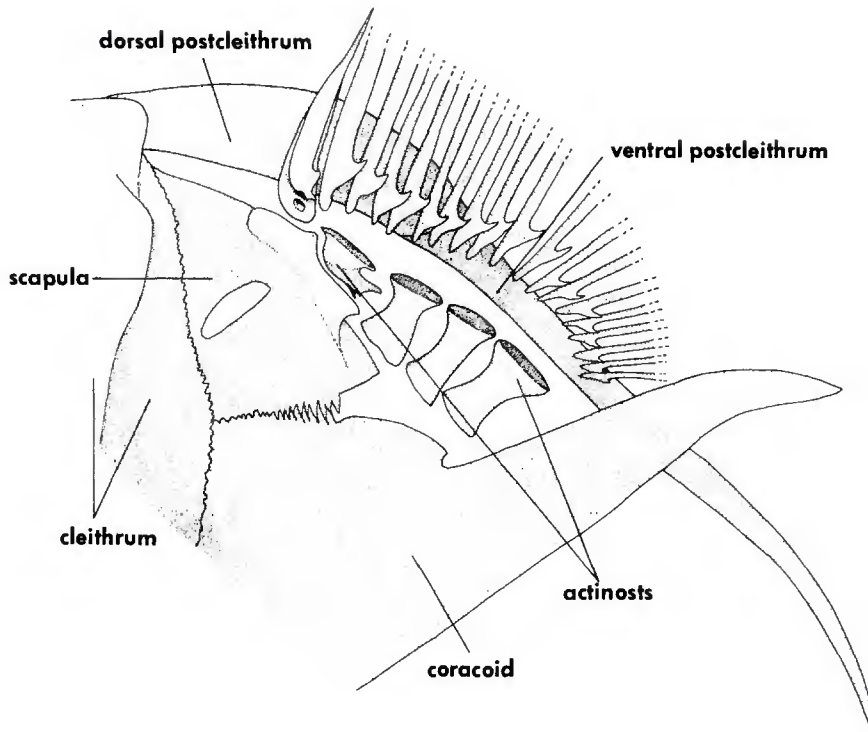


FIGURE 20.—*Luvarus imperialis*, SIO 79-281, 301 mm SL, lateral view of posterodorsal region of pectoral girdle supporting pectoral fin.

articulations of the distal ends of the 21 proximal radials are more pronounced than those of the 79.2 mm specimen, and more nearly approach the degree of interdigitation illustrated for the large 200 lb specimen by Gregory and Conrad (1943). Each middle radial shows some fusion anteriorly with the serially corresponding proximal radial and ventrally with the dorsal surface of the succeeding proximal radial. Perichondral ossification covers the entire dorsal half of all but the last few distal radials.

There are 18 anal soft rays, similar to those of the dorsal fin, each composed of separate right and left halves throughout their lengths, branched distally in single bifurcations but unsegmented. The 17 pterygiophores are as extensively interlocked distally as those of the dorsal fin, the distal radials are similarly ossified and the middle radials appear fused.

Scales

Similar to those described and illustrated for the 79.2 mm specimen. The distal ends of the upright pedicels are more laterally expanded and spinulose, resembling the irregularly edged and flattened cap of a mushroom, and the larger retrorse spiny processes of some of the scale plates are thicker and better developed.

485 mm SL

Caudal Skeleton

The caudal skeleton of this specimen is essentially like those of larger specimens. There are several notable features not found in the smaller specimens (Figures 13 and 21). The parhypural is fully fused to the urostylar centrum, and the hypurapophysis is comparatively small. Hypural 5 is fully fused with the uroneural-urostylar complex.

The haemal spine on preural centrum 3 is fused, but that on preural centrum 2 remains autogenous. There is a very small notch at the midline of the posterior margin of the hypural plate. The hypural plate remains autogenous from the urostylar complex.

980 mm SL

Hyoid Arch, Branchiostegal Rays, and Urohyal

Similar to that of the 301 mm specimen (Figure 19), except that the ceratohyal and epihyal are more elongate and there is extensive interdigitation between them. The urohyal is more rounded in lateral view than in smaller specimens (Figures 9 and 19). The five branchiostegal rays are flat and elongate, with increasing flatness and size gradually from anterior to posterior.

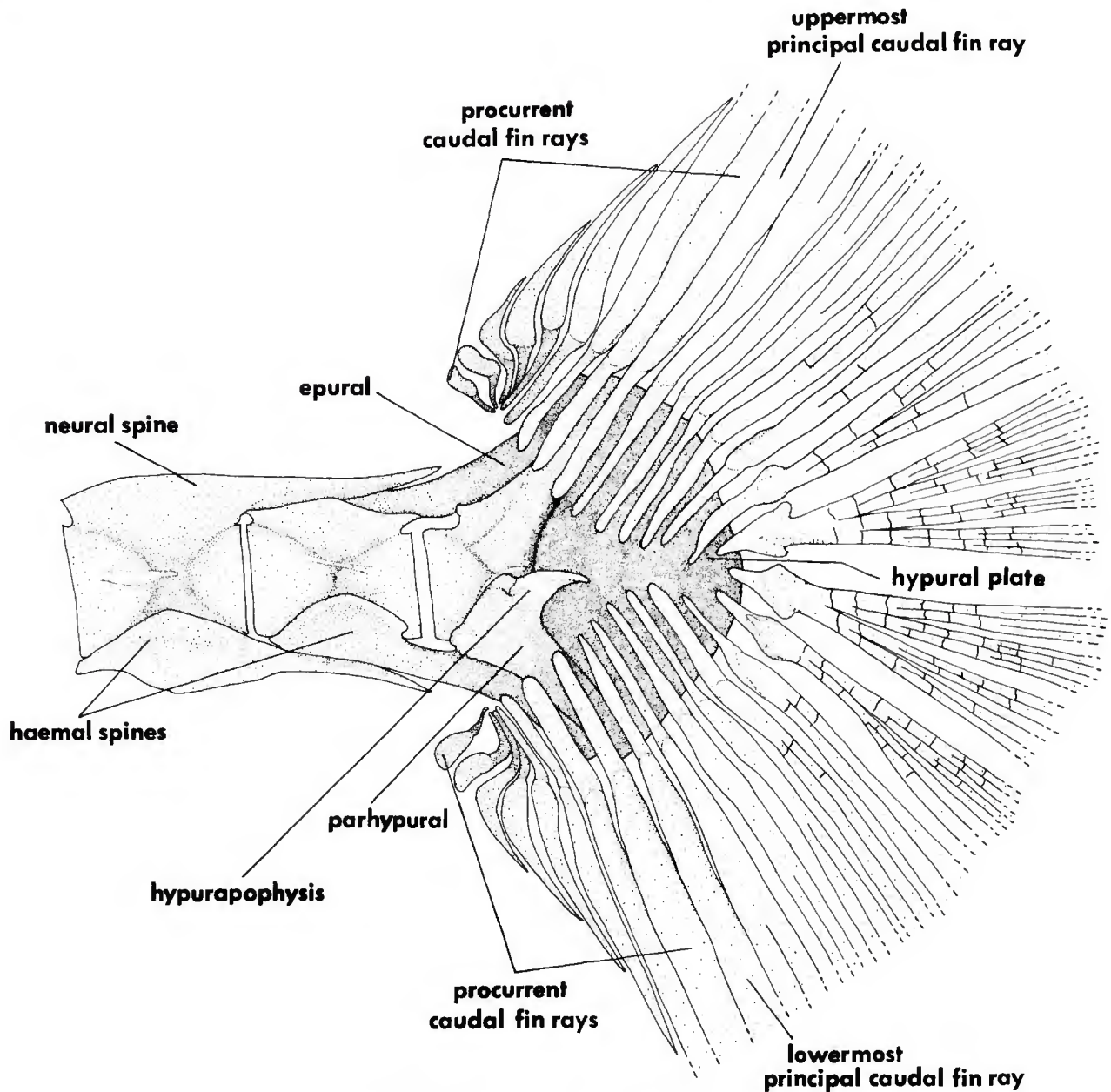


FIGURE 21.—*Luvarus imperialis*, SIO 79-281, 301 mm SL, lateral view of structures supporting caudal fin (last three caudal vertebrae, to last two of which procurrent and principal caudal-fin rays are most closely associated).

Branchial Arches

Similar to those of the 301 mm specimen (Figure 19), except most of the bones stouter, the gill rakers heavier, shorter and less spiny, and the basihyal more rounded than in the smaller specimens (Figures 9 and 19).

Pectoral Girdle

Very similar to that of the 301 mm specimen (Figure 20), except the stay for the first pectoral-fin ray is better developed, the base of the posterior process of the coracoid is thicker and wider, and the scapula and coracoid tightly interdigitate with

each other along the whole suture. The four actinosts are stouter and more tightly associated, with a foramen between them.

Pelvic Girdle

Pelvis with an elongate body with a wing-like process posteriorly. The left and right pelvics are sutured to each other throughout their entire lengths, with a small foramen midway along the suture line. The pelvic fins have a single small spine (left and right elements completely united).

Vertebral Column

There are well-developed blade-like ribs on the 3rd to 9th vertebrae. The vertebrae are essentially similar to smaller specimens (Figure 3), except for stouter centra and stouter and thicker neural and haemal spines.

Caudal Skeleton, Peduncular Keels, and Caudal Fin

The caudal skeleton is similar to the 485 mm specimen. The notch on the posterior margin of the hypural plate is even smaller. A median fleshy keel and two accessory keels above and below it are well developed laterally on the caudal peduncle; these keels have no bony support structure. Caudal notches on the dorsal and ventral parts of the caudal peduncle found on some other specimens are not seen in this individual.

1100 mm SL

Vertebral Column, Caudal Skeleton, Teeth

Seven ribs, on abdominal vertebrae 3 to 9; first and second caudal vertebrae with typical condition of elongate curved haemal spines; caudal-fin rays broadly overlapping hypural plate, almost meeting in midlateral line as in other larger specimens. Remains of at least a dozen teeth on dorsomedial region of premaxilla toward the symphysis, but only a deeply pitted rugose surface without obvious teeth in the corresponding place on the dentary, at least as seen by cursory examination at low power of a dissecting microscope in the specimen as presently cleaned by dermestid beetles. Stout neural spine of first abdominal vertebra apparently separate from its neural arch and centrum, but it is unclear whether this is because of the resorption of the narrow anterior region of the neural arch as seen in smaller specimens or from breakage of the spine away from the arch during skeletal preparation.

1140 mm SL

Vertebral Column and Caudal Skeleton

The vertebrae are similar to those of the 980 mm specimen, but thicker and stouter. The caudal skeleton complex is stout,

with a very small notch at the center of the posterior margin of the hypural plate and several shallow grooves on the hypural plate that receive the deeply forked bases of the caudal-fin rays.

1720 mm SL

Viscera

FIGURE 22

The visceral cavity is compressed and very large, extending to the origin of the anal fin, with the anus situated beneath the thoracic pelvic spine. The stomach is large with thick walls; soft tubercles of various size are present on the inside wall of the cardiac portion, and several thin striae on the inside wall of the pyloric portion. The intestine is highly coiled (Figure 22) and very long, about 8 times in the SL in this specimen (about 5 times in the 301 mm specimen, about 11 times in the 980 mm specimen). "Loop b" of the intestine (see Mok, 1977) lies on the right side of the stomach. Pyloric caeca are few in number (5 in this specimen, 4 in both the 301 mm and 980 mm specimens), short and simple in shape. The liver is small, roughly triangular in lateral view. The spleen is small and round. The gall bladder is elongate. The kidney is relatively massive, triangular in lateral view. The urinary duct is long and thick. The air bladder is large, occupying the entire upper part of the visceral cavity.

Gill Arches

Essentially like those of the 980 mm specimen. The gill rakers are stouter and shorter than in smaller specimens. The gill filament blades are ossified.

Olfactory Rosette

The nostrils are double. Both are elliptical, closely spaced; the anterior one (long diameter 41 mm) slightly larger than the posterior one (long diameter 36 mm). The olfactory rosette is elliptical and small (long diameter 23.8 mm, short diameter 8.9 mm), with smooth fleshy eminence at the outer margin and 26 lamellae in the central part, situated a little posterior to the nostrils.

External Features

Body compressed and fusiform. A shallow groove is present from the snout to the upper margin of the opercle above the eye. There is a median fleshy caudal keel with accessory keels above and below. Very small dorsal and ventral notches are present on the caudal peduncle. The left and right pelvic spines are completely united and the soft rays are absent. A shallow pelvic cavity receives the pelvic spine and opens to the anus. The dorsal spines are absent at this size. The caudal fin is well

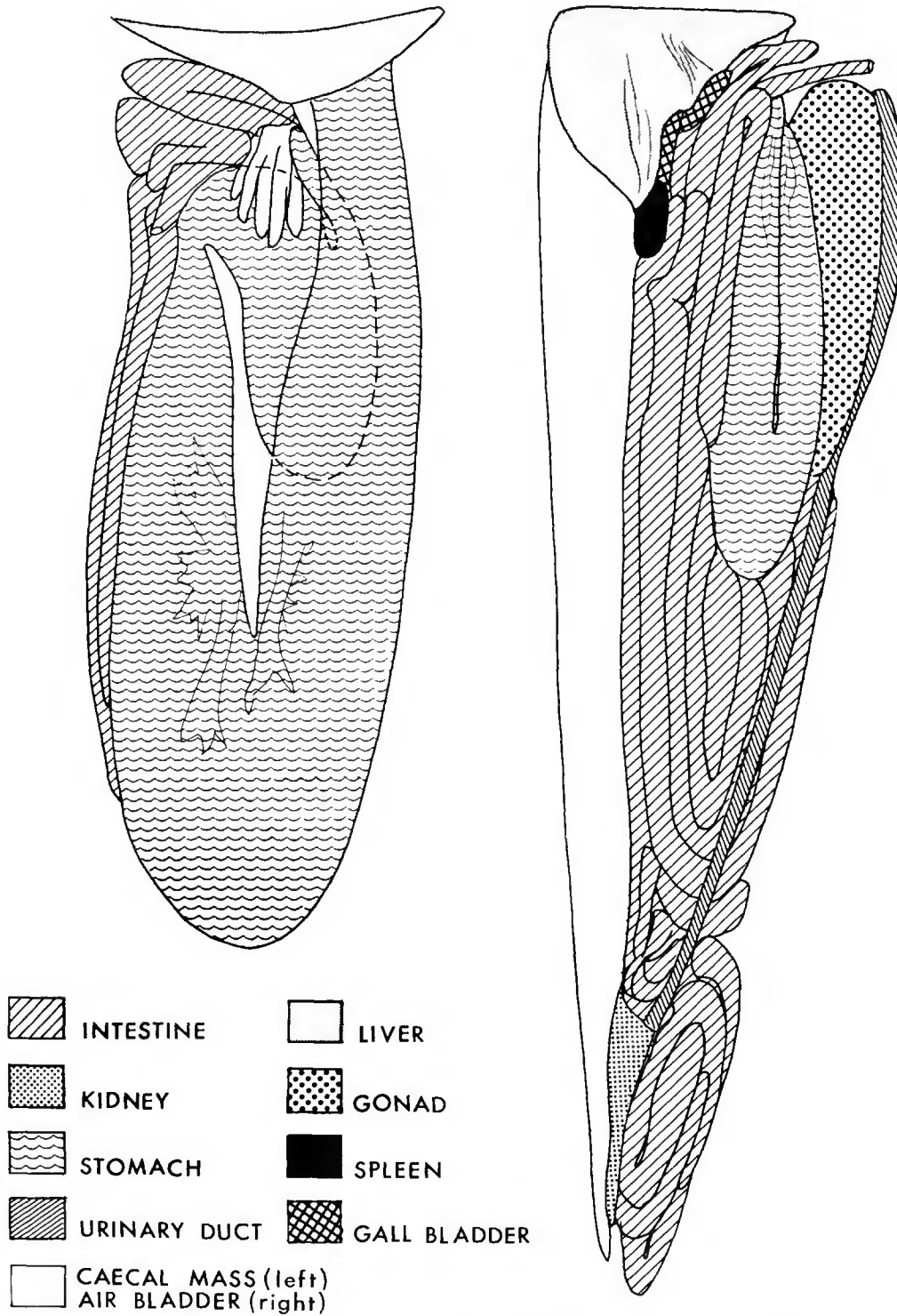


FIGURE 22.—*Luvarus imperialis*, ZMUT P1400, 1720 mm SL, viscera in lateral view of right side (*right*) and the opposite side (*left*; enlarged about two times of *right*, and posterior part of intestine omitted).

developed, with a posterior concavity in lateral view. The bases of most of the caudal-fin rays are deeply forked and broadly overlap the hypural plate.

1780 mm SL

Caudal Skeleton and Caudal-Fin Rays

The hypurapophysis is relatively small. The hypural plate is stout, with an extremely minute notch midway along the posterior margin. The epural is stout, autogenous, and broadly overlain dorsally by the neural spine of the eleventh caudal (preural 3) vertebra. There are 17 principal caudal-fin rays, 5 dorsal procurent rays and 7 ventral procurent rays. All the caudal-fin rays are well ossified, without any segments or branches. The bases of the rays, except for some of the procurent rays, are deeply forked and overlap the hypural plate extensively and deeply, like the condition of the hypural plate and fin rays typically seen in *Thunnus*, *Makaira*, and *Xiphias*. Sagittal shape of the bases of the central principal caudal-fin rays found in smaller specimens (Figure 21) not seen in this specimen.

Relationships

Fossil Record

The fossil record of the Luvaridae is limited but instructive. Two species are known from the Paleocene (?) and Eocene; one, *Eoluvarus bondei*, so closely resembles *Luvarus imperialis* that we consider them congeneric, whereas the other, *Proluvarus necopinatus*, is generically distinct. Another species, *Kushlukia permira*, from the same deposits as *Proluvarus*, probably represents an acanthuroid relative of the Luvaridae. An Oligocene species described as *Luvarus preimperialis* cannot be assigned with confidence to the Luvaridae because there is not enough information about it.

Proluvarus necopinatus Danilchenko (1968:144-147, fig. 17, pl. 35) is based on 10 specimens of 44-330 mm SL, at least some of which are well preserved, from the "Palaeocene" of Turkmenistan in Russia (possibly of Ypresian age in the early Eocene). It closely resembles *Luvarus imperialis* and has 9+13=22 vertebrae, 24-26 dorsal-fin elements, 17-20 anal-fin rays, 16-17 pectoral-fin rays, an indistinct pelvic fin (said to be absent in adults), united pelvic bones, thoracic anus, an unspecified number of caudal-fin rays that appear in the illustration to at least moderately overlap the hypural plate (and are described as covering the wide hypural plate laterally), and scales consisting of small plates of irregular shape. *Proluvarus necopinatus* appears to have about seven well-developed pleural ribs, as in *L. imperialis*, and several epipleural ribs; the latter are absent in the Recent species and provide modest evidence for what we tentatively consider as the generic distinction of *Proluvarus necopinatus* from *Luvarus imperi-*

alis. In any event, in the upper Paleocene or lower Eocene there existed a luvarid rather similar to the Recent species, differing most notably by the presence of epipleural ribs.

Eoluvarus bondei Sahni and Choudhary (1977) is based on a better-preserved specimen (273 mm SL) from the early Eocene (Ypresian) Fuller's Earth (diatomite) at Rajasthan or Barmer, India, and is thus approximately contemporaneous with *Proluvarus*. It is remarkably similar to the Recent species, with 22 vertebrae and about 7 pleural ribs. The caudal peduncular vertebrae are notably like those of *Luvarus imperialis*. The short "pivot" (10th caudal) vertebra is followed by two vertebrae with elongate, almost horizontally oriented neural and haemal spines that support some of the rays of the large caudal fin (degree of overlap of bases of rays on hypural plate unclear). The third preural (11th caudal) vertebra has an autogenous haemal spine but attached neural spine, the second preural (12th caudal) vertebra appears to have both the neural and haemal spines autogenous, and there is a parhypural and fused hypural plate articulated to the ural centrum and urostyle, all exactly as in the Recent *Luvarus imperialis*. It is impossible to distinguish *Eoluvarus* from *Luvarus* on the basis of the available specimen, which lacks certain details in the poorly preserved dorsal and anal fins and the distal ends of their pterygiophores, although the species *bondei* may be valid. We therefore consider *Eoluvarus* a junior subjective synonym of *Luvarus* Rafinesque, 1810, and its only included species should now be known as *Luvarus bondei*, new combination.

Kushlukia permira Danilchenko (1968:147-149, fig. 18, pl. 36) is based on three specimens of 160-184 mm SL, at least the holotype of which is well preserved, from the same Paleocene strata of Turkmenistan as *Proluvarus*. Danilchenko created for it the family Kushlukidae, which he considered to be closely related to the Luvaridae, both of which families he included in the suborder Scombroidei. *Kushlukia* is similar to *Luvarus* in the following: dorsal and anal pterygiophores firmly sutured distally to form a longitudinal truss around the body; bases of caudal-fin rays broadly overlapping the hypural plate; caudal peduncle slender; anus forward; teeth absent; pelvic fins absent or poorly developed; pelvic bones fully fused and attached to coracoid; ribs thin, attached to centra; opercle broad; anterior dorsal-fin elements short. *Kushlukia* differs from *Luvarus* in the following: 27-28 vertebrae (22 in *Luvarus*); posttemporal small but said to be forked (very large and forked in *Luvarus*); pectoral fin high on body (middle of body in *Luvarus*); bones dense (delicate in *Luvarus*); two dorsal-fin rays to each vertebral segment in the caudal series (mostly one to each segment in *Luvarus*); proximal radials of dorsal and anal pterygiophores with wide shafts and distinct median keels, blades of shafts in contact with one another (shafts narrow, slender and well separated in *Luvarus*); pointed beak-like snout with a small, upturned, terminal mouth (snout more rounded and mouth not upturned in *Luvarus*); scales absent (scales present and bearing prominent clusters of spinules in *Luvarus*).

While we do not have enough information about *Kushlukia* to resolve its affinities cladistically, its known features are consistent with the inclusion of the Kushlukiidae as a family of the Acanthuroidei, but not in the family Luvaridae. In certain features (i.e., the broad pterygiophores, beak-like snout, and reduced posttemporal), *Kushlukia* resembles members of the Acanthuridae, particularly the more pelagic species of *Naso* such as *N. thynnoides* (Figure 23). We conclude that *Kushlukia* is probably an acanthuroid, but in light of the mosaic of luvarid and acanthurid features, the precise relationship of this fossil genus cannot be resolved based on the available evidence.

Luvarus preimperialis Arambourg (1956) is based on two incomplete skeletons of about 62 and 111 mm TL from the Oligocene of Iran. Arambourg suggested that these two specimens are similar in form to early developmental stages of *Luvarus imperialis*, but it is difficult to evaluate this surmise based on the information in his description or the photographs of the specimen. The similarities of *L. preimperialis* to *L. imperialis* are general body shape and arrangement of the caudal skeleton, with the bases of the caudal-fin rays broadly overlapping the hypural plate; coalescence and interdigitation of the distal ends of the dorsal and anal pterygiophores to form a bony truss around the middle of the body, and the feeble ossification of the fragile bones in these relatively small specimens. Features in which *L. preimperialis* differs from *L. imperialis* are as follows: 28 to 30 vertebrae (22 in *L. imperialis*); 10 to 13 caudal-fin rays (16 principal in *L. imperialis*); most neural spines short and directed obliquely posteriorly, not extending much beyond the region of the neural canal, only the neural spines under the rear of the dorsal fin more elongate, but still horizontally directed (neural spines slender and elongate in *L. imperialis*); basal pterygiophores especially elongate, reaching to centra (moderately long in *L. imperialis* and reaching one-half to two-thirds the distance to the centra); haemal spines short and horizontally directed like the neural spines, etc. (relatively long haemal spines and shorter shafts of basal pterygiophores in *L. imperialis*); second preural centrum elongate (not elongate in *L. imperialis*).

The heads of the two specimens of *L. preimperialis* are poorly preserved, as are much of the bodies, and it is impossible to state unequivocally to what family they should be assigned. The few luvarid-like features (caudal rays broadly overlapping hypurals, distal ends of pterygiophores interdigitated to form a truss, delicate bones) of *L. preimperialis* are not unique, among perciforms, to the Luvaridae, and the other known characteristics of *L. preimperialis* are not typical of either the established fossil members of the Luvaridae or of *L. imperialis*. Thus, considerable doubt exists as to any possible relationship between *L. preimperialis* and luvarids or acanthuroids.

Parasites

Several parasitic copepods were found attached to the gills of specimens of *Luvarus* from the Indian Ocean (ZMUT P1400,

1720 mm SL) and from off the coast of Oregon (USNM 296183, 850 mm FL). These were identified by Dr. Roger Cressey of the Smithsonian Institution as *Lutkenia asterodermi* Claus, a relatively rare species previously known only from *Luvarus* from the Mediterranean Sea and western Atlantic Ocean. A second species of the genus, *Lutkenia elongata* Shiino, has been described from *Luvarus* from the eastern Pacific Ocean. *Lutkenia* is a member of the Cercropidae, a small family of four genera and ten species. Species of the other three genera are found mostly on the tetraodontiform *Mola mola*, with a few records from elasmobranchs. Thus, the distribution and associations of these parasites seem to have little phylogenetic significance.

Diagnosis of the Family Luvaridae

All of the previous work and that presented here on the anatomy of the Luvaridae indicates that these fishes exhibit a large number of highly specialized features, many clearly associated with an oceanic pelagic existence, and that they have changed little in structure since at least the early Eocene or late Paleocene. The combination of juvenile and adult features that diagnose both the fossil (with one noted exception) and Recent Luvaridae are as follows: a reduced number of vertebrae (9+13); a modified caudal complex featuring, in adults, deeply bifurcate bases of the caudal-fin rays (16 principal rays plus 7 or 8 procurent rays above and below) broadly overlapping the fused hypural plate and supported by 3 vertebrae; uniquely interdigitated dorsal and anal pterygiophores forming a rigid peripheral structure just below the skin around much of the upper and lower edges of the body; dorsal fin initially with two spines (plus the remnant of a third) and 20–22 soft rays, elements becoming reduced in length and the anterior ones being lost with increasing size; anal fin with no spines and initially 18 to 20 soft rays, the anterior elements being lost with increasing size; pelvic fin initially with one spine and four soft rays, the rays absent in large adults; pelvic girdle initially bilaterally divided, the two halves becoming fused to one another in large adults; about 18 pectoral-fin rays; rays of vertical fins slightly branched with increasing size, but unsegmented except for the more medial rays of the caudal fin, which are also the most branched; mouth small and upper jaw non-protractile; jaw teeth small and conical on the premaxilla and dentary in the young, becoming reduced with increasing specimen size and absent in large adults; seven pleural ribs; no epipleural ribs (except in the Paleocene-Eocene *Proluvarus* and thus not diagnostic at the family level) or intermuscular bones; a large forked posttemporal; infraorbital series consisting of the lachrymal and one rudimentary suborbital element; supraoccipital large and anteriorly displaced, forming much of the dorsal surface of the cranium; ethmoid largely cartilaginous, with a small median ossification; vomer and palatines toothless; parietals absent (present in larvae); basisphenoid absent; a relatively generalized branchial apparatus with

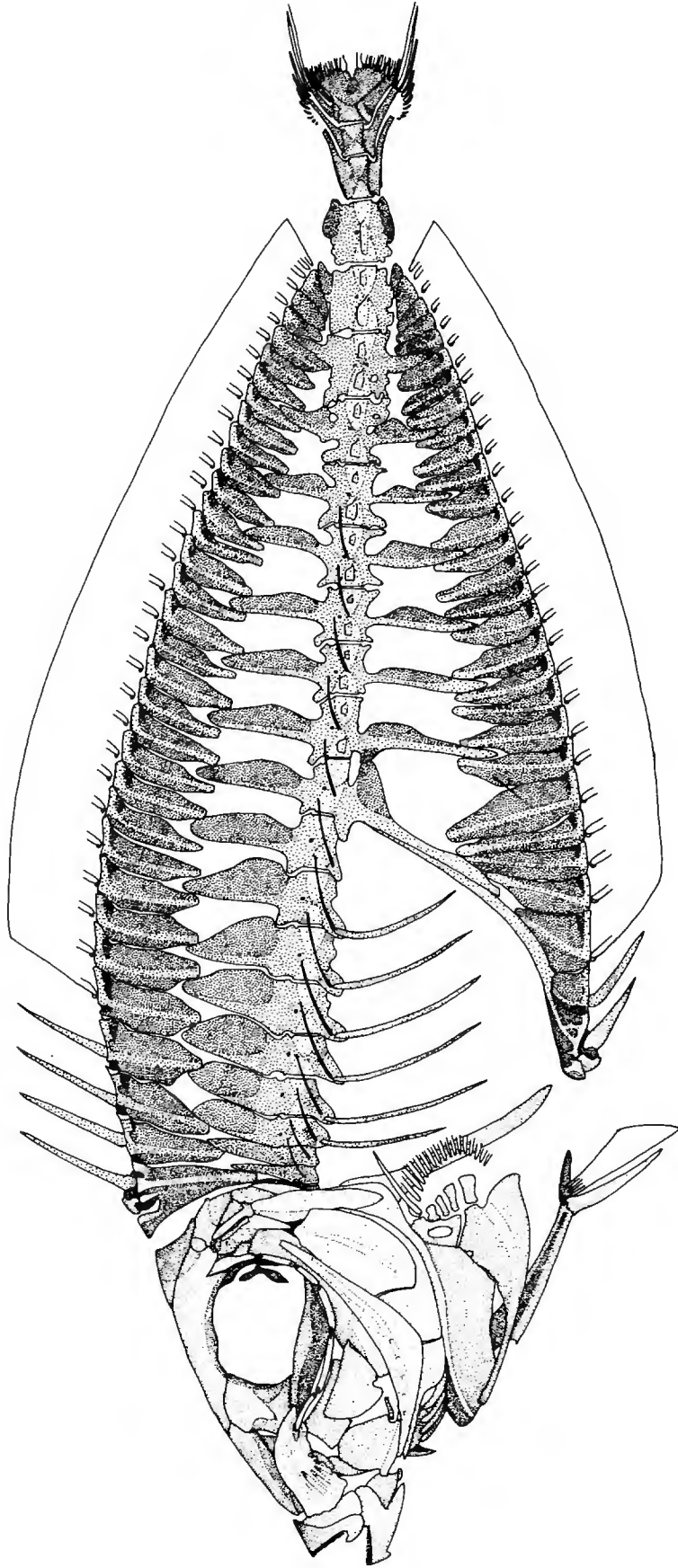


FIGURE 23.—*Naso thynnoides*, RU (JLBSID) 616d, 191 mm SL, lateral view of entire skeleton for comparison with the lateral view of the entire skeleton given in Figure 3 for *L. varus imperialis*.

well-developed gill rakers and large teeth on the lower pharyngeals and on the second to fourth pharyngobranchials (4 basi- (fourth cartilaginous), 3 hypo-, 5 cerato-, 4 epi-, and 4 pharyngobranchials); hyoid arch relatively generalized (1 basi-, 2 hypo-, 1 cerato-, 1 epi-, and 1 interhyal); five branchiostegal rays; scales modified with upright mushroom-like, spinulose, expansions (no true ctenii); long and highly coiled gut, with loop b (see Mok, 1977) on the right side of the stomach; double nostril; restricted gill opening with the membranes broadly attached to the isthmus; a fleshy lateral keel developing on the caudal peduncle with increasing size.

