THE OSTEOLOGY AND RELATIONSHIPS OF THE ANGLERFISH GENUS *TETRABRACHIUM* WITH COMMENTS ON LOPHIIFORM CLASSIFICATION[1]

THEODORE W. PIETSCH[2]

ABSTRACT

The shallow-water anglerfish, *Tetrabrachium ocellatum*, now represented by 36 specimens from Australian, New Guinean, and Indonesian waters, is redescribed and compared osteologically with its allies within the Antennarioidei. Phylogenetic analysis based on a search for shared, derived characters shows that *Tetrabrachium* is most closely related to *Antennarius*, and is classified on this basis as a sister-family of the Antennariidae. That the Tetrabrachiidae has entered a "new adaptive zone" relative to the Antennariidae is evidenced morphologically by a number of unique derived features. The most conspicuous of these include small, close-set eyes protruding from the dorsal surface of the head, and a peculiar webbing between the pectoral fin and the body, and between the pectoral and pelvic fins, characters that reflect a benthic existence in soft substrata (mud or fine sand).

It is further shown that a group including the Antennariidae and Tetrabrachiidae forms the primitive sister group of the Lophichthyidae and that these two groups together form the primitive sister group of the Brachionichthyidae. Although evidence is provided to establish a sister-group relationship between the Chaunacidae and Ogcocephalidae, no convincing synapomorphy is known at the present time that will establish monophyly for a group containing all six families. An analytical key to the major subgroups of the Antennarioidei is provided and a revised classification of the order Lophiiformes is proposed.

One of the more curious forms described by Günther (1880) in his report on the shore fishes procured by the *Challenger* Expedition of 1873-76, was a single specimen of an antennarioid anglerfish from off the southern coast of New Guinea. In reference to a peculiar, double pectoral fin and numerous ocellilike markings on the dorsal half of the body, the species was named *Tetrabrachium ocellatum*. Since the original description perhaps a dozen authors have cited Günther (1880), but none have been able to offer any new information on this species other than a report of the discovery of two additional specimens (Whitley 1935). For the purposes of this study, 36 specimens of *T. ocellatum* have been located, all collected from Australian, New Guinean, and Indonesian waters at depths of between approximately 5 and 55 m. Although a close phylogenetic relationship with the genus *Antennarius* has been implied (by recognition of a subfamily Tetrabrachiinae of the Antennariidae; Regan 1912, Berg 1940, Norman 1966), no evidence for this alignment has been provided.

The objectives of this paper are to describe the structure of *T. ocellatum*, to compare it morphologically with its nearest allies, and to speculate on the phylogenetic relationships of this and other members of the suborder Antennarioidei. Representatives of the six major antennarioid subgroups (here recognized as families) are