Previously Proposed Relationships

Gregory and Conrad (1943:279–281) concluded their extensive comparative description of *Luvarus* by considering three alternative hypotheses of relationships, that *Luvarus* is (1) “an offshoot of the basic carangoid stock”; (2) “a modified scombroid, its nearest relative being the tunny”; or (3) “the sole known representative of a distinct order, Luvariformes (Jordan), and that its resemblances to carangoids and scombroids are due to convergence (Roule).” A fourth hypothesis, not considered by Gregory and Conrad (1943), is that of Regan (1902), who proposed that “the Luvaridae are closely allied to the Acanthuridae.” A discussion of each argument follows.

1. CARANGOID HYPOTHESIS.—According to Gregory and Conrad (1943), the carangoid affinities of *Luvarus* are supported by the following: a low number of vertebrae (23 vs. 31 or more in scombroids, with the exception of the billfishes, which have 24–26); superficial similarities in the interlocking of the expanded distal regions of the basal pterygiophores of the dorsal and anal fins; continuous dorsal and anal fins without separate finlets; low number and sessile condition of the ribs; similarities in the shape of the pelvis, small mouth, and dorsal hump or convexity of the skull as found in some stages of *Luvarus* and *Coryphaena* (the humped condition perhaps advanced), and a few other minor points.

The only substantial considerations of the relationships of *Luvarus* since the work of Gregory and Conrad (1943) are those of Matsubara (1955 and 1963), the latter proposing a close relationship to carangoids. In his treatise on fish morphology and hierarchy, Matsubara (1955:539–540) considered *Luvarus* a highly specialized scombroid that diverged early in the evolutionary diversification of these fishes. In his subsequent analysis of fish classification, Matsubara (1963) gave a more detailed comparison of *Luvarus* with various subgroups of his suborder Scombrina. He noted that *Luvarus* is similar to the suborder Scombrina in having non-protractile premaxillae, abdominal vertebrae without well-developed parapophyses and with ribs originating from the centra, and the hypural plate completely covered by the bases of the caudal-fin rays. Conversely, he noted that *Luvarus* resembled his suborder Stromateina in having non-protractile premaxillae, vertebrae reduced to 23 (urostyler complex apparently counted as two

centra), and dorsal and ventral body profiles supported by a longitudinal truss formed by the extensive interdigitation of the distal ends of the pterygiophores of the dorsal and anal fins. Matsubara also pointed out, however, that *Luvarus* differs from both scombroids and stromateoids in having gill membranes united to the isthmus, pelvic fin reduced to a single small spine and pelvic bones fused into a single piece in adults, and the eye placed lower than the level of the centra of the abdominal vertebrae. Because of these differences, Matsubara placed *Luvarus* in a monotypic suborder, Luvarina, of his order Percida, which he concluded arose from a carangid-like ancestor. He believed that the steep dorsal profile of the head and reduced dorsal spines of *Luvarus* indicated a common ancestry with the coryphaenids of his Carangina. He expressed his conclusions in a phylogenetic tree rooted in a *Ctenothrissa*-like ancestor leading to the perciforms, from one branch of which diverged, in sequence, the Carangina, Stromateina, Luvarina, and Scombrina (Matsubara, 1963:395).

Of the features listed by Gregory and Conrad (1943) and Matsubara (1963) as supporting a *Luvarus*-carangoid connection, those that clearly represent specializations are shared with *Luvarus* by only one or a few carangids (e.g., superficial similarity of pterygiophores in *Trachinotus*, humped head in *Coryphaena*), and furthermore are not borne out as homologous with close inspection of the morphology. The remaining features are common among perciforms and thus fail as synapomorphies of *Luvarus* and carangoids. More importantly, *Luvarus* lacks the two specializations that unite the carangoids (including *Nematistius*) as a monophyletic group: an anterior extension of the nasal canal of the lateralis system and small adherent cycloid scales. *Luvarus* further lacks the three synapomorphies that unite echeneoids (*Coryphaena*, *Rachycentron*, and echeneids) and carangids: two separate prenasal canal units, absence of the bony stay posterior to the ultimate dorsal and anal fin pterygiophores, and presence of a characteristic lamellar expansion on the coracoid (Johnson, 1984; Smith-Vaniz, 1984). We thus reject the hypothesis that *Luvarus* is closely related to carangoids.

2. SCOMBROID HYPOTHESIS.—The second hypothesis proposed by Conrad and Gregory (1943), that *Luvarus* is a modified scombroid, originated with Regan (1903) and has received wide acceptance. Regan had initially (1902) concluded that *Luvarus* is most closely related to the Acanthuridae but reversed his position in 1903 after having considered evidence from the caudal skeleton. In the latter paper, Regan (1903) stated that “*Luvarus* must be considered to be a most abnormal and specialized Scombroid, and that the features in which it approaches the Acanthuridae . . . are to be regarded as the result of convergence.” He further explained that “Mr. Boulenger has pointed out to me that the Scombridae and Xiphiidae are remarkable in that the deeply forked bases of the rays of the caudal fin are inserted nearly vertically and extend over the hypural so as to almost entirely conceal that bone, those of the upper and lower series nearly meeting in the middle

line on each side. This feature is also seen in *Luvarus*, and is well illustrated by Mr. Waite's photograph." Regan further emphasized the similarities of the vertebral structures in the caudal peduncle, stating that scombrids have the centra "square and have broad flat neural and haemal spines, which are directed horizontally backwards, so as to embrace the succeeding vertebrae above and below, and the vertebrae between the procurvent caudal rays are greatly and progressively shortened. A similar condition obtains in *Luvarus* in which, however, the first vertebra of the caudal peduncle [the pivotal 11th caudal vertebra] is only half as long as the one preceding it, but otherwise normal." He also noted that the "sessile blade-like ribs exactly resemble the sessile anterior ribs of a *Thunnus*."

Regan (1903) also compared the skull and pectoral girdle of *Luvarus* with that of scombrids, and illustrated the posttemporal and all but the anterior end of the skull, which was damaged in his specimen. He noted, erroneously, the unique absence of the supracleithrum in *Luvarus* (the supracleithrum actually is well developed in *Luvarus*, see descriptions herein), but also found what he believed to be numerous scombrid-like features: "The post-clavicle is small, the clavicle, scapula, coracoid, and pterygials exactly like those of *Thunnus*. The pelvic bones are completely united [separate in young, see descriptions herein], but do not diverge posteriorly at the vent, as has been erroneously stated." "In the skull, which is best understood by comparison with that of a *Thunnus*, the ossified sclerotic and broad opercular bones are typically Scombroidei features." After describing the main features of the skull of *Thunnus*, Regan (1903) concluded: "The skull of *Luvarus* may be regarded as that of a *Thunnus* in which the posterior, nearly vertical part of the roof has become very long and oblique, the epiotics being greatly enlarged and united in the middle line behind the supra-occipital, whilst the latter bone is carried forwards to the level of the prefrontals and forms the roof of the cavity between the frontals, which is extremely large and is open anteriorly, its floor now being formed mainly by the united alisphenoids and prefrontals."

Regan's arguments for general similarities in the skulls of *Luvarus* and scombrids are ambiguous and in no way convincing. It seems clear that it is primarily similarities in the caudal region, particularly hypurostegy of the fin rays, that led him to favor the scombroidei hypothesis over his original proposal that *Luvarus* is related to acanthurids.

Following the lead of Günther (1866), Regan (1903, 1909), and subsequent authors, Gregory and Conrad (1943) set out to determine if the generally tuna-like external appearance of *Luvarus* is also evident in its osteological structure. They concluded that there is an array of anatomical similarities, and "that both the caudal region and the entire skull abound in many and detailed specializations which may be readily conceived as stages beyond those of the tunnies (*Thunnus*) and bonitos (*Auxis*)." Nonetheless, Gregory and Conrad could not choose definitely between the carangoid and scombroidei hypotheses, stating that "after again comparing the *Luvarus*

braincase with those of several carangids, we now realize that some of the special resemblances between *Luvarus* and the tunny may be partly due to the large size of both of these forms, while some of the differences between *Luvarus* and the carangids may be conditioned by the small size of the latter." They also noted the following: "Perhaps the chief difficulty in deriving the skeleton of *Luvarus* from that of any of the tunny group (Thunnidae, Katsuwonidae) would be that if, as seems highly probable, the vertebral formula in the primitive percomorphs was 10+14, the numbers would have to be increased to thirty-nine in *Auxis* and then decreased again to the 9+12 in *Luvarus*." They thought this unlikely, although they cited *Mola* and ostraciid tetraodontiforms as fishes that have fewer vertebrae than the percoid norm of 24 and discussed the then current experimental research on the relationship of vertebral numbers to water temperature during early developmental stages. Finally, they noted: "Whatever may be the ultimate answer to these problems, the fact remains that among the extant or fossil scombroidei (excluding the Xiphiiformes) none is known in which the vertebral formula even remotely approaches that of *Luvarus* and the carangoids. Consequently, we feel obliged to give this fact its due weight in the present discussion."

The inability of Gregory and Conrad (1943) to resolve the relationships of *Luvarus* can probably be attributed to several factors. First, their approach was mainly phenetic; they emphasized differences over similarities and did not consider polarity of character states. Certain character complexes (e.g., the caudal skeleton) were overemphasized, whereas others (e.g., the gill arches) were treated superficially. Although Roule's (1924) observations on the larvae were discussed, no attempt was made to compare the larval morphology with that of other groups. Finally, and perhaps most importantly, the possibility that *Luvarus* might be related to some percomorph group other than carangids or scombrids was never considered. With considerably more information available now about the larval and adult morphology of *Luvarus* and most other percomorphs, and with cladistic methodology, unequivocal refutation of the carangoid (see 1 above) and scombroidei (2 above) hypotheses is possible.

The most recent definition of the Scombroidei is that of Johnson (1986). Johnson identified six synapomorphies of the Scombroidei, and a total of five that are successively shared with scombroidei by several outgroup taxa. Included among these are distinctive specializations of the primary jaw dentition, neurocranium, and gill arches believed to be unique among percomorphs. Of these 11 synapomorphies that diagnose the scombroidei and support their close relationship to specific percomorph taxa, *Luvarus* exhibits only one, a non-protrusible upper jaw, a feature that has evolved independently numerous times. Within the Scombroidei, *Luvarus* shares some common reductive features, particularly in the caudal complex, with certain subgroups. Of six synapomorphies that unite the gempylids, scombrids, and billfishes, three common

reductions, absence of predorsals, absence of the procurent spur, and ontogenetic fusion of hypurals 1-2 and 3-4, are shared by *Luvarus*. Likewise, of the six synapomorphies uniting scombrids and billfishes, *Luvarus* exhibits three, absence of fang-like premaxillary teeth, absence of the posterior uroneural pair, and well-developed hypurostegy. The first two of these are, again, very common among percoids. The last, hypurostegy, the extreme anterior extension of the caudal-fin ray bases to cover each side of the hypural plate, is the character most emphasized by both Regan (1903, 1909) and Gregory and Conrad (1943) as indicative of a close relationship between *Luvarus* and scombrids and billfishes. However, hypurostegy is not unique to these groups but is found in a variety of obviously unrelated fossil and extant families (see, for example, Le Danois and Le Danois, 1963, and Patterson, 1968) that have stiff caudal fins with high aspect ratios and relatively consolidated caudal skeletons. This type of caudal propulsive unit, specifically adapted to high-speed power and efficiency, has evolved repeatedly in pelagic fishes, and its phylogenetic significance is necessarily suspect without substantial corroborative evidence.

Treatment of hypurostegy as a synapomorphy of *Luvarus* and the Scombridae (including billfishes), i.e., placement of *Luvarus* within or as the sister group of scombrids, is not parsimonious, because *Luvarus* lacks most of the unique innovative specializations that diagnose the suborder Scombroidei and its closest relatives; hypothesized reversals would be required in at least 14 derived characters, including reversion to primitive configurations in dentition, gill arches, and certain aspects of the neurocranium. We conclude that hypurostegy and the other specializations shared by *Luvarus* and scombrids, most of which are reductive features common among percomorphs, were independently evolved, and we reject the hypothesis that *Luvarus* is a highly modified scombroidei or is related to the Scombroidei at all.

3. "LUVARIFORMES".—The third hypothesis considered by Gregory and Conrad (1943) was proposed originally by Roule (1924). Roule argued that the clear-cut differences in the larval morphology of *Luvarus* and scombrids indicated that similarities in adult morphology must be the result of convergence. Accordingly, he elevated Jordan's (1923) division Luvariformes to ordinal rank and implied that its origin might be found among more primitive fishes with cartilaginous skeletons, his only apparent support for this surmise being that there is a considerable amount of cartilage in the skeleton of *Luvarus*. Although there is no basis in fact for Roule's "primitive origin" hypothesis (and we will not belabor it here), his conclusions concerning convergence with carangoids and scombroids were correct, as we have discussed above and as is supported by our final phylogenetic hypothesis.

Before examining the fourth and final hypothesis, two other groups of oceanic perciforms, the suborder Stromateoidei and the order Lampriformes, warrant brief consideration regarding the possible affinities of *Luvarus*. These groups were consid-

ered relatives of *Luvarus* in a classification of the order "Scombres" by Le Danois and Le Danois (1963). This classification is based on the presence of hypurostegy and the presence or absence of an erisme, a crest on the skull (Le Danois, 1963). Le Danois and Le Danois included the scombroids, xiphioids, carangoids, and echeuids as suborders in their group B, "Hypurostèges Anerismatiques," lacking an erisme. Their group C, "Hypurostèges Erismatiques," contains two suborders, the Astrodermoidea (*Luvaridae*, *Coryphaenidae*, *Gastrochismidae*, *Nomeidae*, and *Stromateidae*) and the Selenichthyoidea (*Lampridae*, *Veliferidae*, and four other families).

The Stromateoidei comprises six families (Horn, 1984), two of which, the Centrolophidae and the Stromateidae, superficially resemble *Luvarus* in certain features: a long continuous dorsal fin with a reduced number of spines; relatively small mouth with small conical teeth; pelvic fin sometimes reduced or absent; and a *Luvarus*-like body shape with an inflated, protruding snout. Beyond the superficial similarities with centrolophids and stromateids, there is no evidence to suggest that *Luvarus* is a stromateoid. The osteological data presented by Haedrich (1967) indicate few internal similarities between stromateoids and *Luvarus* aside from general features common to many perciforms, and no synapomorphies between either the Centrolophidae or Stromateidae and *Luvarus*. Moreover, *Luvarus* lacks the complexly toothed, sacular outgrowths of the esophagus that characterize five of the six stromateoid families, including centrolophids and stromateids.

The order Lampriformes (allotriognaths) comprises seven families (Oelschläger, 1983; Olney, 1984) of highly specialized meso- and epipelagic fishes, all but two of which (*Lampridae* and *Veliferidae*) are quite elongate, ribbon-like, and have asymmetrical caudal fins. The *Veliferidae*, which Oelschläger showed to be the most primitive or, at least, generalized, of the order, has an external appearance in many ways similar to that of *Luvarus*, especially at younger stages, including a long continuous dorsal fin, long dorsal- and anal-fin rays, a small mouth, and a moderately convex snout; the body is much deeper than in any except the larval stages of *Luvarus*.

Again, beyond the superficial similarities with *Velifer*, we see no evidence to suggest that *Luvarus* is a lampriform. The osteological data given by Oelschläger (1983) show few trenchant similarities between lampriforms and *Luvarus* and no clear synapomorphies between the *Veliferidae* and *Luvarus*. Moreover, *Luvarus* lacks the single most important synapomorphy that unites the seven lampriform families, maxillae and premaxillae protrusible as a unit, and also lacks palatamaxillary articulations, the diagnostic specialization of the *Veliferidae*, including the highly protrusible and microphagous jaw apparatus and the scaly sheaths on the dorsal and anal fins (Oelschläger, 1983:121).

4. ACANTHUROID HYPOTHESIS.—A fourth hypothesis, not considered by Gregory and Conrad (1943), is the one initially proposed by Regan (1902), but rejected by him a year later in

his defense of the scombroid hypothesis (Regan, 1903); i.e., that "the Luvaridae are closely allied to the Acanthuridae." Regan cited numerous similarities between *Luvarus* and acanthurids, most of which are either primitive or occur commonly as specializations among various percomorphs. These include an elongate, compressed body with a slender caudal peduncle and deep caudal fin, long dorsal and anal fins, lateral line concurrent with the dorsal profile, four gills with a slit behind the fourth, short gill rakers, separate lower pharyngeals, well-developed pseudobranch, and toothless palate. Cited similarities less common in perciforms include anteroposteriorly compressed upper pharyngeals, gill membranes broadly united at the isthmus, five branchiostegal rays, and a small mouth with non-protrusible premaxillae to which the maxillae are immovably attached. Regan also noted similarities in the visceral anatomy, a large, thick-walled stomach, few short, simple pyloric caeca, and a long, highly coiled gut (noted previously by Nardo, 1827, Cuvier and Valenciennes, 1833, and Haller, 1881) and surmised that both *Luvarus* and acanthurids are "vegetable feeders."

Regan (1902) found the most convincing evidence for a *Luvarus*-acanthuroid relationship in the vertebral column, "the vertebrae numbering twenty-two in both cases, the first being very short and more or less regularly convex anteriorly, fitting the concavity formed by the facets of the basi- and exoccipitals, the second without ribs, as usual in Perciform fishes, the next seven bearing ribs, and succeeded by thirteen caudals." Finally, he found specific similarities between *Luvarus* and the acanthurid genus *Naso* (= *Naseus*), "notably in the long anal fin extending to the vent, which is situated just behind the origin of the ventrals, and in the physiognomy of the head," as well as in the small pointed jaw teeth (present only in young *Luvarus*), the keel-like plates on the caudal peduncle, and the small posterior nostril.

Regan (1902) concluded that the "Luvaridae may be considered as ultra-specialized Acanthuridae," being similar to the latter in a number of features but differing as follows: skeleton poorly ossified; dentition weak; posttemporal large and forked; precaudal vertebrae with rudimentary parapophyses; pleural ribs large and sessile; epipeural ribs absent; anterior dorsal spines not pungent; anal spines absent.

Regan (1903), disenchanted with his acanthuroid hypothesis less than a year after its publication, rejected it in favor of the scombroid hypothesis. Apparently because of this, it has not been taken seriously by any subsequent author and was not even cited by Conrad and Gregory (1943). We believe Regan's original hypothesis was correct. The character analysis that follows, based on both larval and adult morphology, demonstrates conclusively that *Luvarus* is a member of the Acanthuroidei.

Acanthuroid Characters

As a preface to our analysis of acanthuroid relationships, a brief synopsis of certain characteristics of the eight genera

usually placed in the Acanthuroidei is summarized from Tyler (1970a). (That paper incorporated data from three previous papers devoted to Recent acanthurid classification, phylogeny, and characteristics: Aoyagi, 1948; Randall, 1955; and Smith, 1966.)

Prionurus (Figure 24): Three or more enlarged fixed scale plates on a slender caudal peduncle; pelvic fin 1, 5; teeth fixed, compressed, with well-developed denticulations; seven to nine dorsal spines; scales with upright spinules; five separate hypurals; three epurals; five branchiostegal rays (1+4, the first on the middle of the ventral edge of the ceratohyal and the other four more posteriorly on the ceratohyal and on the epihyal); first dorsal and anal spines well developed, easily seen externally; lateral expansion of distal ends of first dorsal and anal pterygiophores slight; predorsal bones usually present; suborbital shelf present.

Naso (Figures 23, 25): One or two enlarged fixed scale plates on a slender caudal peduncle; pelvic fin 1, 3; teeth fixed, conical but slightly compressed distally, denticulations variously small, minute or absent; five to eight dorsal spines, one fewer apparent externally, the first greatly reduced and not protruding through epidermis, similar to the first anal spine; scales with upright spinules; five hypurals, all fused into a single plate; three epurals in most species (two in at least one species, *N. thynnoides*, Figure 23) and the single pair of uroneurals (found in all acanthurids) reduced; four branchiostegal rays (0+4); reduced first dorsal and anal spines rotate downward into a deep vertical groove at anterodistal corner of first pterygiophore; lateral expansion of distal regions of first dorsal and anal pterygiophores great, more than twice that of the other genera, except in *N. thynnoides* in which only the anal pterygiophore is greatly expanded; predorsal bones absent; suborbital shelf absent.

Paracanthurus (Figure 26): Folding spine in a broad groove on a deep caudal peduncle; pelvic fin 1, 3; teeth fixed, compressed, with well-developed denticulations; nine dorsal spines; scales with upright spinules; five separate hypurals; three epurals; five branchiostegal rays (1+4); first dorsal and anal spines well developed, easily seen externally; lateral expansion of distal regions of first dorsal and anal pterygiophores moderate; predorsal bones absent; suborbital shelf present.

Zebbrasoma: Folding spine in a shallow groove on a deep caudal peduncle; pelvic fin 1, 5; teeth fixed, compressed, with well-developed denticulations; four or five dorsal spines; scales with upright spinules; five separate hypurals; three epurals; five branchiostegal rays (1+4); first dorsal and anal spines well developed, easily seen externally; lateral expansion of distal ends of first dorsal and anal pterygiophores slight to relatively well developed (but no more than one-half as great as in *Naso*); predorsal bones absent; suborbital shelf present.

Acanthurus (Figure 27): Folding spine in a well-defined deep groove on a deep caudal peduncle; pelvic fin 1, 5; teeth fixed, compressed, with well-developed denticulations; six to nine (usually nine) dorsal spines; scales with short unraised

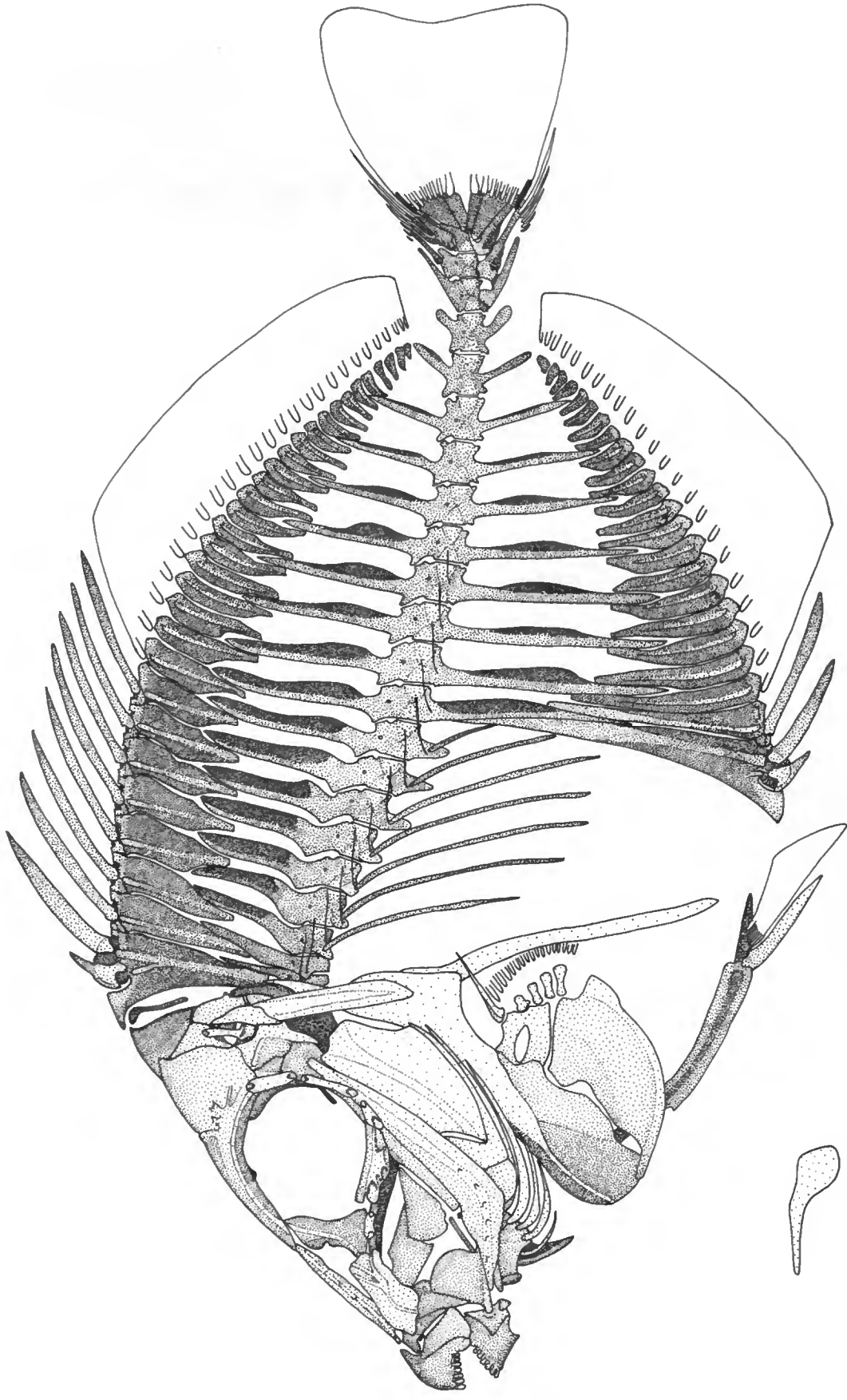


FIGURE 24.—*Prionurus scalprum*, ANSP 109779, 44.3 mm SL, lateral view of entire skeleton.

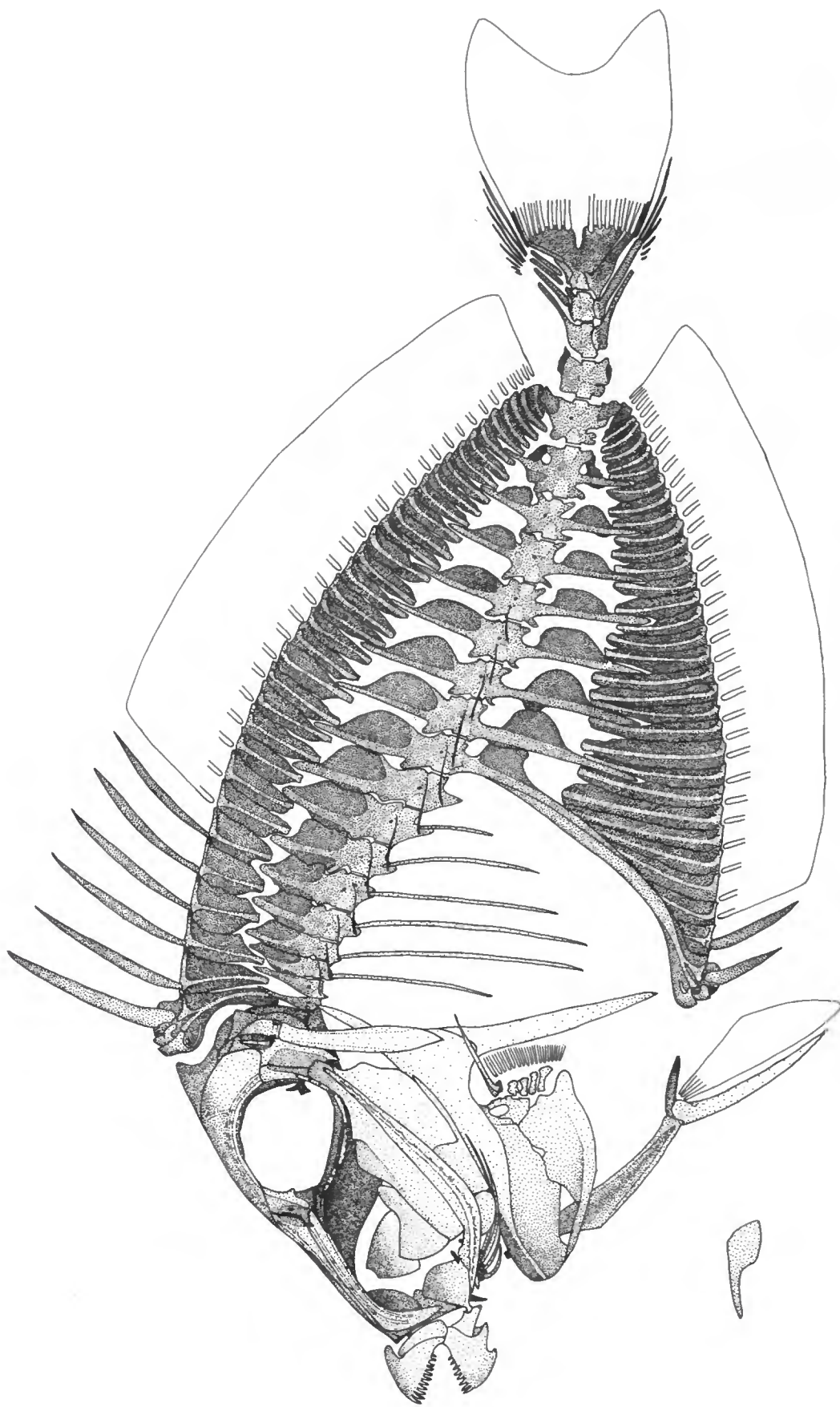


FIGURE 25.—*Naso lateralis*, ANSP 109497, 111 mm SL, lateral view of entire skeleton.

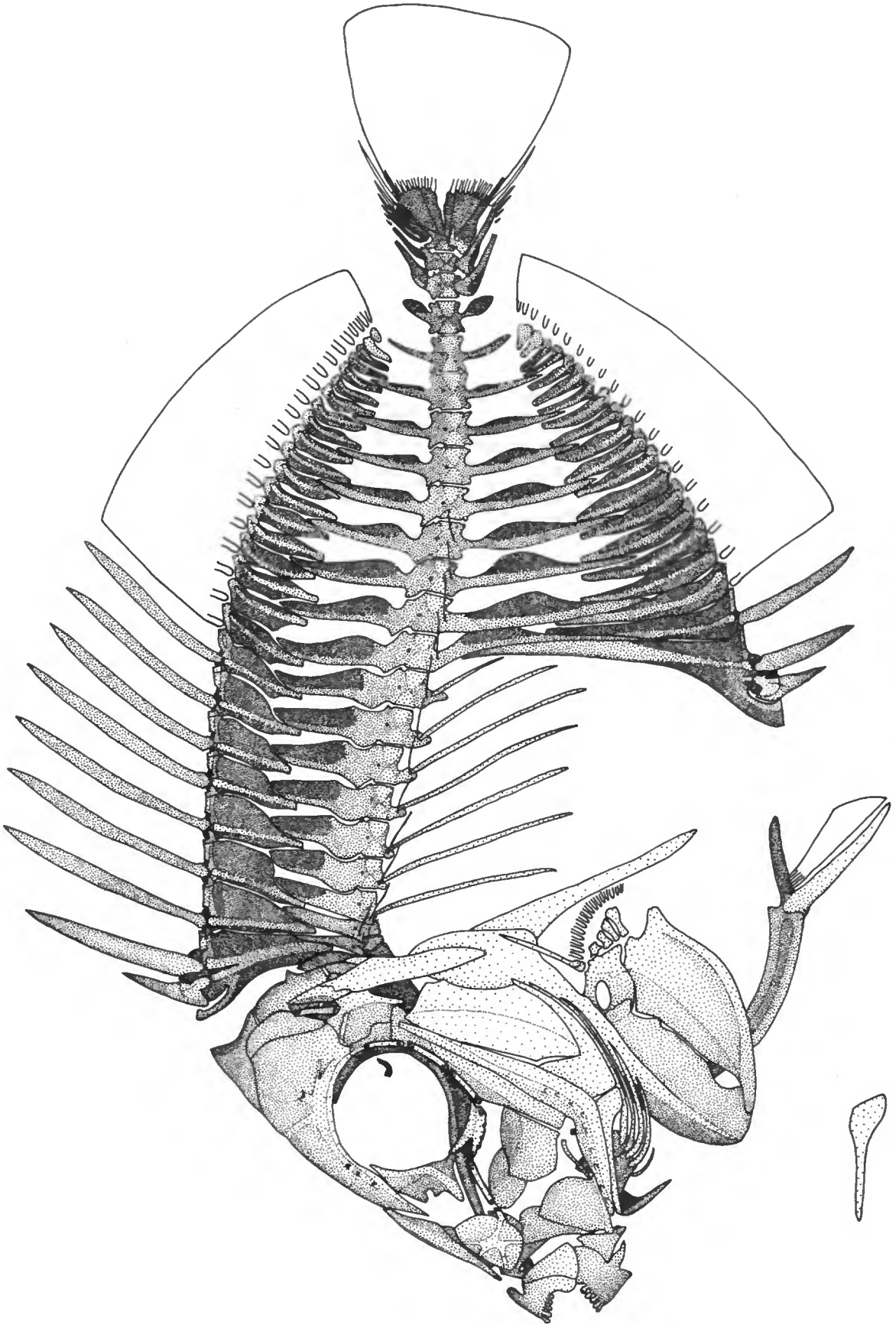


FIGURE 26.—*Paracanthurus hepatus*, ANSP 108444, 31.6 mm SL, lateral view of entire skeleton.

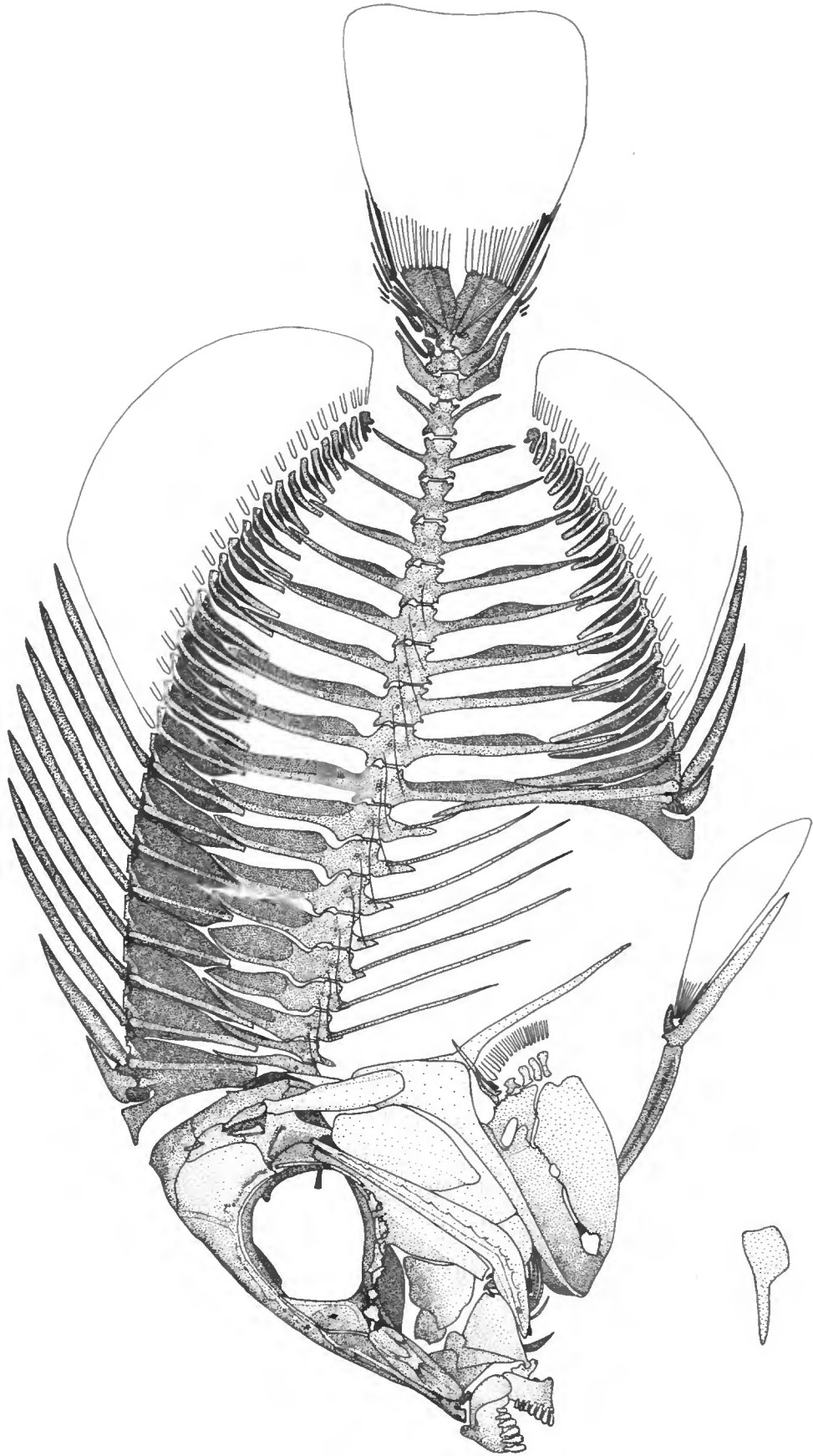


FIGURE 27.—*Acanthurus triostegus*, ANSP 109491, 46.2 mm SL, lateral view of entire skeleton.

ctenii at posterior edges; five separate hypurals; three epurals; five branchiostegal rays (1+4); first dorsal and anal spines well developed, easily seen externally; lateral expansion of distal ends of first dorsal and anal pterygiophores slight; predorsal bones absent; suborbital shelf absent.

Ctenochaetus: Externally like *Acanthurus* except teeth movable, more numerous, elongate and well-denticulated on one side only; dorsal spines always eight; internally like *Acanthurus* except that the first of the five branchiostegal rays is expanded, and the distal ends of the first dorsal and anal pterygiophores are slightly more laterally expanded.

Zanclidae (Figure 28): No folding spine or enlarged fixed scale plates on the deep caudal peduncle; pelvic fin I, 5; teeth numerous, movable, elongate, brush-like, with smooth edges; seven dorsal spines, the third exceptionally elongate; scales rough, with a serrate vertical ridge; five separate hypurals; three epurals; five branchiostegal rays (1+4); first dorsal and anal spines short but well developed, easily seen externally; lateral expansion of dorsal ends of first dorsal and anal pterygiophores slight; one predorsal bone; suborbital shelf present. Zanclids resemble acanthurids in having 16 principal caudal fin rays and no dorsal pterygiophores between the neural spines of the third and fourth vertebrae (Blot and Voruz, 1970, 1975; Blot, 1984), but differ notably in having the first dorsal spine borne on a separate pterygiophore (except in the Eocene *Eozanclus* with two spines on the first pterygiophore, see Blot and Voruz, 1975), greater body depth, longer dorsal spines and smooth edges on comb-like teeth.

Siganidae (Figure 29): No folding spine or enlarged fixed scale plates on moderate caudal peduncle; pelvic fin I, 3, I; teeth fixed, compressed, notched or sharply incised; 13 dorsal spines; scales cycloid; five separate hypurals; three epurals; five branchiostegal rays (1+4, the first expanded as in *Ctenochaetus*); first dorsal and anal spines well developed, easily seen externally; lateral expansions of dorsal ends of first dorsal and anal pterygiophores slight; predorsal bones absent; suborbital shelf absent. Siganids differ notably from acanthurids and zanclids in having 17 principal caudal fin rays, a dorsal pterygiophore between the neural spines of the third and fourth vertebrae and none between the fifth and sixth, more dorsal (13) and anal (7) spines, two pelvic spines, one more vertebra (23), serrate teeth, palatine with two ossifications (see Starks, 1907; Gosline, 1968; and Figure 34d), and cycloid scales.

Outgroups (Figures 30–33): To facilitate comparisons with acanthuroids, we include lateral views of skeletons of representative outgroup taxa: Pomacanthidae, *Holacanthus ciliaris* (Figure 30); Chaetodontidae, *Chaetodon striatus* (Figure 31); Ehippiidae, *Platax teira* (Figure 32); and Scatophagidae, *Selenotoca multifasciata* (Figure 33).

Character Analysis

In order to test Regan's (1902) hypothesis that *Luvarus* is most closely related to the Acanthuridae, we undertook a

cladistic analysis of the intrarelationships of the suborder Acanthuroidei. Previous classifications have most frequently treated acanthuroids as members of the old Squamipinnes (sensu Cuvier, 1817). So that we might identify precise outgroups for the analysis, we re-examined the most recent and only formal cladistic hypothesis of relationships among those families usually included in the Squamipinnes, that of Mok and Shen (1983, fig. 22).

Several authors (see Tyler, 1980) have proposed that acanthuroids are closely related to tetraodontiforms. According to Tyler (1980:15) and Rosen (1984), this idea originated with Dareste's (1872) proposal of a close relationship between the Acanthuridae and balistoids (also see Winterbottom, 1974). Mok and Shen (1983) concluded that the Acanthuroidei (Siganidae, Acanthuridae, and Zanclidae, as they defined the suborder) are the sister group of the Tetraodontiformes, but cited only two characters in support of this hypothesis; i.e., association of pleural ribs with the first or second vertebrae and epipleural ribs lacking on the first vertebra, both of which they misinterpreted. Contrary to Mok and Shen (1983), among acanthuroids the first pleural rib occurs on the second vertebra only in siganids, not in *Naso lituratus* (Figure 25) or *Zanclus* (Figure 28). Rosen (1984) was also mistaken when he stated that "acanthuroids generally have the first pleural rib on the second (vertebra)." Our data on the presence or absence of an epipleural rib on the first vertebra in acanthuroids are also at odds with those of Mok and Shen (1983), and we agree with Rosen's (1984) assessment that this condition is probably not homologous with that of tetraodontiforms.

Rosen (1984) rejected the acanthuroid-tetraodontiform connection and hypothesized that zeoids are the sister group of tetraodontiforms and that caproids are the sister group of zeoids plus tetraodontiforms. Because a full examination of Rosen's hypotheses and the supporting evidence is beyond the scope and objectives of our paper, we tentatively accept them and exclude tetraodontiforms from consideration in our analysis of acanthuroid relationships; nonetheless, we believe these hypotheses need further examination and testing. Rosen's dismissal of Dareste's (1872) evidence for a close relationship between acanthurids and balistoids seems cursory, and some of Dareste's characters (e.g., configuration of the ethmoid, association of the first dorsal pterygiophore with the neurocranium) probably deserve additional careful consideration. Winterbottom (1974) noted that there is considerable myological evidence to support Dareste's idea. Furthermore, a fundamental tenet of Rosen's hypothesis of a zeiform-tetraodontiform connection is that triacanthoids are the sister group of all other tetraodontiforms, and this relationship remains open to question; in Rosen's scheme it is supported by six characters, five of which are reductive. If Rosen's rejection of Dareste's hypothesis proves incorrect, a few of our character polarity assessments might be affected, because balistoids (or tetraodontiforms as a whole) would become the first outgroup for acanthuroids; however, this would not alter our conclusions about the relationships of *Luvarus*.

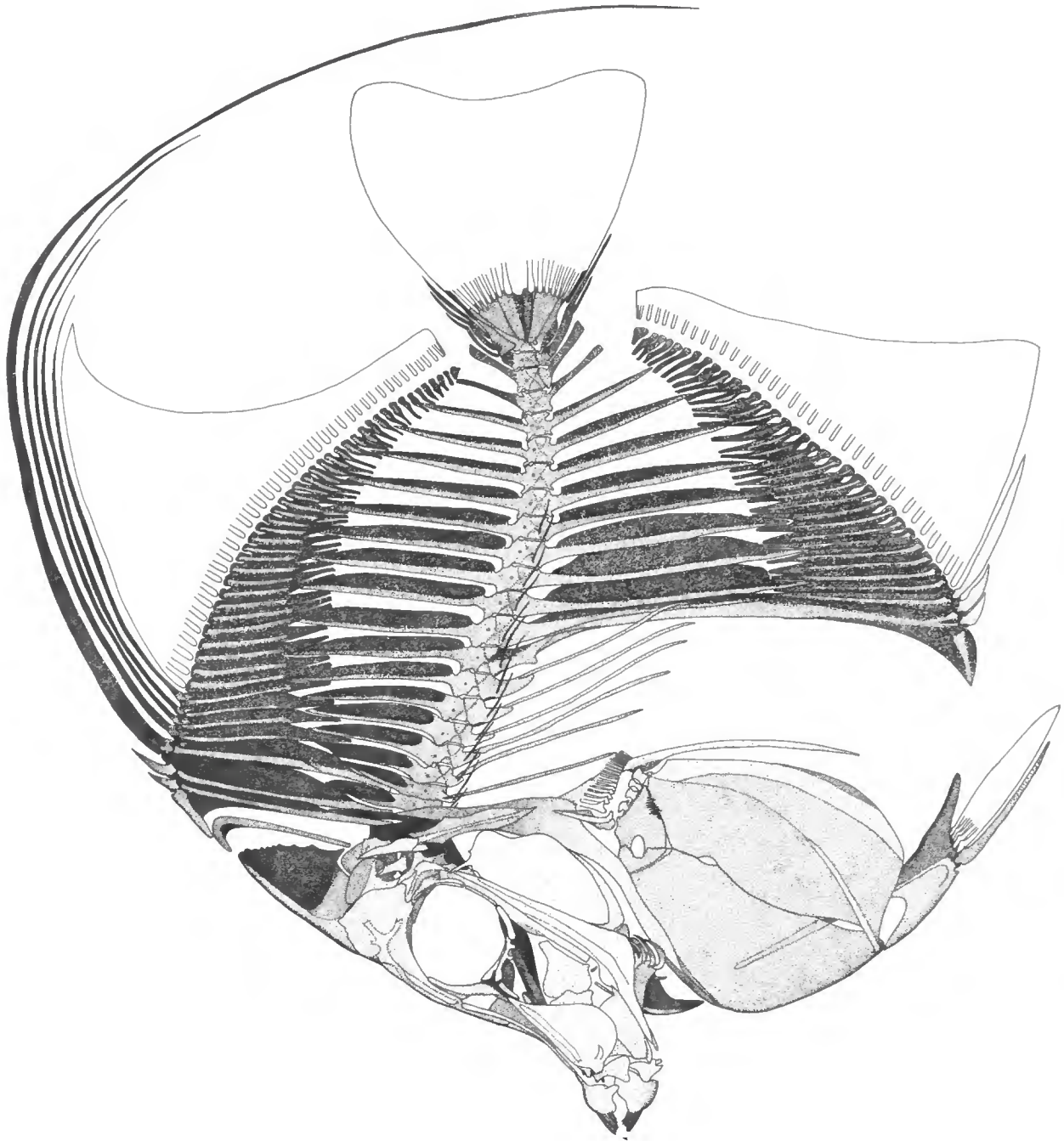


FIGURE 28.—*Zancus cornutus*, ANSP 109502, 66.4 mm SL, lateral view of entire skeleton.

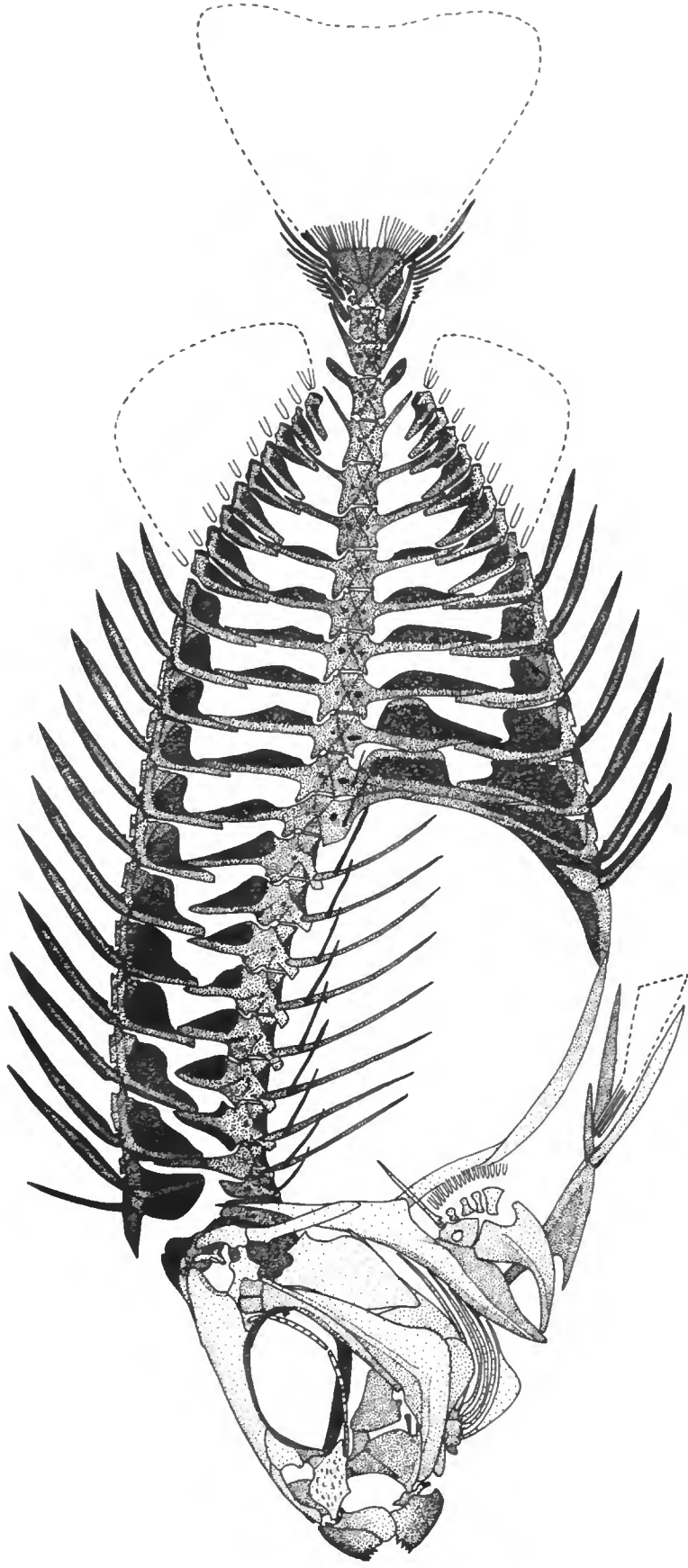


FIGURE 29.—*Siganius canaliculatus*, ANSP 77804, 55.9 mm SL, lateral view of entire skeleton.

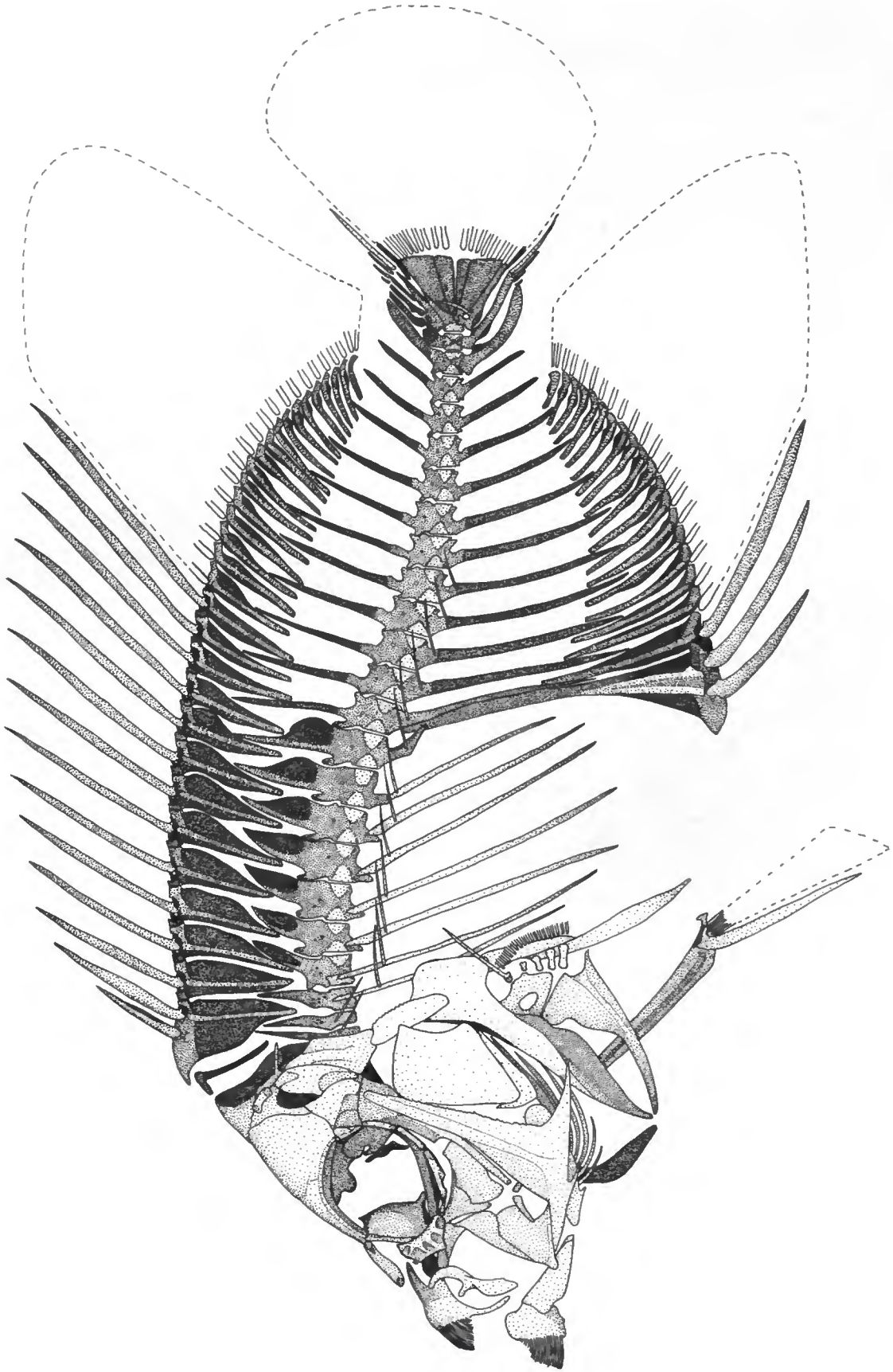


FIGURE 30.—*Holacanthus ciliaris*, ANSP 91094, 54.4 mm SL, lateral view of entire skeleton.

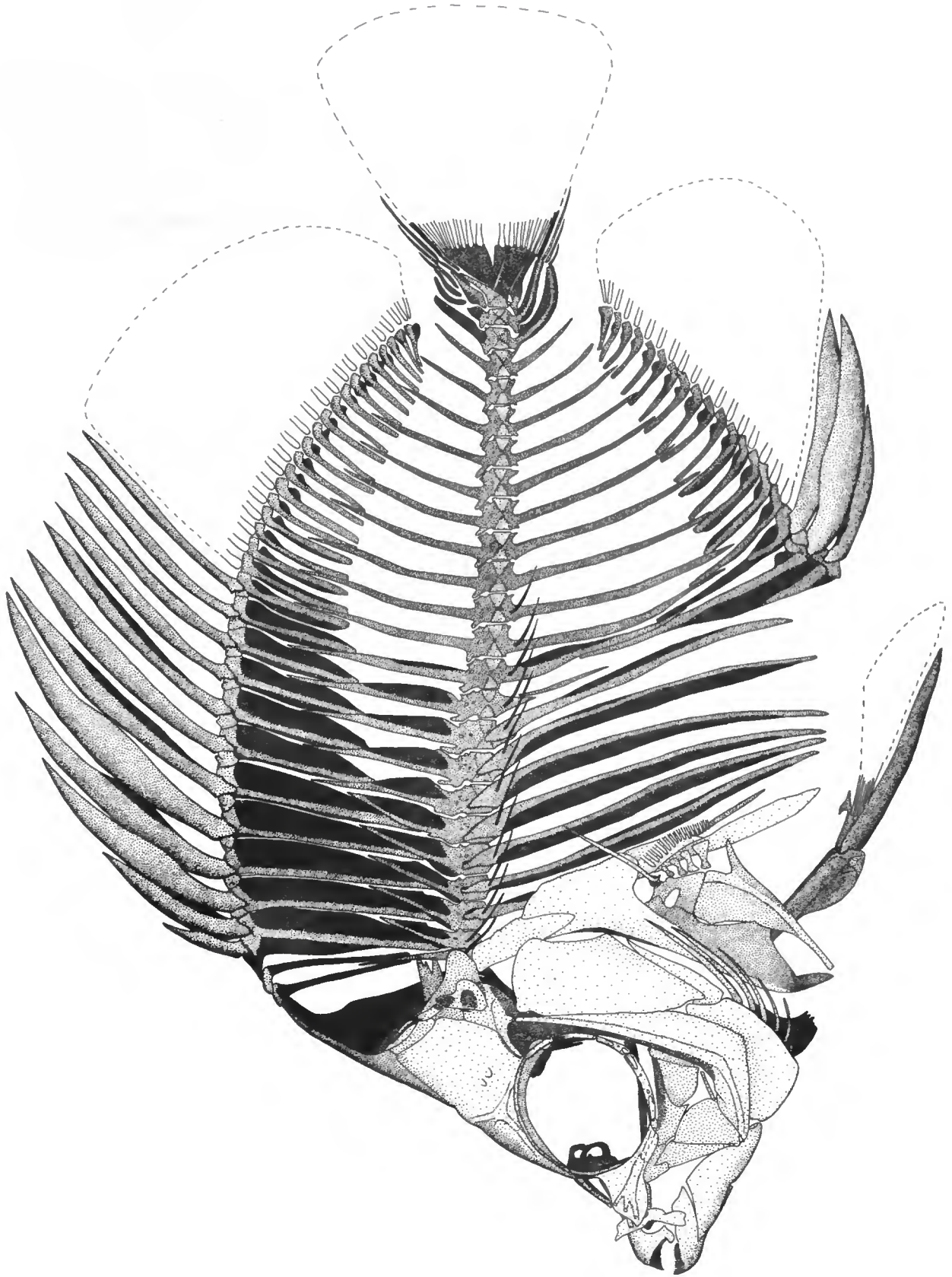


FIGURE 31.—*Chaetodon striatus*, ANSP 9118, 44.6 mm SL, lateral view of entire skeleton.

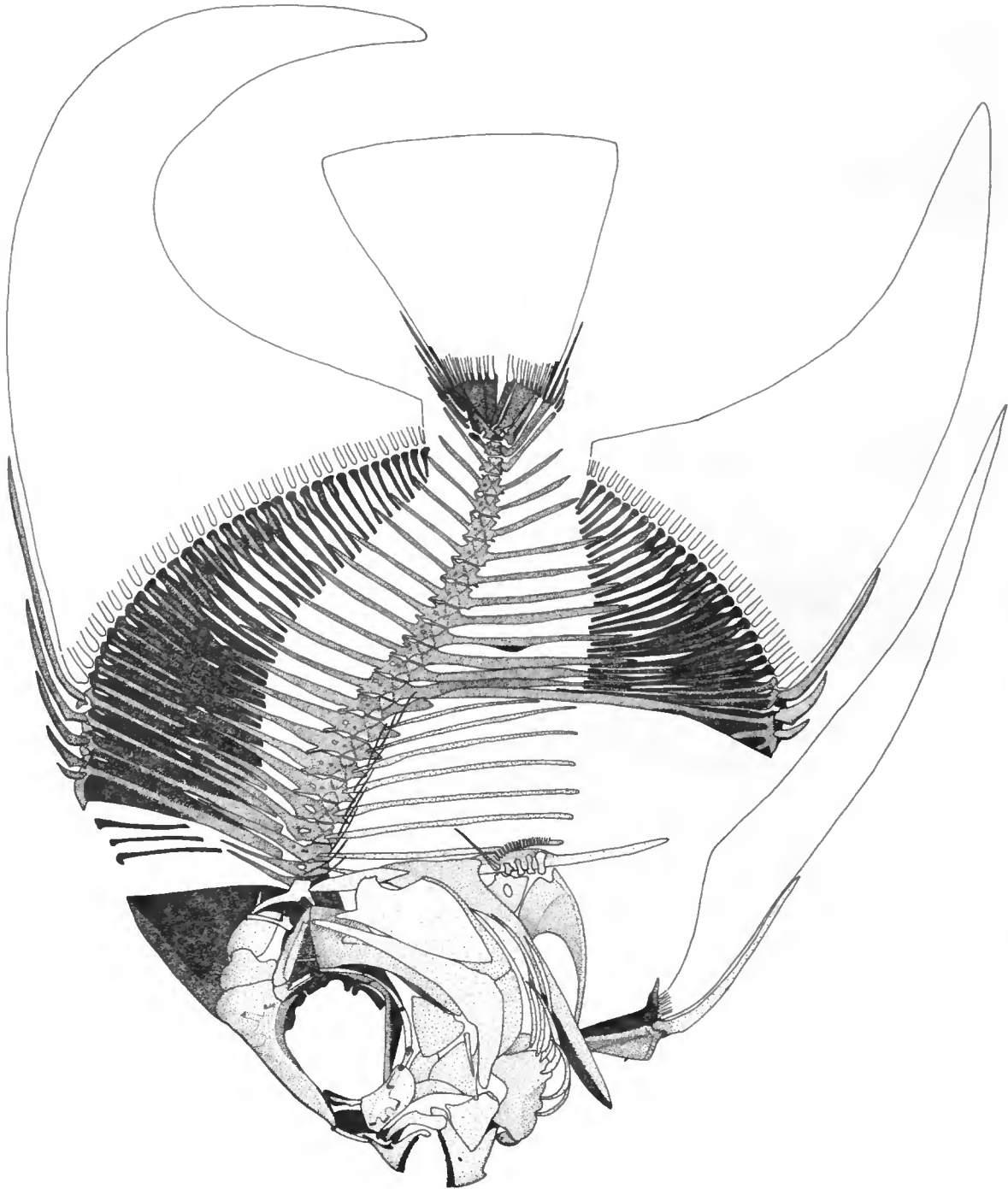


FIGURE 32.—*Platystrophia*, ANSP 109630, 26.0 mm SL, lateral view of entire skeleton.

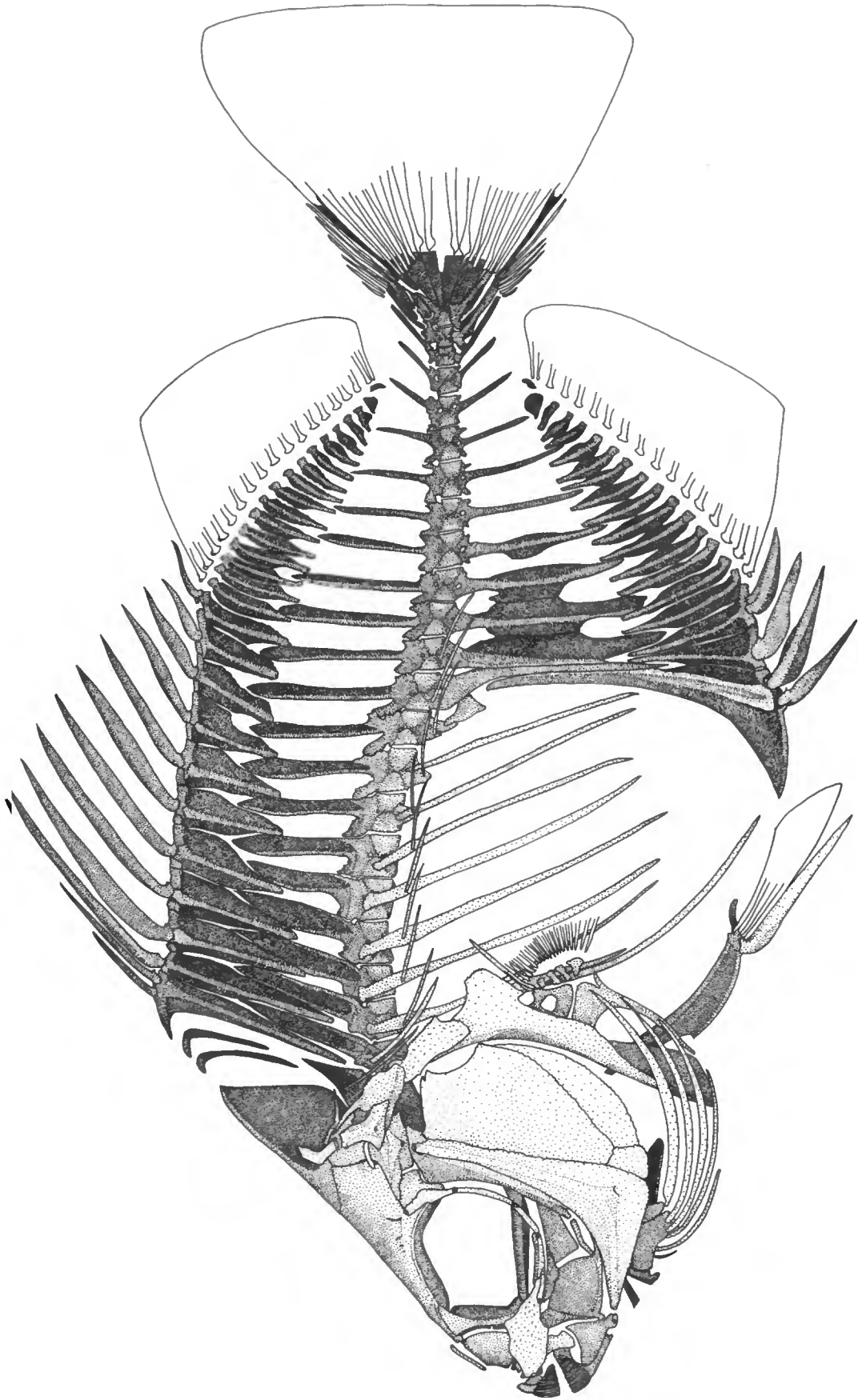


FIGURE 33.—*Selenotoca multifasciata*, USNM 245702, 55.1 mm SL, lateral view of entire skeleton.

Our re-examination of Mok and Shen's (1983) analysis of squamipinne intrarelationships has identified several problems involving both fact and analysis, and we disagree with much of their hypothesized phyletic sequence. In their study, character states for each family were established by examination of only a few of the component genera (e.g., Ephippidae, one of five or six genera; Acanthuridae, two of six genera). Most major nodes in their cladogram are supported by only one or two characters, none complex. The most serious problem is that character states for many taxa are incorrectly reported, and this necessarily requires caution in accepting the accuracy of others. Errors are particularly numerous in descriptions of the gill arches; e.g., scatophagids are erroneously reported to lack a first basibranchial, and the fourth pharyngobranchial cartilage is incorrectly reported to be absent in all squamipinnes except *Monodactylus*, *Kyphosus*, and *Scorpiis*, whereas our observations indicate that it is absent only in siganids (tetraodontiforms not examined). Errors in the reported presence or absence of pleural and epipleural ribs, uncinat process on the first epibranchial and interarcual cartilage are discussed elsewhere in this paper. Another difficulty of the Mok and Shen analysis is that there is no clear outgroup statement and there are some obvious errors in character polarity assessment; e.g., the presence of the second epibranchial toothplate is interpreted as a synapomorphy of *Girella*, *Scorpiis*, and *Toxotes*, whereas the common occurrence of this toothplate among lower percoids indicates that its absence in squamipinnes is derived (see Johnson, 1981). Finally, although parsimony is mentioned, it is not clear how it was used in construction of the cladogram.

In relation to the identification of specific outgroups for the Acanthuroidei, we were not concerned with relationships among the more primitive families considered by Mok and Shen (Monodactylidae, Kyphosidae, Girellidae, Scorpididae, Toxotidae, and Enoplosidae); consequently, we treated those families as a general outgroup for analysis of relationships among the "higher squamipinnes," those obviously more closely related to acanthuroids.

We also excluded the Pentacerotidae from consideration as a possible outgroup. Although pentacerotids have not previously been included within the squamipinne assemblage, Mok and Shen (1983) placed them with the "higher squamipinnes" because they share with chaetodontids, pomacanthids, scatophagids, and acanthuroids a fully interlocked pelvic spine. We found no other evidence to support their relationship to squamipinnes; pentacerotids are primitive with respect to all higher and some lower squamipinnes in having a well-developed dorsal and anal fin stay, generalized gill arches with robust dentition, a large second epibranchial tooth plate, generalized jaw morphology, and no vacant precaudal interneural space (see below). We conclude that the interlocked pelvic spine of pentacerotids evolved independently, and we do not consider the family further here.

Mok and Shen (1983) cited one synapomorphy of higher squamipinnes; presence of a pelvic foramen. Additional

putative synapomorphies include the following: pharyngobranchials (= infrapharyngobranchials) with comma-shaped tooth patches of filiform teeth (Rosen, 1984) (scatophagids are exceptional, apparently through reversal); second epibranchial toothplate absent (incorrectly interpreted as the primitive state by Mok and Shen, 1983); branchiostegal rays six or fewer; and a variously developed parasphenoidal apophysis (Rosen, 1984, erroneously reported that siganids, *Prionurus*, and *Zanclus* lack a distinct apophysis; the latter two genera have a large bony apophysis and in siganids it is present but cartilaginous).

Mok and Shen (1983) placed *Drepane* as the sister group of the platacids (*Platax*) plus ephippidids (we treat the latter two as one family, the Ephippidae, as defined by Johnson, 1984) based on one purported reductive synapomorphy, the absence of an uncinat process on the third epibranchial. But the cited evidence supporting the *Drepane*-Ephippidae node is erroneous. Our observations indicate that, among the groups considered here, only the genus *Ephippus* and some acanthuroids lack an uncinat process; in *Drepane*, *Platax*, and all ephippidids except *Ephippus*, the third epibranchial bears a cartilage-tipped uncinat process. The proposed *Drepane*-ephippidid relationship is further refuted by a unique, complex specialization of the ethmoid shared by *Drepane*, chaetodontids, and pomacanthids, while several synapomorphies unite ephippidids with scatophagids and acanthuroids.

In most percoids, including the "lower squamipinnes" and most higher squamipinnes (Figures 34c,d, 35), the ethmoid extends anterior to the lateral ethmoids and forms a convex, usually wedge-shaped surface anteriorly, along which the rostral cartilage rides during protrusion of the upper jaw. *Drepane*, chaetodontids, and pomacanthids share a striking modification of the ethmoid, first described by Starks (1926; Figure 34a,b). In them, the ethmoid does not extend forward to the lateral ethmoids but is inverted posteriorly, and so its lateral walls extend back into the orbit and form a wedge-shaped or cup-shaped cavity between the lateral ethmoids into which the relatively horizontally oriented rostral cartilage and ascending processes of the premaxillae project. A similar condition has been described elsewhere only in the unrelated Callionymidae (Starks, 1926) where it differs in that the ethmoid forms part of the neurocranial roof. We suggest that this complex specialization represents a unique synapomorphy of *Drepane*, chaetodontids, and pomacanthids. Rosen (1984) was apparently unaware of this feature when he suggested that *Drepane* might be the sister group of zeiforms plus tetraodontiforms and that chaetodontids would probably be shown to be the sister group of acanthuroids; Johnson (1984) was also unaware of it when he suggested a possible sister group relationship between *Drepane* and *Coracinus*.

We propose that ephippidids, not chaetodontids and pomacanthids, are the sister group of scatophagids plus acanthuroids (Figure 36). Monophyly of the Ephippidae plus Scatophagidae plus Acanthuroidei is corroborated by the following synapomorphies.

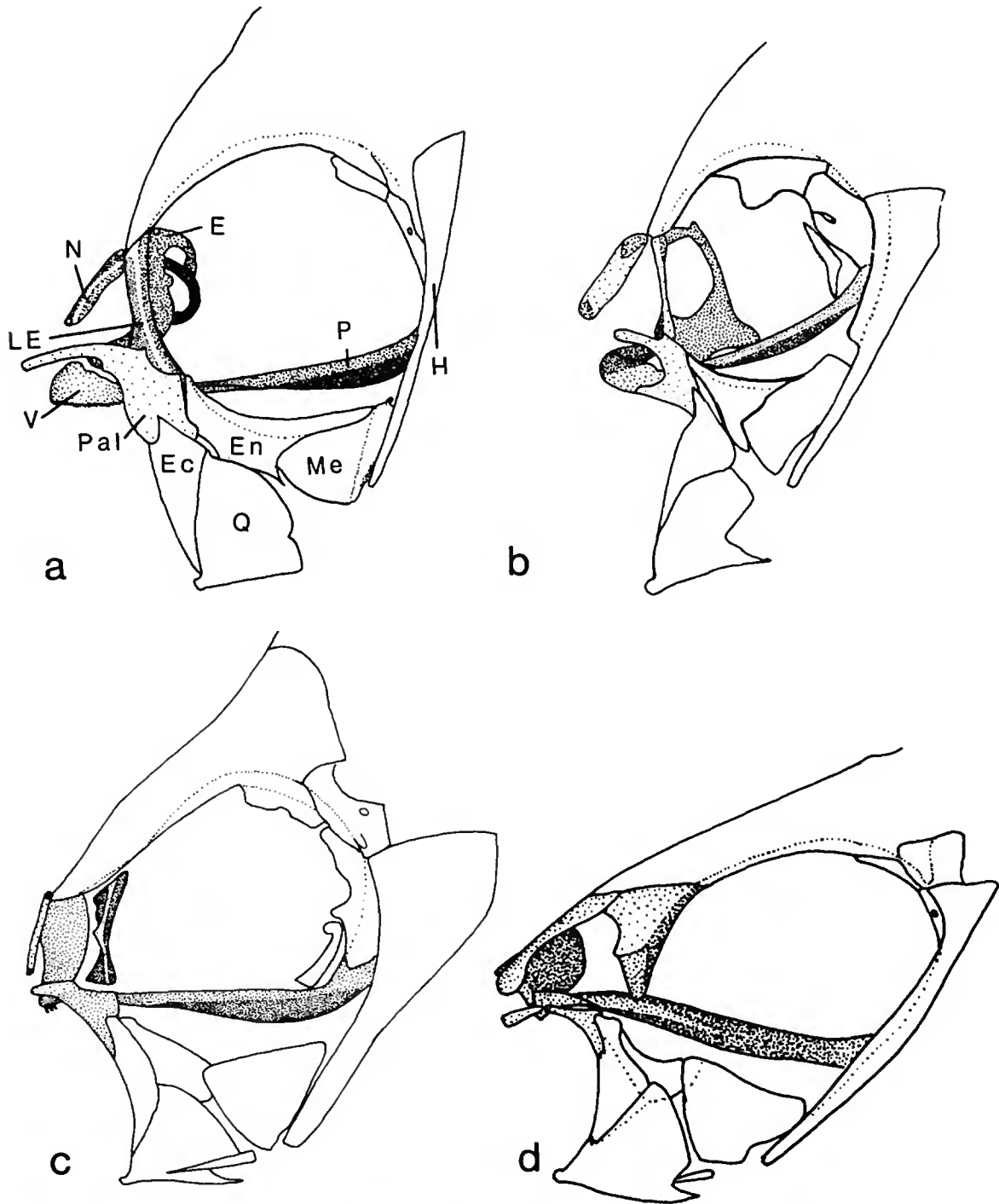


FIGURE 34.—Lateral view of anterior cranium and suspensorium: *a*, *Chaetodon striatus*, ANSP 9118, 44.6 mm SL; *b*, *Holacanthus ciliatus*, ANSP 91094, 54.4 mm SL; *c*, *Platax teira*, ANSP 109360, 26.0 mm SL; *d*, *Siganus canaliculatus*, ANSP 77804, 55.9 mm SL. (E = ethmoid, Ec = ectopterygoid, En = mesopterygoid (entopterygoid), H = hyomandibula, LE = lateral ethmoid, Me = metapterygoid, N = nasal, P = parasphenoid, Pal = palatine, Q = quadrate, and V = vomer.)

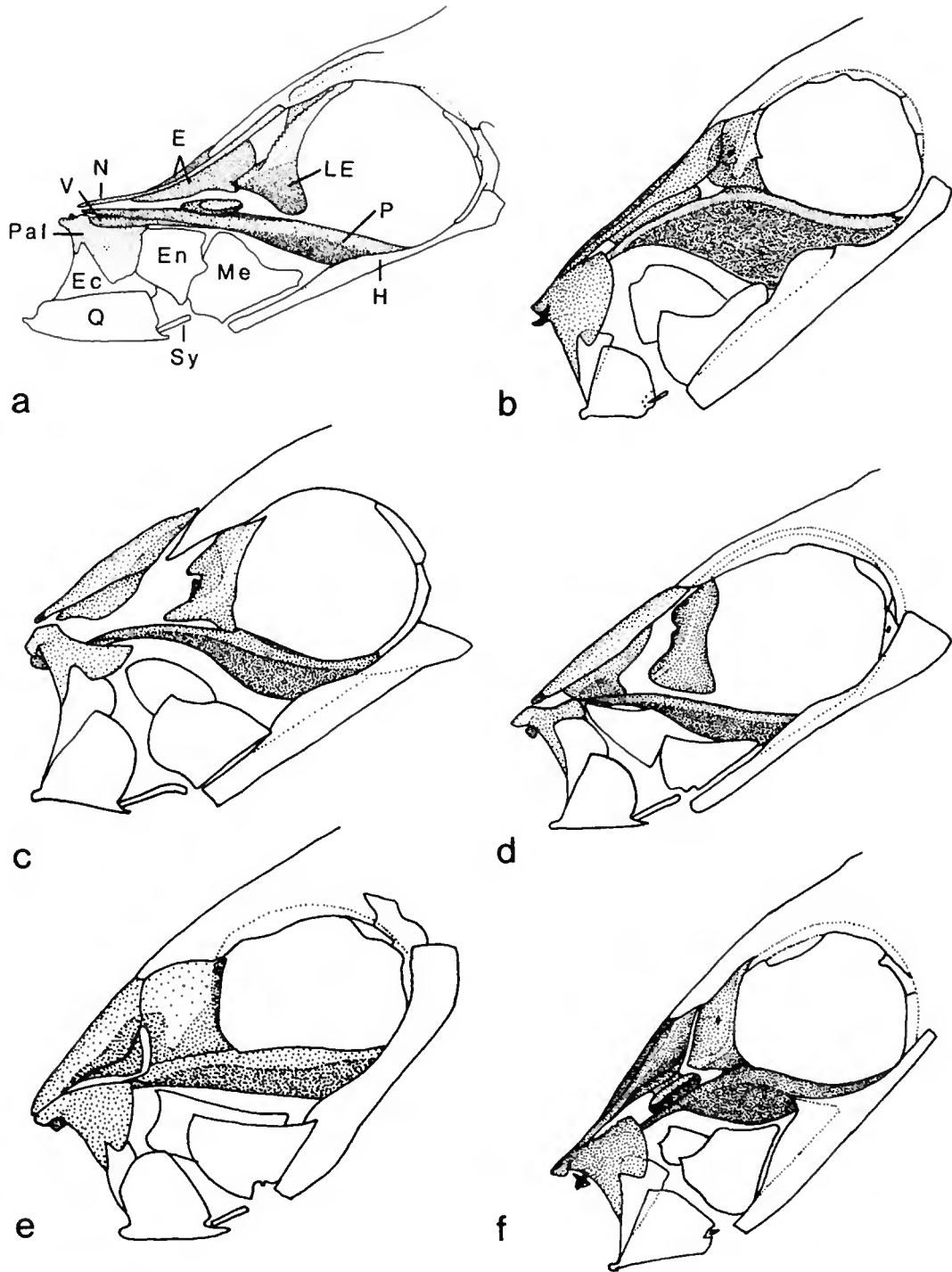


FIGURE 35.—Lateral view of anterior cranium and suspensorium: *a*, *Zanclus cornutus*, ANSP 109502, 66.4 mm SL; *b*, *Naso literatus*, ANSP 109497, 11.2 mm SL; *c*, *Paracanthurus hepatus*, ANSP 108444, 31.6 mm SL; *d*, *Prionurus scalprum*, ANSP 109779, 44.3 mm SL; *e*, *Naso thynnoides*, RU uncat., 191 mm SL; *f*, *Acanthurus triostegus*, ANSP 109491, 46.2 mm SL. (Sy = symplectic; see Figure 34 legend for other bone names.)

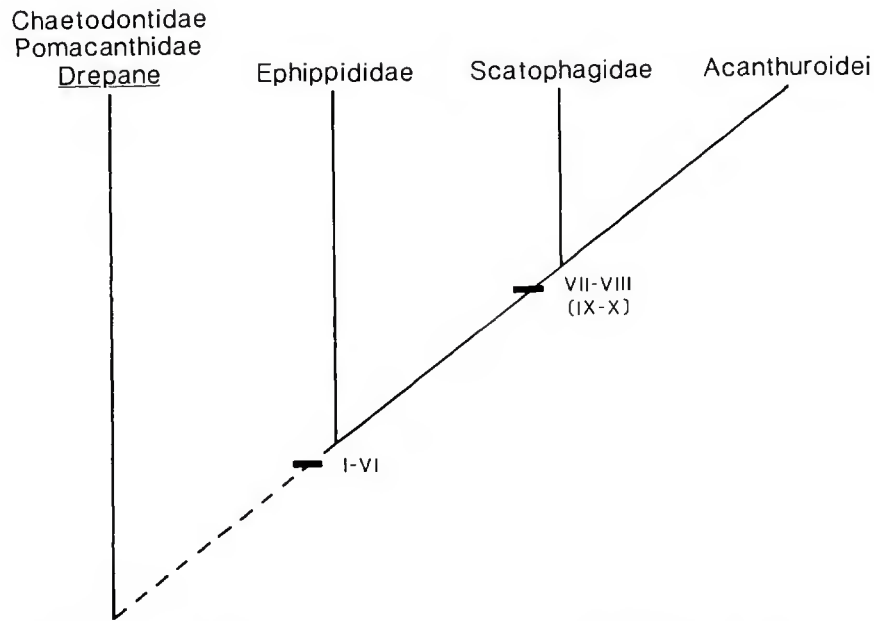


FIGURE 36.—Cladogram of hypothesized relationships among higher squamipinnes. (Roman numerals refer to characters discussed in text.)

I. *The interarcual cartilage is absent.* It is present in all other squamipinnes and most percoids. Mok and Shen (1983) erroneously reported that the chaetodontids, based on their examination of *Heniochus varius* and *Hemitaurichthys polylepis*, and the pomacanthid *Pomacanthus semicirculatus*, lack an interarcual cartilage. We found a well-developed interarcual cartilage in these three species, and other chaetodontids and pomacanthids we examined also have a well-developed interarcual cartilage.

II. *The interopercle is distinctively shaped, being broad posteriorly with the dorsal portion continuing forward as a narrow extension (scatophagids and acanthurids) or as a narrow, ligamentous band (ephippidids)* (Figures 37, 38). In all other squamipinnes and most percoids, the interopercle is roughly ovoid. The ovoid interopercle in *Luvarus* is interpreted as a reversal.

III. *The articular is equal to or shorter than the dentary* (Figures 37, 38). In all other squamipinnes and most percoids, the articular is longer than the dentary.

IV. *The premaxillae are non-protrusible or only slightly so and the maxillae and premaxillae move relatively little independently* (Figures 37, 38). In other squamipinnes and most percoids, the maxillae and premaxillae function independently and the premaxillae are protrusible.

V. *The gill membranes are broadly united at the isthmus, restricting the branchial aperture ventrally.* In other squamipinnes, the gill membranes are either not

continuous ventrally, or, if united, are not connected to the isthmus.

VI. *The frontal and supraoccipital bones are cancellous.* In ehippidids deep, tubular hollows in the bone surface are filled with dense connective and fatty tissue. In scatophagids the tubes are smaller and shorter and there is no thick layer of fatty-connective tissue associated with them. Among acanthuroids this cancellous condition is best developed in siganids, while it is reduced but still evident in acanthurids. Cancellous cranial bones apparently have been lost secondarily in *Luvarus* and may have arisen independently in *Drepane*. In all other squamipinnes and most percoids, the surfaces of the cranial bones are relatively smooth.

We agree with Mok and Shen (1983) that scatophagids and acanthuroids are sister groups. They share at least two reductive specializations lacking in ehippidids.

VII. *There are only 13 caudal vertebrae, 22 (9+13) or 23 (10+13) total.* Ehippidids and all other squamipinnes have 14 caudal vertebrae, 24 (10+14) total. Among percoids, only priacanthids have 23 (10+13) vertebrae; all others have 24 or more (see Johnson, 1984).

VIII. *Only the anterior uroneural pair is present* (Figure 39). Ehippidids, chaetodontids, pomacanthids, and *Drepane* have two pairs of uroneurals. Among lower squamipinnes, only girellids and toxotids lack the posterior uroneural pair. Most percoids have both uroneural pairs, but the posterior pair has been lost in a

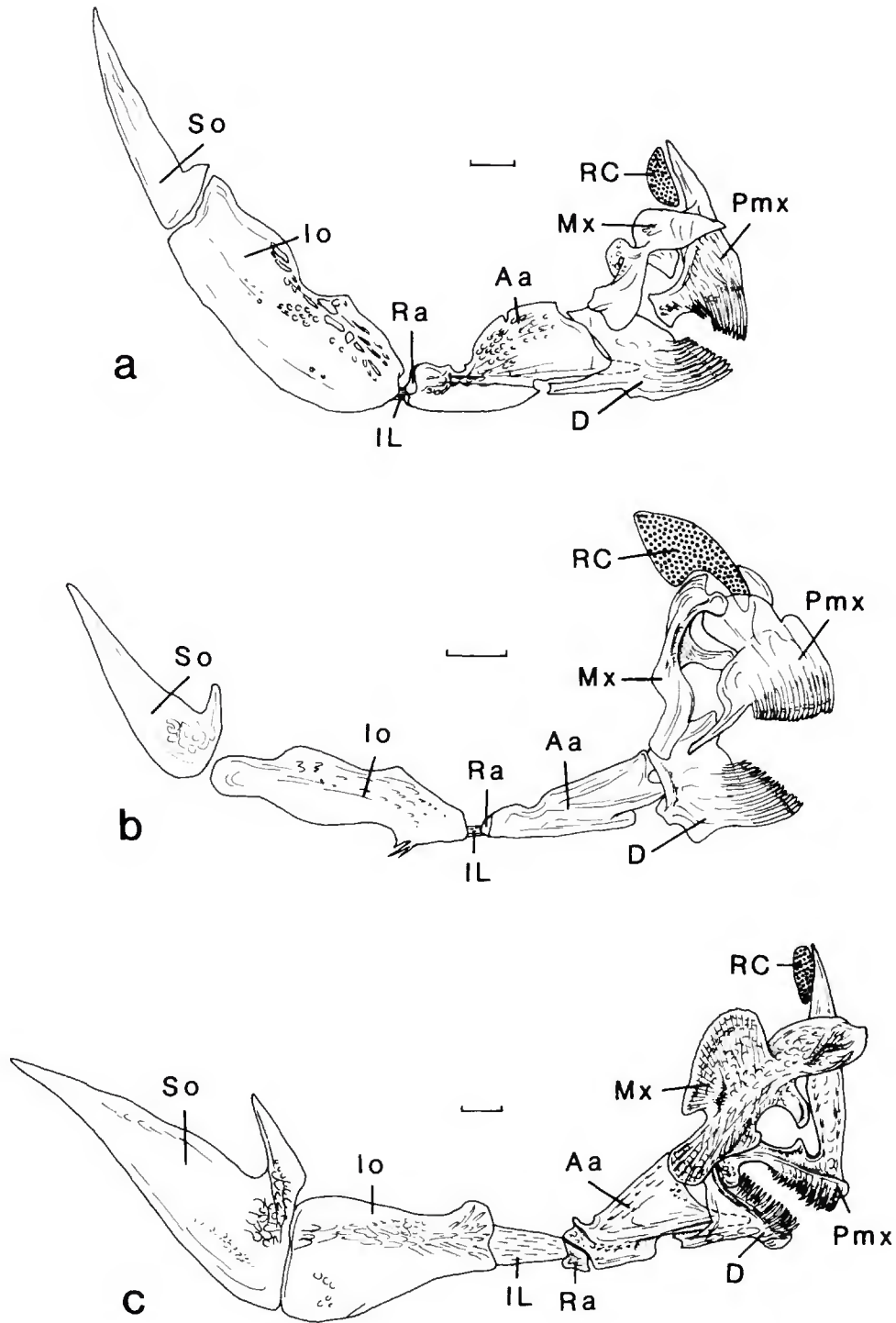


FIGURE 37.—Lateral view of jaws and part of opercular series: *a*, *Chaetodon unimaculatus*, USNM uncat., 46.2 mm SL; *b*, *Centropyge loriculatus*, USNM uncat., 46.2 mm SL; *c*, *Drepane punctata*, USNM 261421, 48.8 mm SL. (Aa = articular (anguloarticular), D = dentary, IL = interoperculo-mandibular ligament, Io = interopercle, Mx = maxilla, Pmx = premaxilla, Ra = angular (retroarticular), RC = rostral cartilage, So = subopercle; scale bars = 1 mm.)

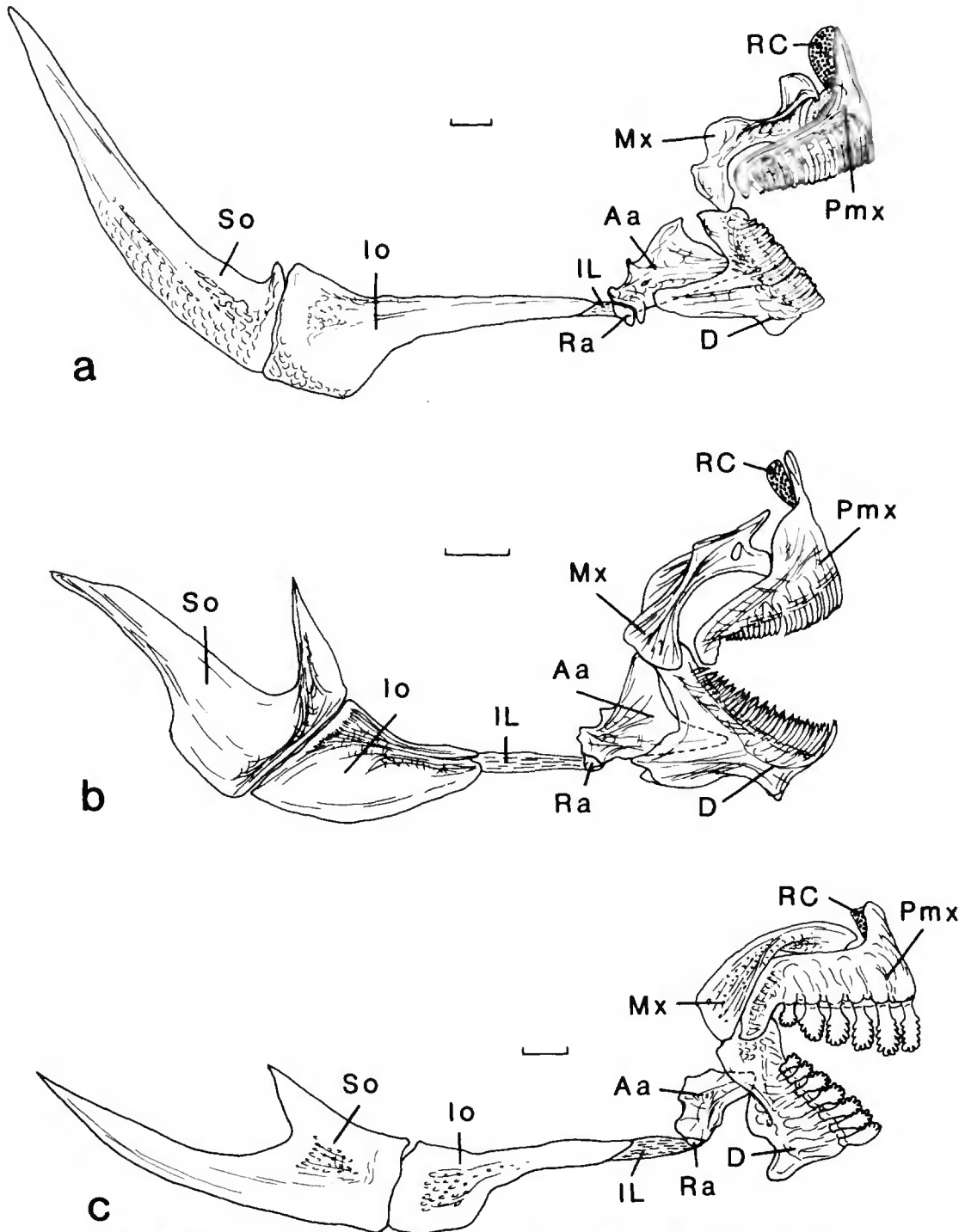


FIGURE 38.—Lateral view of jaws and part of opercular series: *a*, *Selenotoca multifasciata*, USNM 245702, 55.1 mm SL; *b*, *Chaetodipterus faber*, USNM uncat., 29.2 mm SL; *c*, *Acanthurus triostegus* USNM 218866, 52.1 mm SL. (See Figure 37 legend for bone names; scale bars = 1 mm.)

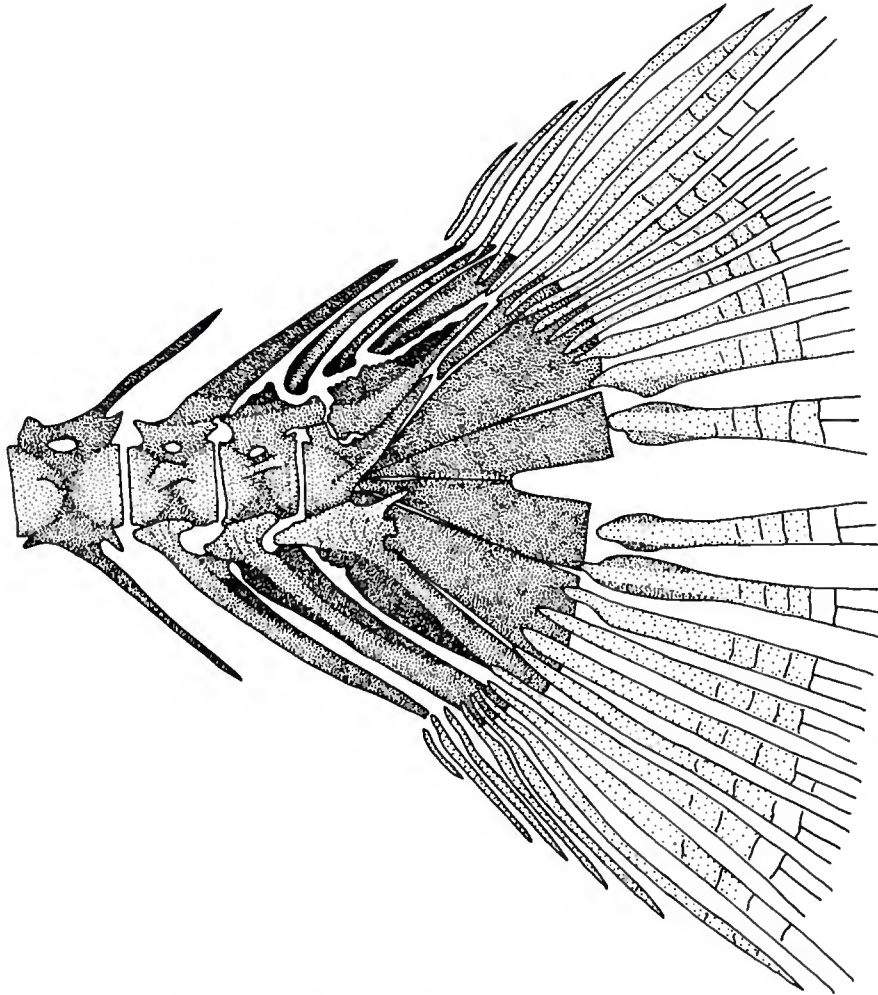


FIGURE 39.—Lateral view of caudal skeleton of *Selenotoca multifasciata*, USNM 245702, 55.1 mm SL.

number of groups (see Johnson, 1984).

Two additional reductive specializations may be synapomorphies of scatophagids and acanthuroids.

IX. *There are 8+8 principal caudal fin rays* (Figures 21, 39), *except in siganids, which have 9+8*. The latter number characterizes ephippidids, all other squamipinnes, and most percoids. If 8+8 caudal fin rays is a synapomorphy at this level, the additional upper ray has re-emerged in siganids. Equally parsimonious is the hypothesis that the upper ray was lost independently in scatophagids and other acanthuroids.

X. *Parietals are absent in scatophagids* (Figure 40) *and siganids but are present in Luvarus (only in the larvae), Zanclus and the Acanthuridae*. Ephippidids, all other squamipinnes, percoids, and most perciforms have parietal ossifications. Absence of parietals is an uncom-

mon feature among acanthopterygians, this absence being found among non-perciforms only in tetraodontiforms and some cyprinodontoids, and among perciforms in gobioids (Springer, 1983) and *Elassoma* (Johnson, 1984). If parietals were absent in the common ancestor of scatophagids and acanthuroids, they must have re-emerged in the common ancestor of *Luvarus*, *Zanclus*, and the Acanthuridae. An equally parsimonious hypothesis is that parietals were independently lost in scatophagids and siganids. A third possibility, that loss of parietals is a synapomorphy of scatophagids and siganids, is refuted by numerous synapomorphies, described below, that place siganids as the sister group of other acanthuroids.

At least one derived character supports the hypothesis that ephippidids are the sister group of acanthuroids. In all members of these two groups, except *Luvarus*, there are no gill filaments

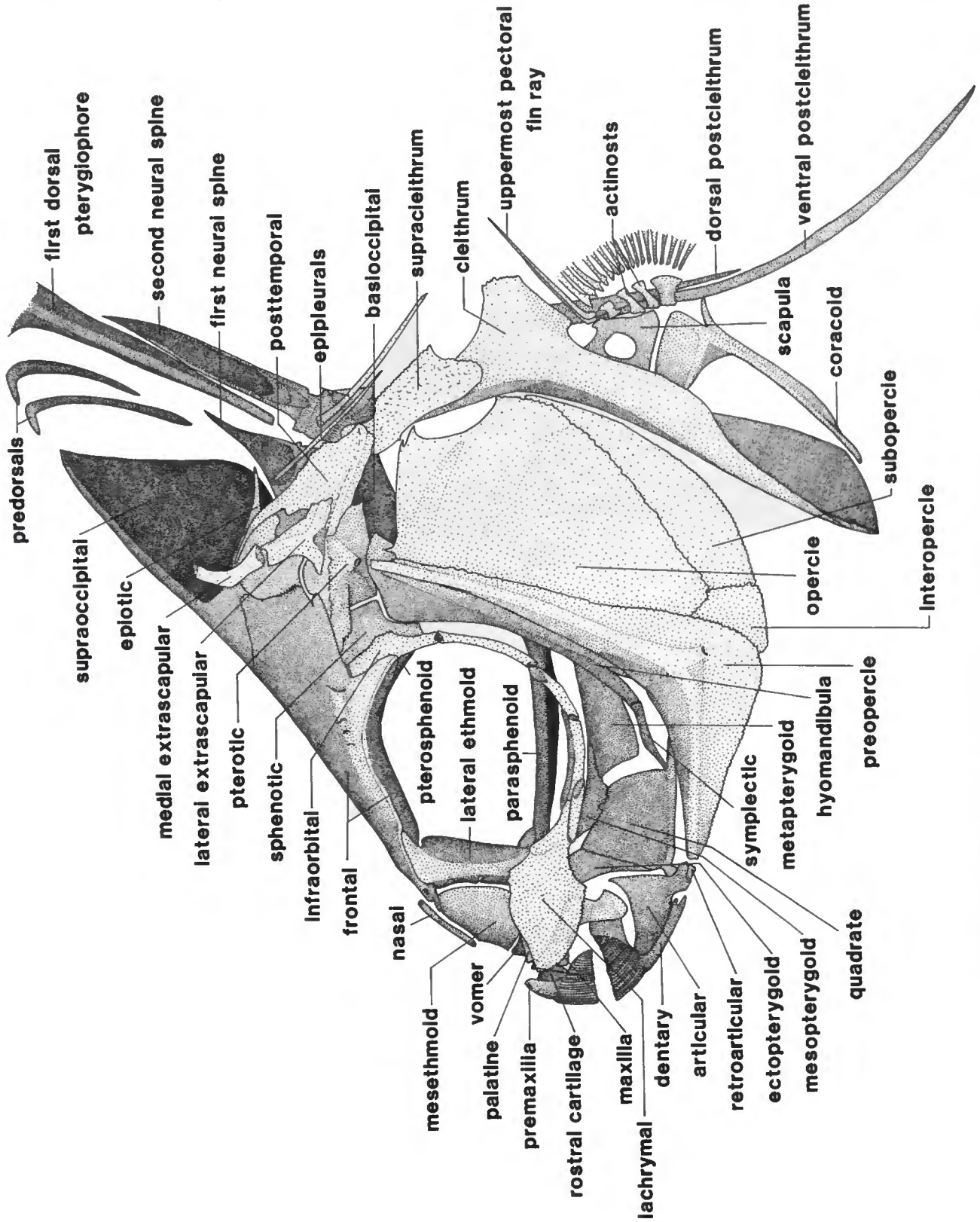


FIGURE 40.—Lateral view of skull and pectoral girdle of *Selenotoca multifasciata*, USNM 245702, 55.1 mm SL.

associated with the epibranchials; instead, the row of filaments on each gill arch continues posteriorly from the end of the ceratobranchial with only a slight dorsal curvature, thereby completely bypassing each epibranchial. Scatophagids exhibit the primitive condition found in all other squamipinnes and most percoids, wherein the gill filament rows curve sharply around the ceratobranchial-epibranchial junction and are thus borne along at least the proximal portion of each epibranchial. In the absence of information about the importance of this innovative specialization relative to the two (and possibly four) reductive synapomorphies of scatophagids and acanthuroids, we hypothesize that the Scatophagidae is the sister group of the Acanthuroidei and postulate that a specialized gill filament arrangement either has arisen independently in ehippidids and acanthuroids or that it has been lost secondarily in scatophagids. In either case, absence of this specialization in *Luvarus* is a reversal.

In the analysis of acanthuroid intrarelations that follows, we considered scatophagids as the first and ehippidids as the

second outgroup and established hypothetical character polarities following the methods of Maddison et al. (1984). For most characters, change in the hypothesized phyletic sequence of the first two outgroups would not affect polarity assessment, because the primitive state characterizes both of them and, usually, other squamipinnes as well. In each outgroup statement we give character states not only for the first two outgroups but also for other squamipinnes, and we note the state that is most common among percoids.

The cladogram (Figure 41) was constructed based on parsimony argumentation using a total of 90 characters. Sixty of these characters are based on morphological features of adults; 30 are based on morphological features found only in the larvae. No assumptions were made concerning the probability of occurrence of reductive versus innovative specialization or reversals versus independent acquisition. Homoplasies (reversal and independent acquisition) were hypothesized based on the most parsimonious distribution of all character states.

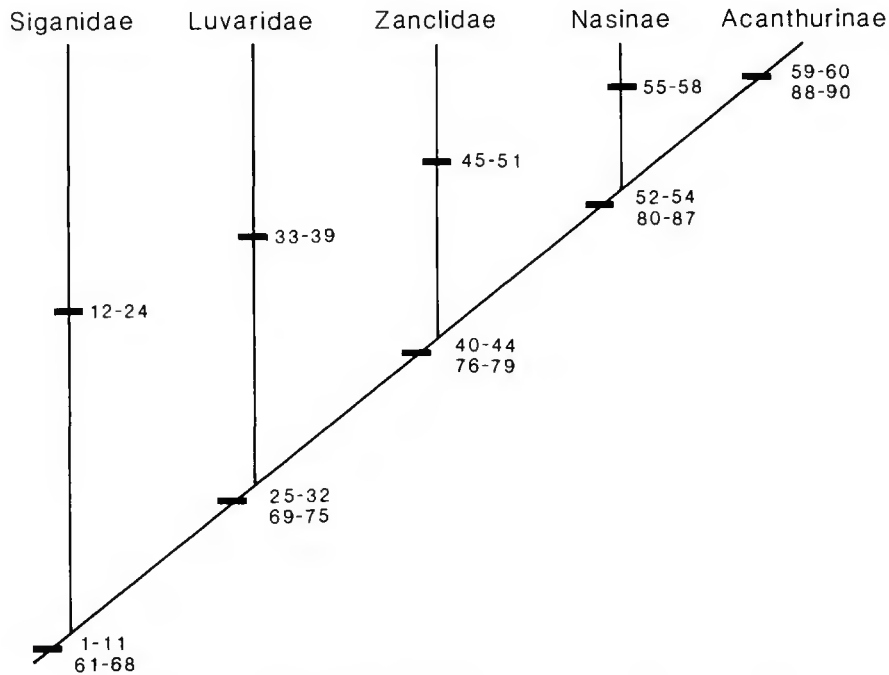


FIGURE 41.—Cladogram of hypothesized relationships of Acanthuroidei. (See text for characters represented by Arabic numerals.)

ADULT MORPHOLOGY.—The following 11 synapomorphies corroborate the monophyly of the Acanthuroidei, comprising Siganidae, Luvaridae, Zanclidae, and Acanthuridae.

1. *The first neural spine is fused to its centrum.* In both outgroups, other squamipinnes, and most percoids, it is autogenous.

2. *There are five (1+4) or four (0+4, only in Naso) branchiostegal rays (Figure 42b–d).* In both outgroups (Figure 42a), chaetodontids, pomacanthids, and girellids there are six (2+4); other squamipinnes and most percoids have seven (3+4) (see Johnson, 1984). A few chaetodontids have five, but the primitive number for the family is six (S. Blum, pers. comm.)

3. *The second infraorbital articulates loosely with the lachrymal and, in most species, does not actually contact it.* In addition, the point of connection is at the posteroventral corner of the lachrymal, so the main body of the lachrymal lies above the projected path of the infraorbital ring (Figure 43). In both outgroups, other squamipinnes, and most percoids, there is a more intimate association between the lachrymal and second infraorbital, and the main body of the lachrymal lies below the path of the infraorbital ring.

4. *The first dorsal pterygiophore interdigitates anterior to the second interneural space.* In siganids it lies between the open neural arch of the first centrum; in all other acanthuroids it is anterior to the neural spine of that centrum, fully within the first interneural space. In both outgroups, other squamipinnes, and most percoids (see Johnson, 1984) it is located more posteriorly, in the second or third interneural space.

5. *The supracleithral sensory canal is absent, and the main trunk lateral line canal communicates directly with the posttemporal canal.* In both outgroups, other squamipinnes, and most percoids, the posttemporal canal joins the main trunk lateral line through a short bony canal at the dorsal end of the supracleithrum.

6. *The maxillae and premaxillae are closely bound together, so they essentially function as a single unit.* Movement of the upper jaw is limited primarily to rotation, the variously developed rostral cartilage serving as a pivot point against the vomer; protrusion is extremely limited or impossible. The upper jaw configuration of scatophagids and ephippidids is similar but less specialized and appears to represent a more primitive stage in transformation to the acanthuroid condition. The maxillae and premaxillae are capable of some independent movement, and the premaxillae can be protruded slightly, although rotation seems to be more prominent. The upper jaws of *Drepane*, chaetodontids, and pomacanthids are capable of extensive protrusion. The maxillae and premaxillae are fully independent. The premaxillary ascending processes and/or rostral cartilage

are extremely long and extend posteriorly into the ethmoid between the lateral ethmoids. They are oriented almost horizontally and slide along the dorsal surface of the vomer. Our observations contradict Rosen's (1984) statement that "in some chaetodontids and pomacanthids the maxilla is greatly reduced so that the two upper jaw bones can act only in concert."

7. *The angular (= anguloarticular) is much smaller than the dentary (Figure 42a), except in Luvarus (Figure 44).* In ephippidids, scatophagids, and *Luvarus*, the angular is about equal in length to the dentary. In *Drepane*, chaetodontids, pomacanthids, other squamipinnes, and most percoids, the angular is notably longer than the dentary. We interpret the presence of the outgroup condition in *Luvarus* as a reversal. It is equally parsimonious to hypothesize independent acquisition of the relatively shorter articular in siganids.

8. *The supraoccipital does not contact the exoccipitals ventrally.* In both outgroups, other squamipinnes, and most percoids, the ventral extension of the supraoccipital (spina occipitalis of Allis, 1909) is embraced laterally by dorsal extensions of the exoccipitals that are tightly attached to the supraoccipital on each side of the extension. In acanthuroids there is no bony contact between the supraoccipital and exoccipitals, although the spina occipitalis is present in siganids.

9. *The supraoccipital crest is reduced to a low short ridge.* In both outgroups, and other squamipinnes, the supraoccipital crest forms a large, triangular peak with a thickened anterior edge. The outgroup condition occurs among acanthuroids only in *Zanclus*; the parsimonious conclusion is that the apparent primitive state in *Zanclus* represents a reversal.

10. *Predorsal bones are absent, except in Zanclus and Prionurus.* Both outgroups, other squamipinnes, and most percoids have one or more predorsal bones (see Smith and Bailey, 1961, and Johnson, 1984). The single predorsal bones in *Zanclus* and *Prionurus* represent independent reversals.

11. *The narrow fourth pharyngeal toothplate is oriented longitudinally, and so the tooth rows are approximately parallel rather than perpendicular to the body axis (Figure 45), except in Luvarus.* In both outgroups, other squamipinnes (some pomacanthids are exceptional), most percoids, and *Luvarus*, the fourth pharyngeal toothplate is oriented transversely, so its long axis and tooth rows (if the teeth are arranged in rows) are perpendicular to the body axis. The primitive state in *Luvarus* is interpreted as a reversal.

Siganids are remarkably specialized in many aspects of their anatomy. There are 13 autapomorphies (12–24) of the Siganidae (plus the unique I,3,I pelvic fin not shown on the cladogram).

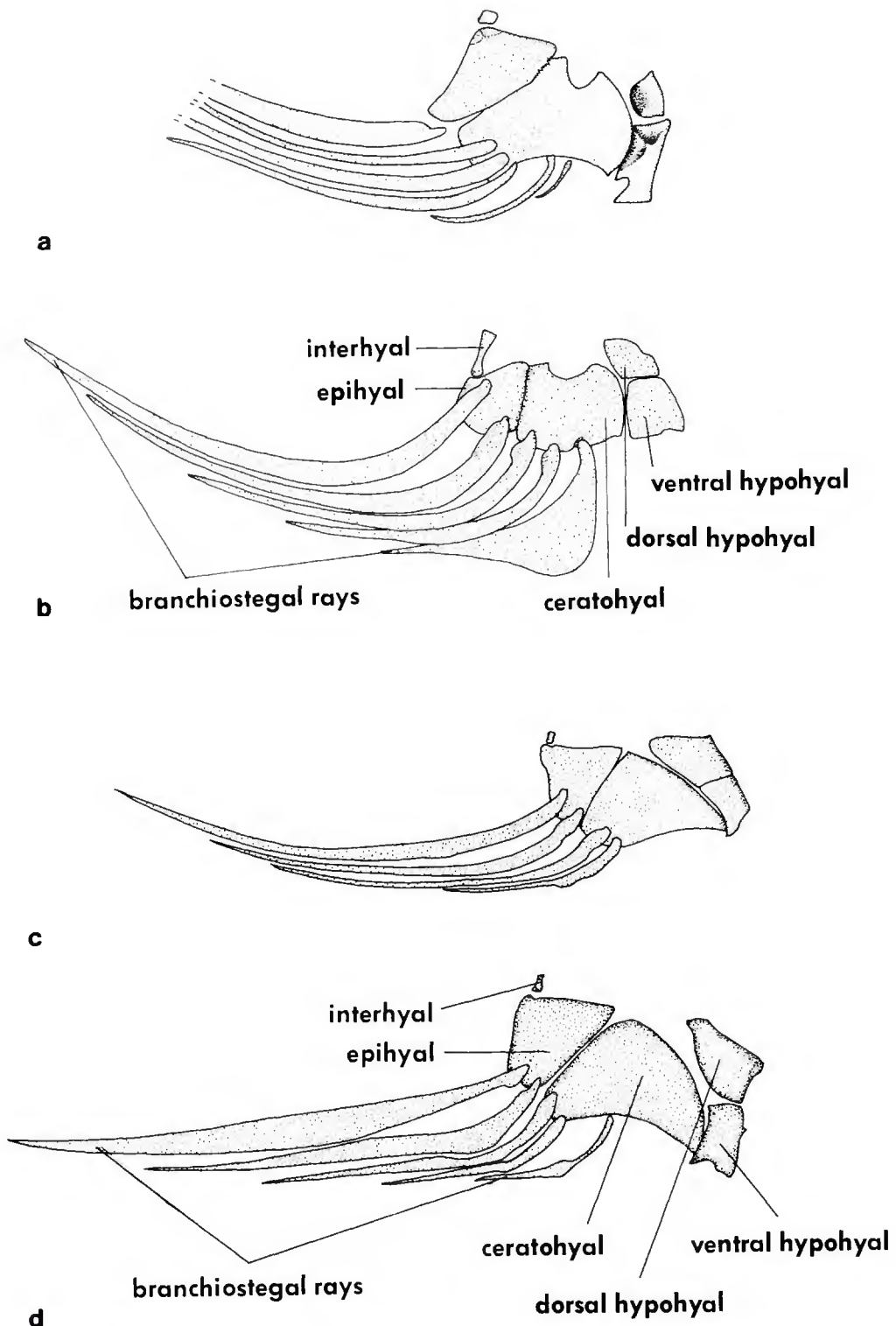


FIGURE 42.—Lateral view of right hyoid series: *a*, *Selenotoca multifasciata*, USNM 245702, 55.1 mm SL; *b*, *Siganus corallinus*, ANSP 49224, 139 mm SL; *c*, *Naso literatus*, ANSP 109497, 209 mm SL; *d*, *Acanthurus triostegus*, ANSP 109491, 52.1 mm SL.

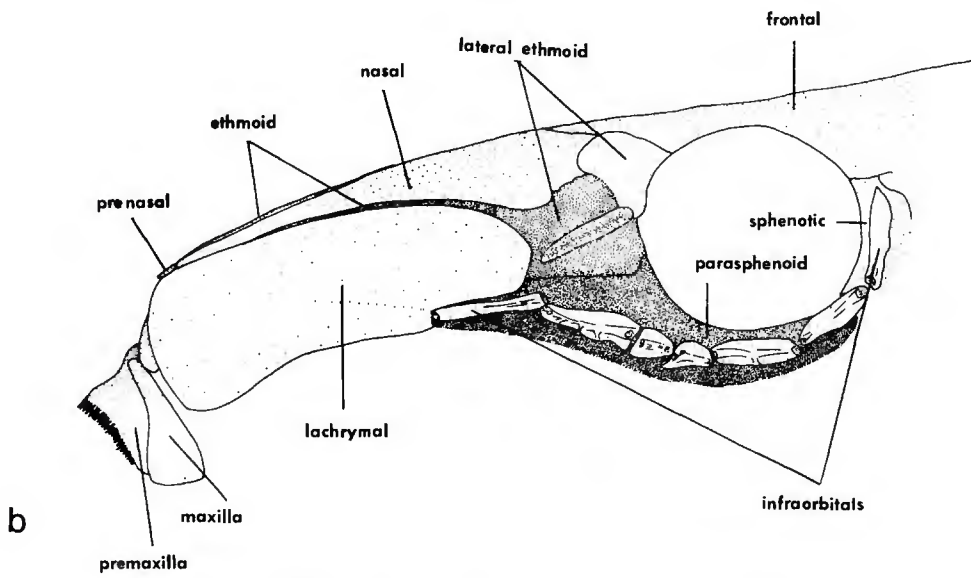
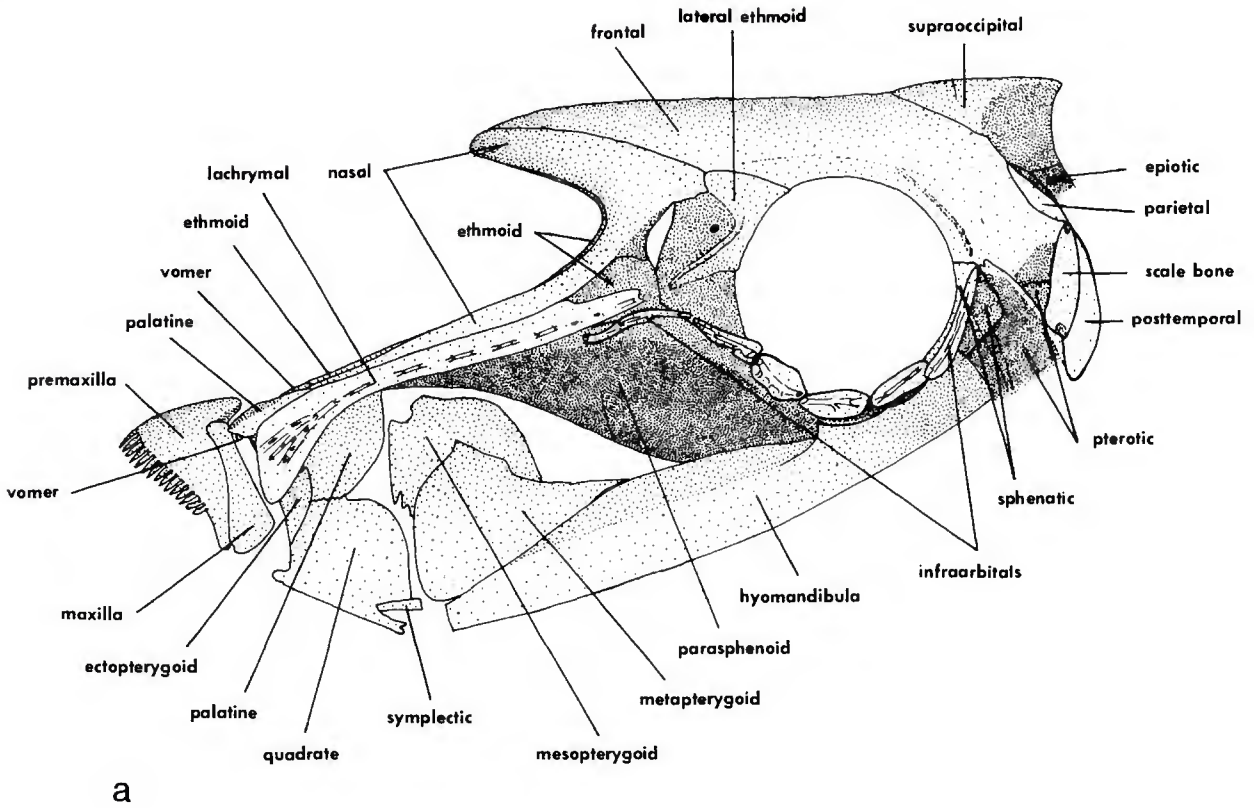


FIGURE 43.—Lateral view of snout and infraorbital series: a, *Naso unicornis*, ANSP 89114, 267 mm SL; b, *Naso fageni*, ANSP 103532, 514 mm SL.

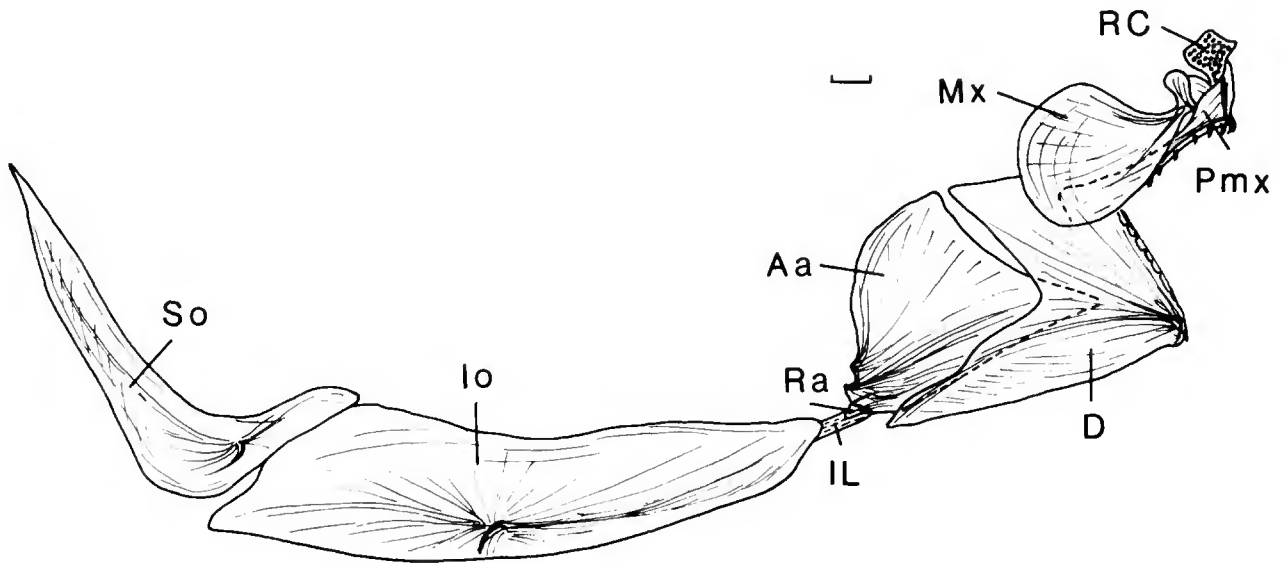


FIGURE 44.—Lateral view of jaws and part of opercular series in *Luvarus imperialis*, USNM 228612, 79.2 mm SL. (See Figure 37 legend for bone names; scale bar = 1 mm.)

12. *There are only ten dorsal and nine anal soft rays.* In other acanthuroids dorsal soft rays range from 19 to 41 and anal soft rays from 19 to 35. Among the higher squamipinnes dorsal and anal soft ray counts are as follows: scatophagids, 16–18, 14–16; ephippidids, 18–40, 15–28; chaetodontids, 15–30, 14–23; pomacanthids, 15–33, 14–25.

13. *The scales are cycloid and very small.* Other acanthuroids have spinulose or true ctenoid (only in *Acanthurus* and *Ctenochaetus*) scales. Cycloid scales are found among squamipinnes only in the ephippidids *Ephippus* and *Rhinoprenes*; they have apparently evolved several times among percoids, where ctenoid scales are most common and presumably primitive (Johnson, 1984).

14. *The parasphenoidal apophysis (see outgroup discussion above) is cartilaginous.* It is bony in all other acanthuroids, both outgroups, and in other squamipinnes where it occurs. Because the parasphenoid is a dermal bone, this cartilaginous apophysis in siganids may not be homologous with the bony apophysis of other groups.

15. *Each palatine consists of separate anterior and posterior ossifications.* This condition is probably unique among perciforms.

16. *The anterior uroneural pair is reduced to two small nubbins of bone (Figure 29) lying free in the space between the urostyle and the anterior two epurals.* In other acanthuroids, both outgroups, other squamipinnes, and most percoids, this uroneural pair is much longer and the anterior portion forms a saddle that embraces the

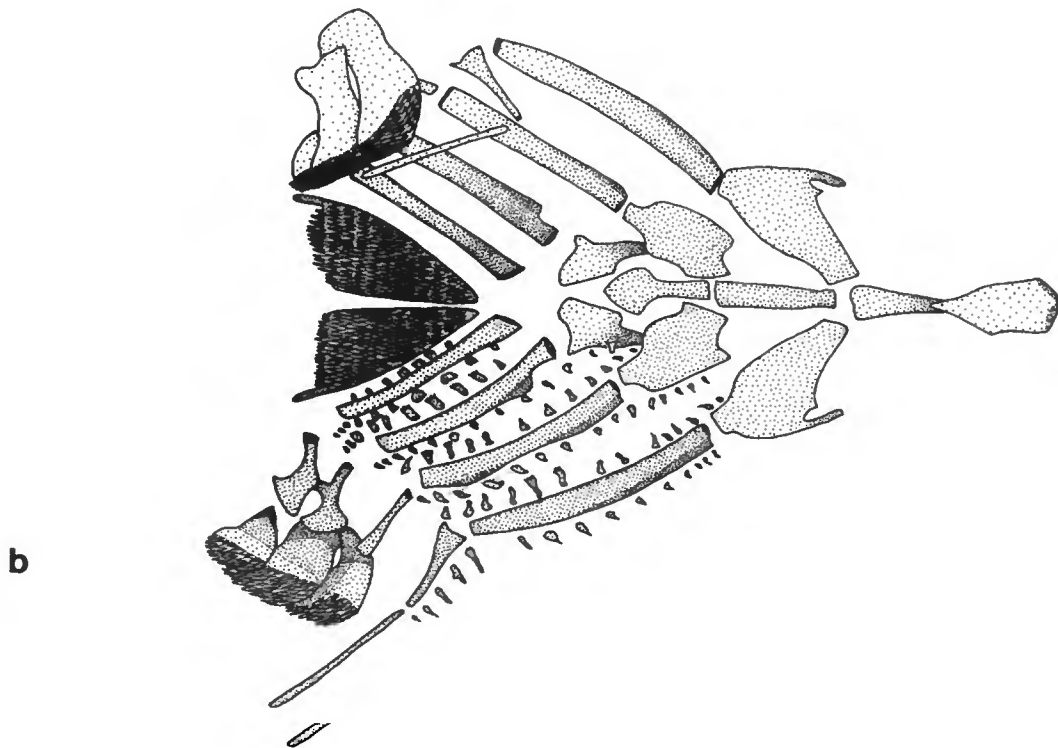
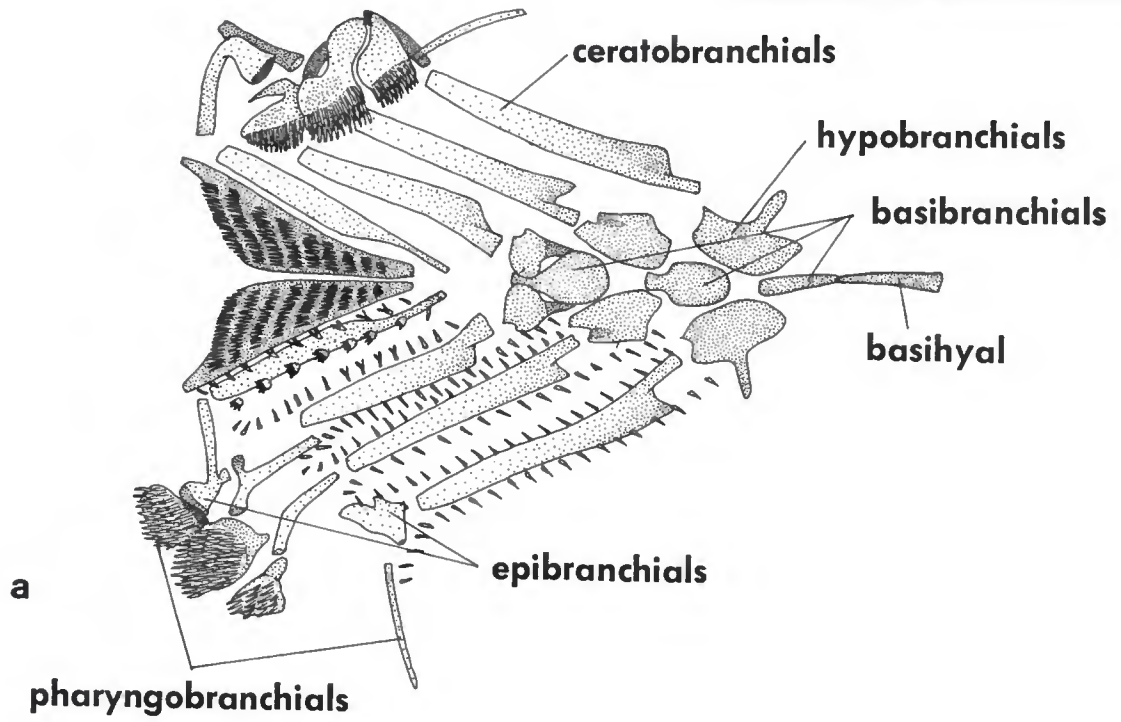
dorsolateral surface of the urostyle, while the posterior portion tapers to a point along the dorsal surface of the fifth hypural.

17. *The first pleural rib inserts on the second vertebra.* In other acanthuroids, both outgroups, and most percoids, the first pleural rib is borne on the third vertebra. Our observations contradict the reports of Mok and Shen (1983) and Rosen (1984) (see general outgroup discussion).

18. *The anterior surface of the ethmoid is vertical and forms a shallow, concave facet that receives the broad base of the large, conical rostral cartilage.* See character 42 for a description of the ethmoid in other acanthuroids and the general outgroup discussion for a description of its configuration in *Drepane*, chaetodontids, and pomacanthids.

19. *A pair of longitudinally oriented, rod-shaped cartilages lies above the pharyngobranchials on each side.* The medial of these (described as two separate cartilages by Mok and Shen, 1983) articulates anteriorly with the second pharyngobranchial; the lateral one lies free next to the medial one. A median accessory cartilage is associated with the dorsal gill arches of some acanthuroids, but, to our knowledge, paired cartilages like those of siganids do not occur elsewhere among perciforms.

20. *A small, autogenous, triangular cartilage is present lateral to the fourth pharyngobranchial toothplate, between the anterior cartilaginous tip of the third epibranchial and the posterior cartilaginous tip of the*



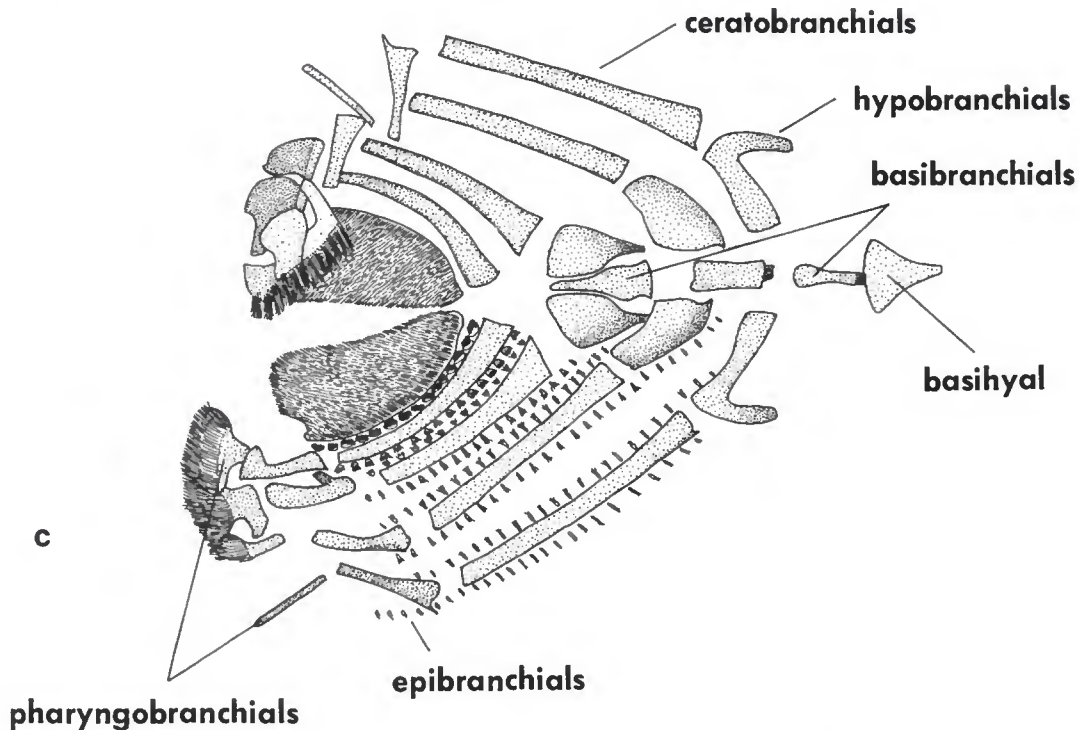


FIGURE 45.—Dorsal view of branchial apparatus: *a*, *Siganus corallinus*, ANSP 49224, 139 mm SL; *b*, *Naso literatus*, ANSP 109497, 209 mm SL; *c*, *Acanthurus triostegus*, ANSP 109491, 52.1 mm SL.

second pharyngobranchial. The position of this cartilage lateral to the fourth pharyngobranchial toothplate suggests that it could be the fourth pharyngobranchial cartilage; if so, it is unusual in being free from the toothplate. In other acanthuroids, both outgroups, other squamipinnes, and most percoids, there is a fourth pharyngobranchial cartilage firmly attached to the dorsal (lateral in *Zanclus* and acanthurids) surface of the fourth pharyngeal toothplate.

21. *The configuration of the fourth pharyngeal toothplate is unique in having a T-shaped dorsal process; the long, tapering, anterior process of the "T" extends along the lateral side of the third pharyngobranchial, and the posterior process extends posteriorly above the main body of the toothplate. To our knowledge, this process is unique among perciforms.*

22. *Replacement teeth on the jaws and pharyngobranchials are not enclosed in bone, but instead lie free in connective tissue. Replacement teeth are enclosed in bone in all other acanthuroids, both outgroups, other squamipinnes, and most percoids.*

23. *There is a thin, elongate rod of cartilage between the haemal spines of the second and third preural centra. As noted by Mok and Shen (1983), such an elongate*

radial cartilage does not occur elsewhere among acanthuroids or squamipinnes.

24. *There is an overlapping articulation between the proximal-medial and distal radials in the spinous dorsal and anal pterygiophores; the distal portion of the proximal-medial radial is flattened and extends posteriorly below the anterior portion of the flattened distal radial. We have observed a similar condition among perciforms only in the unrelated scombroid family Gempylidae (Johnson, 1986).*

There are eight synapomorphies (25–32) of *Luvarus*, *Zanclus*, and the Acanthuridae.

25. *There are 9+13 vertebrae. Siganids and scatophagids have 10+13. All other squamipinnes have 10+14. Among percoids only priacanthids have as few as 23 (10+13) vertebrae, and only *Bathyclupea* (9+22) has fewer than 10 precaudal vertebrae.*

26. *The first dorsal pterygiophore inserts fully in the first interneural space, and the anterior portion of its proximal tip is embraced laterally by posteriorly directed, vertically oriented flanges on the exoccipitals, so this tip extends into the dorsal area of the foramen magnum (Figure 46b,c). In siganids, the first dorsal*

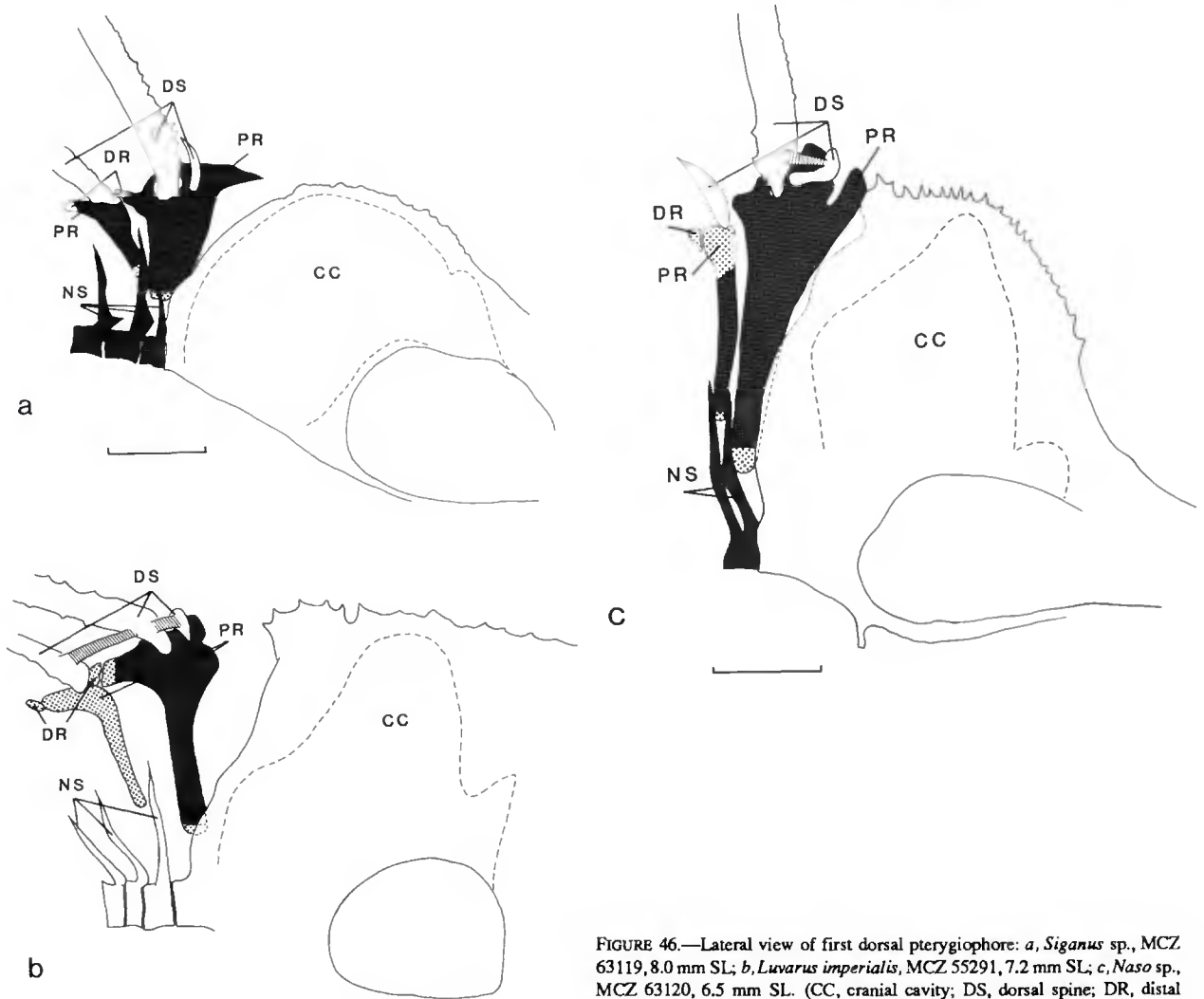


FIGURE 46.—Lateral view of first dorsal pterygiophore: *a*, *Siganus* sp., MCZ 63119, 8.0 mm SL; *b*, *Luvarus imperialis*, MCZ 55291, 7.2 mm SL; *c*, *Naso* sp., MCZ 63120, 6.5 mm SL. (CC, cranial cavity; DS, dorsal spine; DR, distal radial; PR, proximal radial; NS, neural spine; scale bars = 1 mm.)

pterygiophore lies between the open neural arch of the first centrum (Figure 46*a*); it thus extends only partway into the first interneural space and is not associated with the neurocranium. Other squamipinnes and most percoids (see Johnson, 1984) have the first dorsal pterygiophore inserting in the second or third interneural space.

The relationship between the first dorsal pterygiophore and the exoccipitals is evident as soon as these elements begin to ossify. At this point the exoccipital flanges stain darker than the surrounding bone, and their configuration appears identical to that of neural arches. Similar structures are not evident in the developing exoccipitals of siganids. Because *Luvarus*, *Zanclus*, and acanthurids have one fewer precaudal vertebra than siganids, one might speculate that the exoccipital flanges represent the first neural arches of siganids, which also embrace the

first dorsal pterygiophore. There is, however, no ontogenetic evidence that the exoccipital flanges originate from fusion of neural arches; furthermore, distribution of pleural ribs in these groups seems to argue against it. In siganids, pleural ribs begin on the second vertebra, whereas in *Luvarus*, *Zanclus*, and the acanthurids they begin on the third vertebra; if the first vertebra of siganids was lost in the common ancestor of the latter three taxa, one would expect to find pleural ribs beginning on the second vertebra, rather than the third.

27. *The infraorbital series turns anteriorly below the lateral ethmoid and extends forward along the side of the snout.* The lachrymal is thus displaced anteriorly, so it is removed from the anterior border of the orbit and does not articulate with the lateral ethmoid. In siganids, both outgroups, other squamipinnes, and most percoids, the

lacrimal has a condylar articulation with the lateral ethmoid and its posterodorsal margin conforms to the anteroventral border of the orbit.

28. *The palatine lies well forward of the lateral ethmoid and has no articulation with it.* In siganids, both outgroups, other squamipinnes, and most percoids, the posterior portion of the palatine has a condylar articulation with the lateral ethmoid.

29. *There is no spina occipitalis (Allis, 1909), and the epiotics (= epioccipitals) meet synchondrally along the posterior midline of the neurocranium, broadly separating the supraoccipital from the exoccipitals and foramen magnum.* According to Stiassny (1986), the presence of the spina occipitalis is a synapomorphy of the Acanthomorpha. In both outgroups, other squamipinnes, and percoids, a well-developed spina occipitalis extends ventrally between the epiotics to the dorsal margin of the foramen magnum and is embraced laterally by the dorsal processes of the exoccipitals. In siganids, the supraoccipital does not contact the exoccipitals, but a spina occipitalis extends ventrally to the dorsal margin of the foramen magnum, thus separating the epiotics posteriorly. *Zanclus* has a very short ventral extension of the supraoccipital crest, but it does not separate the epiotics posteriorly. Both parsimony and ontogenetic evidence suggest that this short ventral process is secondarily derived. The spina occipitalis of siganids and other perciforms appears very early in larval development, near the onset of ossification of the supraoccipital, whereas there is no evidence of the ventral process in *Zanclus* in a 20 mm juvenile.

30. *The soft rays of the dorsal, anal, caudal, pectoral, and pelvic fins bear small spinules laterally along all or most of their length.* In *Luvarus*, *Zanclus*, and *Naso*, the spinous rays are also spinulose. Spinules appear early in larval development and are retained variously in the adults. For example, *Zanclus* and *Naso* retain all of them, *Luvarus* loses those on the dorsal and anal rays, and *Zebbrasoma* loses all but those on the dorsal and anal soft rays. Fin-ray spinules never develop in *Paracanthurus*, *Acanthurus*, and *Ctenochaetus*, and their absence in those genera is most parsimoniously attributable to reversal. Spinulose fin rays are found in a few percoids, but are lacking in siganids, both outgroups and all other squamipinnes.

31. *The scales of adults consist of circular to ovoid plates from the surface of which project variously arranged upright spinules; unlike the scalelets of true ctenoid scales, these spinules are continuous with the scale plate.* They may be irregularly distributed on the plate, project in a single row along the margin of a transverse keel (*Zanclus*) or be approximately radially arranged at the end of an upright central pedestal (see Tyler, 1970a). Within the Acanthuridae, *Acanthurus* and

Ctenochaetus are exceptions; they have true ctenoid scales (see Johnson, 1984), representing a reversal to the most common percoid condition. The other four genera of acanthurids have spinulose scales like those described above, but strict homology with the spinulose scales of other acanthuroid families is questionable because adult scales do not develop directly from larval scales in all genera (see character 60). The scales of siganids are cycloid (see character 13). Scatophagids, pomacanthids, and some ephippidids have spiny scales that are not truly ctenoid but in the latter two groups the spinules are not upright and are borne on the posterior margin, rather than the surface of the scale plate. In scatophagids, small, flat, triangular "ctenii" project obliquely from the mid-surface of the scale. If these are precursors of the more robust and numerous spinules of acanthuroids, non-marginal projections of the scale plate represent a synapomorphy of scatophagids and acanthuroids. Other squamipinnes and most percoids have true ctenoid scales.

32. *There is a single postcleithrum, although we cannot be certain of strict homology.* In *Luvarus* and *Zanclus*, the dorsal and ventral postcleithra fuse in juveniles, whereas acanthurids never have the dorsal and ventral elements separate (see character 84). Adult siganids, squamipinnes, and most percoids have separate dorsal and ventral postcleithra.

There are seven autapomorphies (33–39) of *Luvarus*.

33. *The dorsal and anal pterygiophores are uniquely modified.* Only the first dorsal pterygiophore lacks a separate middle radial; that pterygiophore supports one (two in the larvae, see characters 43 and 75) spine in supernumerary association and one in serial association. All remaining pterygiophores support only soft rays and have three separate ossifications. The dorsal portions of the proximal ossifications are interlocked with one another in an extensive, suture-like interdigitation, forming a firm infrastructure around the dorsal and ventral margins of the body just beneath the skin. The middle ossifications are trough-like plates of bone that are bound to the dorsal surface of the interlocked proximal ossifications. The distal ossifications are the typical ovoid distal radials that lie between the bases of each soft ray in most perciforms. Separate middle radials are absent in the dorsal and anal pterygiophores of other acanthuroids, most ephippidids, and all chaetodontids and pomacanthids but present in the more posterior soft dorsal and anal pterygiophores of scatophagids, *Ephippus*, other squamipinnes, and most percoids. In scatophagids, *Ephippus*, other squamipinnes, and most percoids with middle radials, these radials are cylindrical structures, not concave, flat plates as they are in *Luvarus*. The extensive interdigitation of the proximal radials in *Luvarus* does not occur elsewhere among acanthuroids,

squamipinnes, or percoids.

34. *Epipleural ribs are absent.* Other acanthuroids, both outgroups, other squamipinnes, and most percoids have epipleural ribs associated with each precaudal vertebra.

35. *Three epurals are present in the larvae, but these eventually consolidate into a single element that fuses to the neural arch of the second preural centrum.* Other acanthuroids (except *Naso thynnoides*, with two), both outgroups, other squamipinnes, and most percoids (see Johnson, 1984) retain three separate epurals as adults.

36. *Hypurals 1-4 fuse to form a single hypural plate.* In all other acanthuroids, except *Naso* (where a similar fusion has occurred independently, see character 58), hypurals 1-4 remain separate as they do in both outgroups and other squamipinnes.

37. *Hypural 5 remains separate from hypural 4 but fuses to the uroneural pair which in turn fuses to the urostyle.* A similar pattern of fusion is found elsewhere among perciforms in some scombrids. In other acanthuroids, both outgroups, other squamipinnes, and most percoids, hypural 5 and the anterior uroneural remain autogenous.

38. *The caudal-fin rays deeply embrace the hypural plate, and so, by 300 mm, it is nearly fully covered by the proximal ends of the rays.* Such extensive overlap of the caudal-fin rays, or hypurostegy, does not occur in other acanthuroids (although moderate overlap occurs in some species of *Naso*), either outgroup, other squamipinnes, or most percoids.

39. *There are only two dorsal spines and no anal spines.* Among other acanthuroids the number of dorsal spines ranges from IV to XIV and there are II-VII anal spines. Squamipinnes have at least IV dorsal spines and III anal spines.

There are five synapomorphies (40-44) of *Zanclus* and the Acanthuridae.

40. *The fourth interneural space is consistently vacant; i.e., dorsal pterygiophores never insert between the neural spines of the third and fourth vertebrae* (Blot, 1980; Blot and Voruz, 1970, 1975). In *Luvarus*, siganids, all squamipinnes, and most percoids, at least one dorsal pterygiophore inserts between these two neural spines. *Luvarus* has no vacant precaudal interneural spaces. In siganids, either the fifth or sixth interneural space is vacant. Among most higher squamipinnes, the seventh or eighth interneural space is vacant (sixth in *Drepane*); the ephippidids *Platax* and *Rhinoprenes* and the chaetodontid *Parachaetodon* have no vacant precaudal interneural space.

41. *The main body of the longitudinally oriented fourth pharyngeal toothplate lies lateral to the third pharyngobranchial, and the medial surface of the former*

extends dorsally, and so the fourth pharyngobranchial cartilage lies lateral to it and has its main articular surface directed laterally or dorsolaterally. In *Luvarus*, siganids, squamipinnes, and most percoids, the main body of the fourth pharyngeal toothplate is posterior to the third pharyngobranchial, and the fourth pharyngobranchial cartilage (absent in siganids) lies dorsal to the former and has its articular surface directed dorsally.

42. *The ethmoid cartilage is more or less wedge-shaped and not fully ossified anteriorly, so the anterior-most part of the wedge separates the main body of the vomer from the ethmoid ossification.* The ethmoid is an oblong block of bone (initially ossifying as a saddle or tube around the cartilage) that extends forward from the lateral ethmoids along most of the length of the ethmoid cartilage. It is truncate anteriorly, and the ethmoid cartilage continues forward above the parasphenoid and vomer to the tip of the snout. In all but *Prionurus*, a dorsal plate of bone extends forward beyond the truncate portion of the ethmoid to overlie the ethmoid cartilage. In some species, this dorsal plate is sutured anteriorly to a posterodorsal laminar extension of the vomer, but there is still cartilage between most of the vomer and the ethmoid. The anterior end of the ethmoid is always a simple, flat, horizontal or slightly oblique plate. In *Luvarus*, the ethmoid cartilage is enormous and remains largely unossified posteriorly, but it is truncate anteriorly and does not separate the ethmoid and vomer in adults. In *Luvarus*, siganids, both outgroups, and most percoids, the ethmoid articulates with the dorsal surface of the vomer ventrally and its anterior surface is approximately vertically oriented. In chaetodontids, pomacanthids, and *Drepane*, the ethmoid is inverted posteriorly between the lateral ethmoids (see general outgroup discussion).

43. *The first dorsal (first three in *Zanclus*, see character 47) and first anal pterygiophores bear a semicircular, ribbed, median flange around which the first supernumerary spine can be rotated and locked at various positions* (see Tyler, 1970b; Figure 46b,c). A rudimentary spinous dorsal locking mechanism is present in larval, but not adult *Luvarus* (see character 75). We interpret its retention in adults as a synapomorphy of *Zanclus* and the acanthuroids. Siganids, all squamipinnes, and most percoids lack a dorsal and anal spine locking mechanism.

44. *As described by Mok (1977), "loop b" of the gut lies on the left side of the stomach.* In siganids, *Luvarus*, both outgroups, other squamipinnes, and percoids examined by Mok, "loop b" is on the right side of the stomach.

There are seven autapomorphies (45-51) of *Zanclus*.

45. *There is a conical, spine-like protuberance on each frontal near the anterodorsal margin of the orbit.*

Comparable structures are absent in other acanthuroids, squamipinnes, and percoids.

46. *All but the first two dorsal spines are produced and distally filamentous.* No other acanthuroids have elongate filamentous dorsal spines, and, among squamipinnes, they are found only in some ehippidids (e.g., *Platax*).

47. *There are median locking flanges on the first three dorsal spines.* See character 43 for outgroup discussion.

48. *The first dorsal pterygiophore bears a single supernumerary spine.* Other acanthuroids and scotophagids have two supernumerary spines on the first dorsal pterygiophore (in *Luvarus* only the larvae have two, the first being lost in juveniles, see characters 43 and 75). See Johnson and Washington (1987) for a discussion of the serial homology of dorsal spines in *Zanclus* and the acanthuroids. Most squamipinnes have two supernumerary spines on the first dorsal pterygiophore. However, the ehippidids *Platax* and *Monodactylus* have a single supernumerary spine and the ehippidid *Rhinoprenes* and the *Toxotidae* have no supernumerary spines on the first dorsal pterygiophore.

49. *There are 38–42 dorsal and 31–35 anal soft rays.* No other acanthuroids have more than 33 dorsal or 32 anal soft rays. Among squamipinnes dorsal soft ray counts as high as those of *Zanclus* are found only in the

ehippidid, *Platax*, and anal soft ray counts as high as those of *Zanclus* are found only in *Monodactylus*.

50. *There is a single predorsal bone.* The presence of a predorsal bone in *Zanclus* represents a reversal. See character 10 for outgroup discussion.

51. *There is a triangular, peak-like supraoccipital crest with a thickened anterior edge, representing a reversal.* See character 9 for outgroup discussion.

There are three synapomorphies (52–54) of the Acanthuridae.

52. *The ethmoid cartilage extends from the tip of the snout to at least mid-orbit and usually to the posterior border of the orbit.* At its posterior termination, it is clasped ventrally by bony medial flanges on the ventral surface of the frontals that project medially below the cartilage to meet in the midline (Figure 47). In all except *Prionurus*, these flanges also join the frontals posteriorly to form an oblique to vertical transverse wall separating the ethmoid cartilage from the cranial cavity, which is thus restricted from extending into the supraorbital space below the frontals. In other acanthuroids, all squamipinnes, and most percoids, the ethmoid cartilage does not extend much beyond the anterior border of the orbit (and usually ends anterior to it) and is not supported posteriorly by ventromedial frontal flanges.

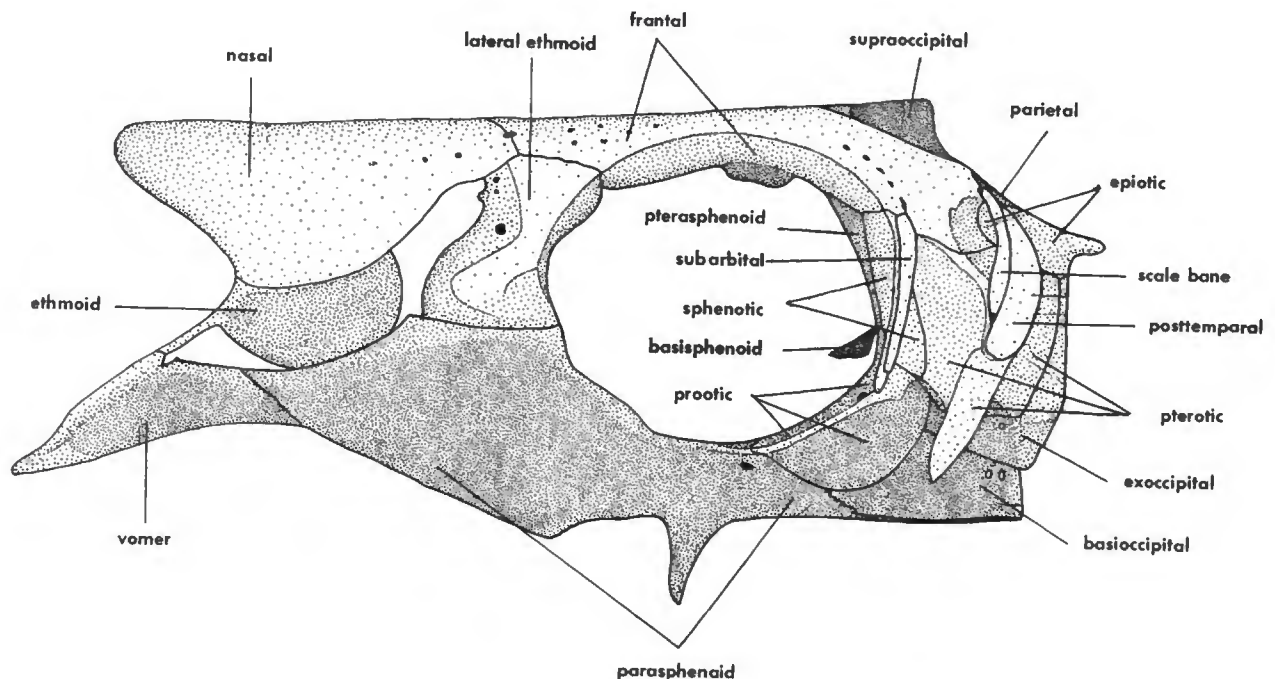


FIGURE 47.—Lateral view of neurocranium of *Naso* sp., MCZ uncat., 370 mm SL.

cavity extends anteriorly into the supraorbital space below the frontals.

53. *The locking mechanism on the first dorsal and anal pterygiophores is further specialized, and a deep vertical groove accommodates the short first spine as it rotates around the crescentic median flange.* Tyler (1970b) gave detailed descriptions and illustrations of this locking mechanism and associated morphology. See character 43 for outgroup discussion.

54. *One or more fixed (Naso and Prionurus) bony plates or a single folding spine (others) are present on the caudal peduncle.* These peduncular structures are apparently homologues; both develop by enlargement and modification of one or more of the specialized scales that cover most of the body of larval acanthurids. Contrary to the statement of Leis and Richards (1984), our observations indicate that the folding spine that characterizes four of the six genera passes through a fixed plate stage in its transformation from larval scale to folding spine. Comparable peduncular structures are absent in other acanthuroids, squamipinnes, and percoids. In larval *Luvarus*, some of the scales with fan-shaped laminar projections become relatively large and, in juveniles, resemble the peduncular plates of juvenile *Naso* and *Prionurus*. These larger "keeled" scales are scattered over the body of *Luvarus*, but those on the caudal peduncle are the largest. We believe it is unlikely that these structures in *Luvarus* are homologous with the peduncular plates of acanthurids; the latter structures develop from larval scales with a configuration very different from those of *Luvarus* (see characters 80–82). If the two structures are homologous, then peduncular plates are a synapomorphy at the *Luvarus* node, and they have been lost in *Zanclus*.

There are four autapomorphies (55–58) of the Nasinae (*Naso*).

55. *There are only four (0+4) branchiostegals* (Figure 42c). In other acanthuroids there are five (1+4); the single anterior element borne on the ceratohyal has been lost in *Naso*. Squamipinnes and most percoids have six or seven (2–3+4) branchiostegals.

56. *The spinous dorsal and anal fin locking mechanism is specialized relative to other acanthurids* (see Tyler, 1970b, figs. 10, 11). The first supernumerary spine on the first dorsal and anal pterygiophore is reduced and lacks a pointed distal tip; it lies beneath the surface of the skin. The anterodistal corner of the first dorsal and anal pterygiophore is expanded to form a broad, anteriorly rounded shield that houses the reduced first spine as it rotates around the ribbed locking flange. See characters 43 and 75 for outgroup discussion.

57. *The single uroneural pair is notably shorter than that of other acanthuroids (except siganids), squamipin-*

nes, and most percoids. In siganids the uroneurals are reduced to small nubbins of bone, a reduction apparently independent of that in *Naso*.

58. *Hypurals 1–4 fuse to form a single hypural plate; only hypural 5 remains autogenous.* In other acanthuroids (except *Luvarus*) and squamipinnes, hypurals 1–5 remain autogenous. Hypural fusion in *Luvarus* (see character 36) arose independently of that in *Naso*.

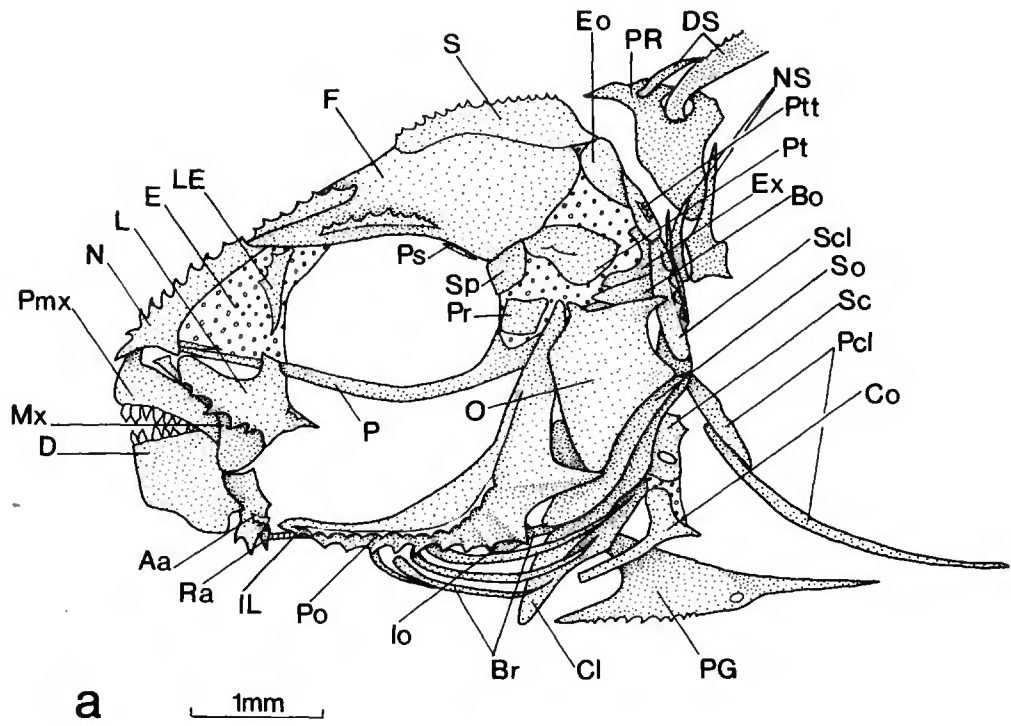
The following are synapomorphies of the Acanthurinae (*Prionurus*, *Zebrasoma*, *Paracanthurus*, *Acanthurus*, and *Ctenochaetus*).

59. *The jaw teeth are spatulate, with strong, multi-lobate, denticulations* (see Tyler, 1970a, fig. 16). Most species of *Naso* have conical teeth; in some the tips of the teeth are flattened (but not spatulate), with weakly denticulate edges. The jaw teeth of *Zanclus* are simple, flexible, elongate, and laterally compressed. In siganids the teeth are robust, somewhat compressed at the tips and, in at least some species, asymmetrically bifid. Tooth configuration varies among squamipinnes, but none resemble the distinctive, multi-lobate, spatulate teeth of acanthurines.

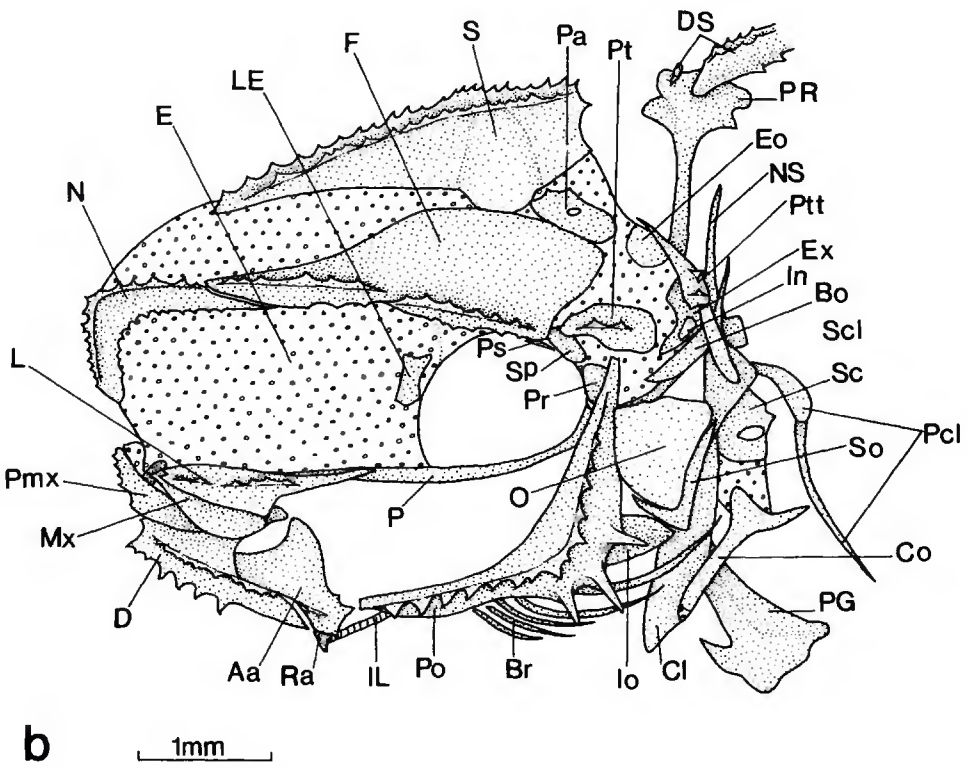
60. *Some or all of the specialized scales, where present in the larvae (absent in Paracanthurus and Zebrasoma), are resorbed and some or all adult scales form anew rather than transforming directly from existing larval scales* (see characters 71 and 81). In other acanthuroids, squamipinnes, and percoids with larval scales, the larval scales transform directly into the adult scales.

LARVAL MORPHOLOGY.—The larvae of acanthuroids exhibit a complex morphology that differs trenchantly from that of the adults. Shape and ornamentation of head bones are illustrated in Figures 48, 49. We discuss characters of the larvae below and list them separately on the cladogram. Only synapomorphies are considered. As treated here, larval characters provide an independent test of our hypothesis of acanthuroid intrarelationships based on the adult characters described above.

FIGURE 48.—Lateral view of skulls: a, *Siganus* sp., MCZ 63119, 9.5 mm SL; b, *Luvarus imperialis*, MCZ 55291, 10.5 mm SL (from Johnson and Washington, 1987). (Osteological abbreviations: Aa = anguloarticular (articular); Bo = basioccipital; Br = branchiostegal; Cl = cleithrum; Co = coracoid; D = dentary; DR = distal radial; DS = dorsal-fin spine; Eo = epioccipital (epiotic); Es = extrascapular; Ex = exoccipital; F = frontal; I = infraorbital; IL = interoperculo-mandibular ligament; In = intercalar; Io = interopercle; L = lachrymal; LE = lateral ethmoid; MK = midventral keel; Mx = maxilla; N = nasal; NS = neural spine; O = opercle; P = parasphenoid; Pa = parietal; Pcl = postcleithrum; Pd = predorsal; PG = pelvic girdle; Pmx = premaxilla; Po = preopercle; PR = proximal-middle radial; Pr = prootic; Ps = pterospheonoid; Pt = pterotic; Pu = posttemporal; Ra = retroarticular (angular); S = supraoccipital; Sc = scapula; Scl = supracleithrum; So = subopercle; and Sp = sphenotic.)



a



b

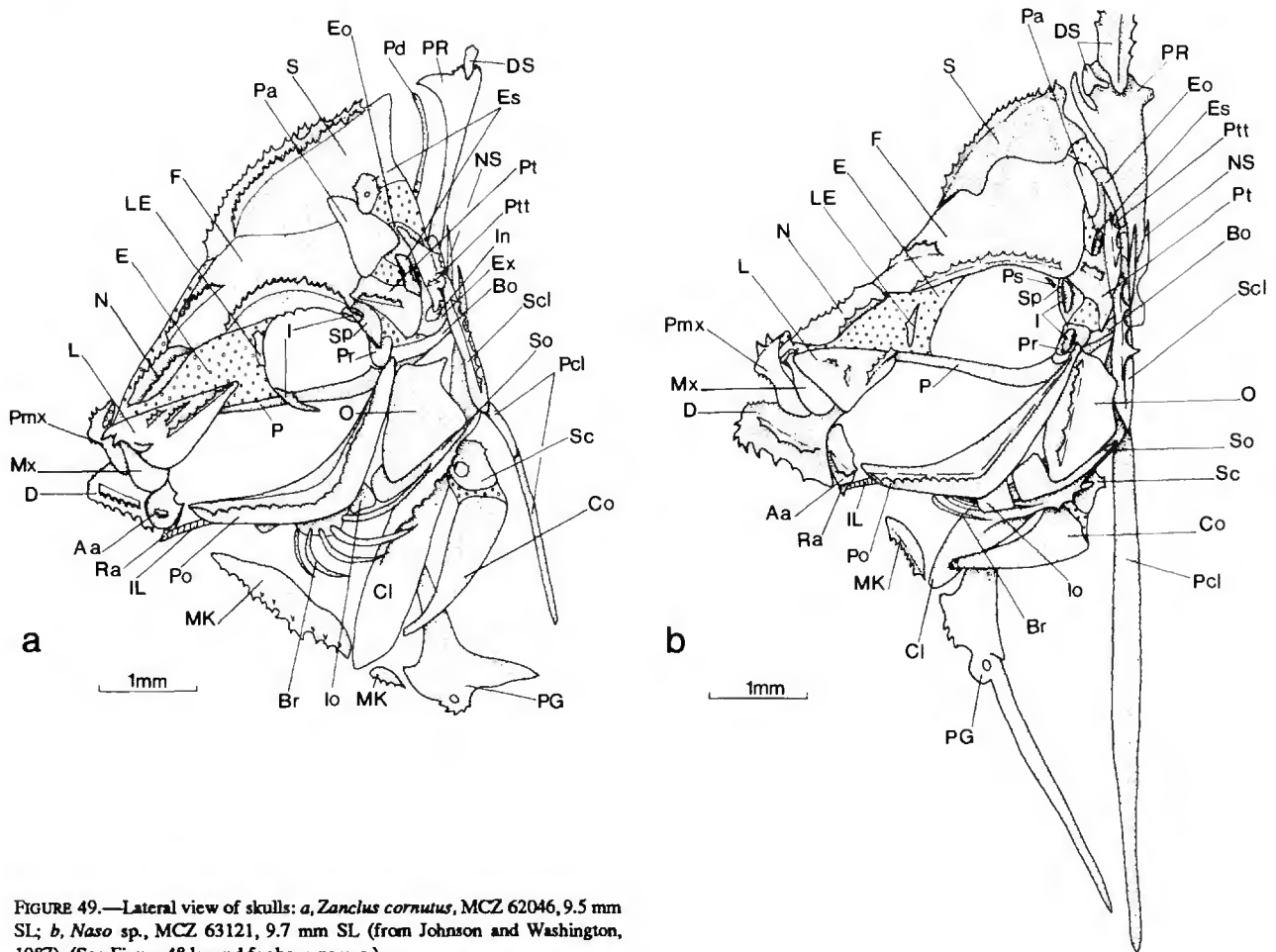


FIGURE 49.—Lateral view of skulls: *a*, *Zanclus cornutus*, MCZ 62046, 9.5 mm SL; *b*, *Naso* sp., MCZ 63121, 9.7 mm SL (from Johnson and Washington, 1987). (See Figure 48 legend for bone names.)

Larvae of the Acanthuroidei share the following eight specializations (61–68).

61. *The second (third in Zanclus) dorsal and pelvic spines are the first fin rays to form and they rapidly become enlarged and serrate. The first dorsal pterygiophore and pelvic girdle also are precocious and relatively very large and robust. Elongate, serrate and/or precocious dorsal and pelvic spines are absent in both outgroups and occur among squamipinnes only in a few chaetodontids, where the corresponding supporting structures are not particularly large or robust. Zanclus is exceptional in having the third, rather than the second, dorsal spine elongate. See Johnson and Washington (1987) for a discussion of the apparent lack of serial homology between the elongate dorsal spines of Zanclus and other acanthuroids.*

62. *The pelvic girdle has a unique configuration, being essentially T-shaped and so oriented that the*

primary ramus extends upward at a steep angle to the horizontal. Dorsally, the cartilaginous tip of the primary ramus articulates between the cleithra at a point about halfway from the scapula to the cleithral symphysis. Ventrally, the subpelvic keel and postpelvic process extend anteriorly and posteriorly, respectively, forming the horizontal to oblique head of the inverted "T." (This configuration is much less distinctive in adults, being most evident in siganids and Zanclus.) The subpelvic keels are exposed and serrate in all but Luvarus and Zanclus. To our knowledge, this distinctive pelvic girdle configuration and the serrate subpelvic keels are unique to acanthuroids.

63. *A thin, slightly curved spine projects ventrally from the posteroventral corner of the angular (= retro-articular), below the insertion of the interoperculo-mandibular ligament; it is the first area of the angular to ossify. When an angular spine is evident in squamipinne larvae (some ephippidids and pomacanthids), it is much*

shorter and does not project below the insertion of the interoperculo-mandibular ligament.

64. *There is a low, distinctly serrate ridge on the supraoccipital.* Comparable supraoccipital ornamentation does not occur in larval squamipinnes, although it is found in some larval percoids (see Johnson, 1984).

65. *On each frontal, there are two well-developed serrate ridges, a slightly arched (straight in *Luvarus*) ridge above the orbit, and a longitudinal ridge anteromedial to the supraorbital ridge.* The latter is absent in all known squamipinne larvae and secondarily in the acanthurines *Paracanthurus* and *Zebrasoma*; the former is absent in larvae of both outgroups, found among larval squamipinnes only in pomacanthids, and is characteristic of larvae of several percoid families (see Johnson, 1984).

66. *The trough-shaped nasal bone bears serrations along one (siganids) or both edges.* Serrate nasal bones are absent in larvae of both outgroups; they are found among squamipinne larvae only in pomacanthids and also characterize the larvae of several percoid families (see Johnson, 1984).

67. *There is a serrate, ventrolaterally-directed, longitudinal ridge on the angular.* A similar ridge is absent in larvae of both outgroups and is found among larval squamipinnes only in pomacanthids.

68. *There is a laterally directed, partially exposed ridge on each lateral ethmoid usually bearing one to several small spines; the ridge is lacking in *Luvarus*, where its absence is interpreted as a reversal.* Larvae of squamipinnes and percoids lack a comparable ridge.

There are seven synapomorphies (69–75) of larval *Luvarus*, *Zanclus*, and the Acanthuridae.

69. *The body is extremely compressed and kite-shaped (the uniquely truncate ethmoid cartilage of *Luvarus* disrupts the anterodorsal outline of the "kite" shape).* A similar shape is not seen in larval siganids or among the larvae of squamipinnes.

70. *The midbrain is dome-shaped, being deeper than it is long, and is housed in a vertically elongate, dome-like cranial cavity.* A smaller, similarly shaped cavity lies just anterior to the main cavity, from which it is separated by a small triangular block of cartilage. In larval siganids, squamipinnes, and most percoids, the midbrain is relatively broad and there is no discrete cranial dome.

71. *The early forming, specialized scales each bear a single, broad-based (fan-shaped or triangular) lamina that projects upright from the basal plate (Figure 50).* Larval scales are absent in siganids and, secondarily, in the acanthurines *Paracanthurus* and *Zebrasoma*. Larval scales occur in both outgroups, but there, as in other squamipinnes (e.g., *Chaetodipterus*) and most percoids with larval scales, the upright projections are more

rounded or spindle-like, and there are usually several on each scale. The narrow-based, elongate projections (two or more per scale) on the larval scales of pomacanthids eventually become flattened basally, but, unlike those of acanthuroids, they initially pass through a rounded, spindle-like stage. Leis' (1984) statement that the larval scales of acanthurids pass through an "intermediate spinule stage" is not borne out by our observations.

72. *There is an anteriorly directed, vertical ridge on the ascending process of each premaxilla, bearing two or three somewhat dorsally directed spines.* Spines on the ascending processes of the premaxillae are unique to these groups among larval perciforms.

73. *There are two or three serrate ridges on the lateral surface of the lachrymal.* The dorsal and ventral margins of the lachrymal are serrate in larval siganids and pomacanthids, but the lateral surface is smooth, as it is in larvae of both outgroups, other squamipinnes, and most percoids. The absence of serrate ridges on the lachrymal in *Paracanthurus* and *Zebrasoma* represents a reversal.

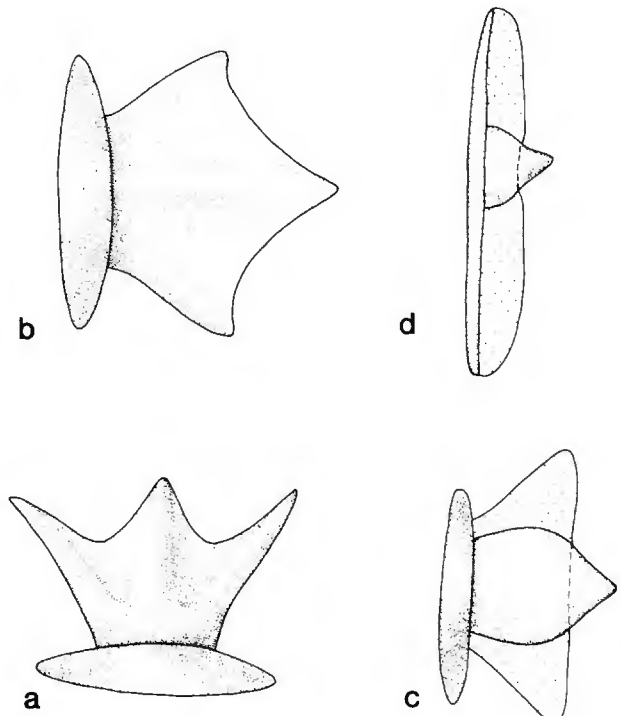


FIGURE 50.—Larval scales, oriented as they are along body; sparser stippling represents specialized connective tissue: a, *Luvarus imperialis*, MCZ 55291, 10.5 mm SL, ventral view; b, *Zanclus cornutus*, MCZ 62046, 9.5 mm SL, posterior view, right side; c, *Naso* sp., MCZ 63121, 11.0 mm SL, posterior view, right side; d, *Acanthurus* sp., USNM 240072, 10.4 mm SL, posterior view, right side (from Johnson and Washington, 1987).N

74. *There are two serrate, longitudinal ridges on the dentary, one along the side (absent in Paracanthurus and Zebrasoma) and another along the ventral margin.* Larvae of both outgroups and all other squamipinnes, except pomacanthids, lack serrations on the dentary. Pomacanthid larvae and larvae of a few percoid families (see Johnson, 1984) have serrate ridges on the dentary similar to those described above; in those groups dentary serrations are most parsimoniously hypothesized to have been acquired independently of those in acanthuroids.

75. *There is a locking mechanism for the elongate second (third in Zanclus) dorsal spine, as described for adults (see character 43).* The first (first three in *Zanclus*, character 47) dorsal pterygiophore bears a crescentic, ribbed flange on its dorsal midline around which the first supernumerary spine can be rotated and locked. The first supernumerary spine is connected to the elongate second (second and elongate third in *Zanclus*) by a stout ligament, providing a means for locking the longer spine in an upright position.

A rudimentary locking flange is present on the first dorsal (but not first anal, as in *Zanclus* and acanthuroids) pterygiophore in larval *Luvarus* (Figures 46, 48), but that pterygiophore is gradually modified with growth, and so the flange is absent by about 50 mm SL. Larval *Luvarus* also bear a tiny first supernumerary spine on the first dorsal pterygiophore, the serial homologue of the first supernumerary spine that functions as a locking device in larval and adult acanthuroids. This spine is gradually reduced with growth in *Luvarus*, eventually fusing to the dorsal surface of the pterygiophore (fused in our 301 mm SL specimen). Thus, a functional spinous-dorsal locking mechanism is present in *Luvarus* only in the larvae. This mechanism also appears early in larval *Zanclus* and acanthuroids, where it is present in the anal fin as well and is retained in the adults. We postulate that a spine-locking mechanism evolved originally within acanthuroids as a larval specialization to support the elongate dorsal and anal spines of the larvae (see character 61) and interpret its retention in adults as a synapomorphy of *Zanclus* and the acanthuroids. Larvae of siganids, squamipinnes, and most percoids lack spine-locking mechanisms in the median fins.

There are four synapomorphies (76–79) of larval *Zanclus* and the Acanthuridae.

76. *There are one (long) to several (short) serrate bony keels along the ventral midline between the angle of the lower jaw and the cleithral symphysis and, except in Naso, posterior to the cleithral symphysis also.* In larval *Luvarus* the scales in this area are somewhat enlarged, and it seems likely that the keels originated by enlargement and/or consolidation of larval scales. Midventral bony keels are absent in the larvae of

siganids, squamipinnes, and percoids.

77. *The obliquely oriented lateral ridge of the cleithrum is serrate along about half of its length.* Larvae of *Luvarus*, siganids, squamipinnes, and most percoids (see Johnson, 1984) lack serrations on the cleithrum.

78. *There is a weakly ribbed crescentic flange on the pelvic girdle against which the pelvic spine can be locked.* This flange resembles those of the first dorsal and anal pterygiophores, but unlike them it is present only in the larvae. Larvae of *Luvarus*, siganids, squamipinnes, and most percoids lack a locking flange on the pelvic girdle.

79. *The scales (absent in Paracanthurus and Zebrasoma) are so arranged that the bases of their laminar projections are distinctly vertically oriented.* In *Luvarus* larvae the fan-shaped projections are horizontally oriented. Siganids lack larval scales, and larval scales of squamipinnes and percoids have spindle-like projections, usually with no specific orientation; however, the slightly flattened, narrow-based projections on the scales of larger pomacanthid larvae are also vertically oriented.

There are eight synapomorphies (80–87) of larval Acanthuridae.

80. *The scales are arranged in ordered vertical rows.* In larval *Zanclus*, *Luvarus*, and those squamipinnes and percoids with larval scales, there is no apparent order to the arrangement of the scales.

81. *The scales have a unique configuration (see Johnson and Washington, 1987; Figure 50).* The basal plates are ovoid to very narrow and elongate and the laminae are triangular. In *Zanclus* and *Luvarus*, the scale plates are approximately round and the laminae are fan-shaped; in squamipinnes and percoids with larval scales the basal plates are also round and the projections are spindle-like.

82. *There is a rounded ridge of firm, non-bony, connective tissue along the entire length of the basal plate of each scale.* This tissue stains definitively with alcian blue; superficially, it has a resilient cartilage-like texture, but the characteristic "cellular" matrix of true cartilage is not evident, even in histological sections. Among perciforms, a ridge of specialized connective tissue along the scale plate is unique to the scales of larval Acanthuridae.

83. *Although the pelvic spine is precocious, as in other acanthuroids, the soft rays of the pelvic fin appear late (6–8 mm SL) in development and remain relatively short and poorly developed to sizes as large as 15 mm SL.* Pelvic soft rays appear much earlier in larvae of other acanthuroids, squamipinnes, and most percoids. In siganids, the rays may appear as late as 6–7 mm (probably a relatively earlier stage in development when compared to the deep-bodied, precocious acanthuroids),

but they are well-developed by 10 mm SL.

84. *The single postcleithrum (on each side) ossifies very early (3 mm) and forms a strong, almost vertically oriented strut that extends to the ventral body margin where it abuts and braces the anteroventral corner of the enlarged first anal pterygiophore.* In larvae of other acanthuroids, squamipinnes, and most percoids, the postcleithra (on each side) comprise separate dorsal and ventral elements, ossify much later, do not form an enlarged strut and do not extend to the ventral body margin.

85. *The posterior margin of the preopercle develops two minute spines near the angle, but these are lost by 5 mm SL or less, and the posterior margin remains smooth for the remainder of the larval period.* Larval *Zanclus* and *Luvarus* develop three relatively large spines on the preopercular margin, one at the angle (the largest) and one on either side of it. In *Zanclus*, these spines diminish with development and are lost by about 9 mm SL; *Luvarus* retains them throughout the larval period, and the larger spine at the angle is still evident, although reduced in a 35 mm SL specimen. Large preopercular spines also characterize the larvae of siganids, squamipinnes, and many percoids (see Johnson, 1984).

86. *There is a vertically oriented, serrate ridge on the lateral surface of the opercle.* A comparable ridge is absent in larvae of other acanthuroids, squamipinnes, and most percoids.

87. *The second anal spine is notably elongate and the first anal pterygiophore is an enormous, columnar strut, several times larger than the succeeding pterygiophores.* This pterygiophore extends dorsally, and its cartilaginous tip is tightly embraced by needle-like parapophyses on the posterior three to four precaudal vertebrae. In larvae of other acanthuroids, squamipinnes, and most percoids, the second anal spine is robust, but not notably elongate, and the first anal pterygiophore, although relatively large in some (e.g., *Zanclus*), does not approach the massive strut described above, nor is it embraced dorsally by several vertebral parapophyses.

The following are autapomorphies of larval Acanthurinae.

88. *The vertically oriented ridge on each lateral ethmoid lacks spines.* In larvae of *Naso*, *Zanclus*, and siganids, there are one to several minute to small spines along this ridge. The ridge is absent in larvae of *Luvarus* (apparently secondarily), squamipinnes, and most percoids.

89. *The scales are extremely long and narrow (the long axis is vertically oriented).* *Naso* larvae have ovoid scales, and those of other acanthuroids, squamipinnes, and percoids are circular.

90. *Scales on the head and cheek and most of those on the body anterior to the postcleithra lack the central*

upright projections (triangular laminae or "spines") that are borne on the remaining scales. In larvae of *Naso*, *Zanclus*, and *Luvarus* all scales bear upright laminar projections. In larvae of squamipinnes and those percoids with larval scales having spinulose projections, these projections are borne on all scales.

Summary of Character Analysis

Evidence from both larval and adult morphology convincingly supports the hypothesis that *Luvarus* is a highly derived member of the Acanthuroidei and that, within the acanthuroids, it is the sister group of *Zanclus* plus the Acanthuridae. Homoplasy as indicated by the most parsimonious solution to the distribution of 90 characters is minimal, consisting of a single hypothesized convergence (hypural fusion in *Luvarus* and *Naso*) and 12 hypothesized reversals.

We identified 19 synapomorphies that diagnose the Acanthuroidei. *Luvarus* shares all but three of these: an articular much shorter than the dentary (character 7); a longitudinally oriented fourth pharyngeal toothplate (11); and presence in the larvae of a distinct ridge on the lateral ethmoid (68). The primitive states exhibited by *Luvarus* are interpreted as reversals. Reversals among the 19 acanthuroid synapomorphies in other taxa are as follows: *Zanclus* has reacquired a peak-like supraoccipital crest (9) and a predorsal bone (10); *Prionurus* has independently reacquired a predorsal bone (10); larval *Paracanthurus* and *Zebrasoma* have lost (failed to develop) an anterior ridge on the frontal (65).

A total of 15 synapomorphies unite *Luvarus*, *Zanclus*, and the Acanthuridae as a monophyletic clade. *Luvarus* exhibits all of these. The following reversals are hypothesized in other taxa: *Paracanthurus*, *Acanthurus*, and *Ctenochaetus* have lost fin-ray spinules (30); *Acanthurus* and *Ctenochaetus* have reacquired true ctenoid scales (31); larval *Paracanthurus* and *Zebrasoma* have lost specialized larval scales (71), serrate ridges on the lachrymal (73), and the lateral serrate ridge on the dentary (74). Among nine synapomorphies that unite *Zanclus* and the Acanthuridae and 11 that diagnose the Acanthuridae there are no reversals.

Three additional conflicts, interpreted as reversals in *Luvarus*, occur among the 8 to 10 derived characters that acanthuroids share with immediate outgroups. *Luvarus* lacks cancellous frontal and supraoccipital bones (present in all other acanthuroids, scatophagids, and ephippidids), lacks a specialized gill filament arrangement (present in all other acanthuroids and ephippidids) and has an ovoid interopercle (roughly ax-shaped in all other acanthuroids, scatophagids, and ephippidids).

Evolution and Adaptation

As the single truly pelagic member of the suborder Acanthuroidei, a group that otherwise comprises strictly shore

fishes (sensu Springer, 1982), *Luvarus* represents a remarkable example of evolutionary adaptation. Although its specific habits remain largely a mystery, *Luvarus* apparently spends its entire life in the epipelagic zone of the open ocean, and grows to a length at least twice that of any other acanthuroid. Most of its highly specialized morphology involves adaptation to this pelagic existence and, as with the pelagic scombroid fishes, centers around locomotory mechanics and hydrodynamic efficiency. The body, although not classically fusiform because of the deeply truncate forehead, is well-streamlined, suggesting that *Luvarus* at least occasionally swims rapidly. The absence of dorsal and anal spines and of pelvic fins contributes to streamlining, as does the flat, relatively consolidated opercular series. The prominent narrow groove extending along the sides of the head above the eye from the snout to the pectoral fin is probably in some way hydrodynamically efficacious. The precise function(s) of the peripheral bony truss of interdigitated pterygiophores is unclear, although it certainly serves to substantially stiffen and decrease lateral undulation of the body from the head to the caudal peduncle and thus has some effect on locomotion.

Finally, there is the extreme modification of the entire caudal propulsive unit, including the fin, supporting elements, and peduncular vertebrae. The large fleshy median keel on the caudal peduncle is a common feature of large pelagic fishes (e.g., scombrids and lamnid sharks), serving to direct water flow and streamline the lateral movements of the caudal peduncle. The caudal fin itself is stiff and relatively inflexible, the bases of the rays deeply embracing the hypurals and other supporting elements, which are fused into a single plate. In these features *Luvarus* closely resembles the scombroids. Striking morphological convergences, presumably in response to similar locomotory demands, have resulted in the continued misplacement of *Luvarus* in or near the Scombroidei.

Ironically, *Luvarus* may regularly swim in a mode quite unlike that of scombroids, which swim continuously at relatively high speeds. We suspect that *Luvarus* spends much of its time slowly sculling with its caudal fin, which is capable of considerable lateral and some dorsoventral movement around the short, loosely articulated, "pivotal" nineteenth vertebra. Two small bundles of red muscle extend along the lateral midline of the body to insert on the hypural plate and bases of the caudal-fin rays. Contraction of these muscles essentially "wags the tail" posterior to the eighteenth vertebra, to which the terminus of the peripheral bony truss is anchored. We propose, then, that the normal swimming mode of *Luvarus* is basically ostraciiform, a slow sculling with the tail (and probably the pectoral fin as well) while most of the body remains unflexed, and that high-speed, carangiform swimming occurs only in bursts, probably mainly for predator avoidance. The skeletal bone in *Luvarus* is light and delicate and the swim bladder is relatively large, so neutral buoyancy should be easily maintained even at very slow speeds. As might be expected, the caudal fin, although deeply forked and relatively rigid, has

more surface area and a lower aspect ratio than that of scombrids, perhaps a compromise between efficiency for speed and the need for rapid acceleration from the sculling mode. The spinulose, pediculate scales that cover the body of *Luvarus* may also increase efficiency of acceleration for burst swimming, much as the spinulose scales have been postulated to function in *Ruvettus* (Bone, 1972), by generating microturbulence and thus preventing separation of the boundary layer as the body accelerates (suggested by R.H. Rosenblatt, pers. comm.).

Information on the feeding habits of *Luvarus* is scant, but the small, edentulous mouth and long, extensively coiled intestine indicate that *Luvarus* does not feed on large, fast-swimming fishes or invertebrates. The stomachs of most specimens mentioned in the literature have been empty, but several have been reported to contain jellyfish and ctenophores (Gotshall and Fitch, 1968). If coelenterates, salps, etc., constitute a major source of the diet of *Luvarus*, a slow sculling mode of foraging seems not only reasonable but necessary. It appears that *Luvarus* may simply have taken the browsing habits typical of the herbivorous, reef-associated acanthuroids into the oceanic realm.

If one were to select a group of shore fishes from which a pelagic form was most likely to arise, the Acanthuroidei would at first seem a strange choice, but upon more reflection a logical one. The pelagic acronurus stage of acanthuroids is not only one of the most highly specialized larval/prejuvenile forms among percomorphs, but it is also among the largest, reaching at least 60 mm SL in *Zanclus* and acanthurids (Leis and Rennis, 1983), and the longest in planktonic duration. A larval *Naso*, 30.6 mm SL, had 84 daily increments in the otolith (Brothers et al., 1983); thus, an individual twice that size may have been in the plankton for as much as four to five months. It is tempting to speculate that this extended pelagic existence during the early life history of acanthuroids in some way facilitated the evolution of the pelagic *Luvarus* from shore-associated ancestors. In acanthuroids, as in many marine shore fishes, transformation from larval to juvenile/adult morphology is a fairly abrupt process that occurs after settling from the plankton, a phenomenon presumably tied to specific environmental cues. In the absence of the appropriate physical stimuli, settling may be substantially delayed. One can envision a heterochronic scenario for the evolution of *Luvarus* whereby the planktonic duration of the ancestral pelagic prejuvenile was gradually extended, eventually delaying settling and the usual abrupt morphological transformation associated with it into the period beyond the onset of sexual maturity. This is "postdisplacement" in the terminology of Alberch et al. (1979), and one would expect at least some of the larval morphology to be expressed paedomorphically in the pelagic adult. In fact, none of the numerous distinctive specializations that characterize larval acanthuroids (including those of *Luvarus*) are retained in adult *Luvarus*.

The absence of larval specializations in the adult, however, is not surprising and probably does not provide a valid test of the

role of paedomorphosis in the evolution of *Luvarus*. Although adults and larvae share the same general oceanic space, the plankton is a separate microcosm, with unique interactions, physical conditions, and associated problems not encountered by a large epipelagic fish. Furthermore, there is probably a substantial hydrodynamic scale factor involved. Much of the specialization of larval acanthuroids encompasses bony ornamentation, e.g., spines, serrate ridges, and embellished scales; the hydrodynamic properties of these various projections are surely drastically different over the range of sizes and swimming speeds encompassed in the transition from the tiny larvae to the giant adults. A larval feature such as the elongate, serrate locking-fin spines that presumably provide protection against predation would not only be ineffective in a large pelagic fish but also would be hydrodynamically disadvantageous.

It would seem that evidence of paedomorphosis is more likely to be manifest in characters that are not so obviously adapted for survival in the plankton. In the context of the hypothesized phylogeny, paedomorphic expression in *Luvarus* would be interpreted as reversal due to truncation with respect to the ontogenetic trajectory of other acanthuroids. Six reversals are hypothesized for *Luvarus* in our analysis. Four of these (transverse orientation of the fourth pharyngeal toothplate, subequal articular and dentary, attached epibranchial gill filaments, and ovoid interopercle) are not interpretable as ontogenetic truncations. The primitive (reversed) state that characterizes *Luvarus* is never evident in the early development of acanthuroids, e.g., the fourth pharyngeal toothplate is not initially transversely oriented. The remaining two reversals (smooth frontal and supraoccipital bones and lack of a lateral ethmoid ridge in the larvae) appear in the early larval

development of acanthuroids and thus can be viewed as paedomorphic in *Luvarus*. Other reductive features that appear paedomorphic include failure of epipleural ribs and adult dentition to develop and the feeble bone and relatively large proportion of cartilage remaining in the ethmoid region.

We conclude that paedomorphosis, probably through postdisplacement, has contributed to the evolution of the highly specialized pelagic *Luvarus* from nonpelagic ancestors, but not as the dominant process. *Luvarus* is not simply a giant larva. Just as the larvae of other acanthuroids abruptly transform at settling and develop an entirely new morphology adapted for their shore-associated habitus, so the larvae of *Luvarus* transform, albeit more gradually, and the adults acquire a distinct suite of specializations, adapted for exploiting the oceanic realm in a mode altogether different from that of the larvae. Certain aspects of the morphology of *Luvarus* do appear to be the result of ontogenetic truncations presumably related to extended planktonic duration of the larva and the concomitant postponement of transformation. However, most aspects of its morphology (e.g., the numerous locomotory specializations) are clearly peramorphic, development having proceeded beyond (and eventually in a different direction from) that in other acanthuroids to new and unique morphologies ("hypermorphosis" in the terminology of Alberch et al., 1979). We propose that gradual protraction of the planktonic residence of the larva expanded temporally and spatially the evolutionary arena in which selection might work on pelagic adaptation, while the accompanying heterochronic processes facilitated novel morphological combinations for selective experimentation. In this way *Luvarus* entered a new and extraordinarily different adaptive zone.

Note

In a recent study on the phylogenetic relationships of the Chaetodontidae, completed after our study, Blum (1988) analyzed outgroup relationships for the family based on over 30 characters. His conclusions concerning relationships among higher squamipinnes agree with ours, with one exception. When additional characters are considered, placement of *Drepane* as the sister group of chaetodontids and pomacanthids is less parsimonious than placement with the ehippidids, even though the latter placement requires independent evolution of the unique ethmoid-upper jaw complex. Although a more in-depth analysis (including larval morphology and additional skeletal characters) will be required to resolve the relationships of *Drepane*, we tentatively accept Blum's conclusions, because they are based on more characters than ours. Because polarity assessment for the acanthuroids is not affected by the placement of *Drepane*, we have not altered our analysis.

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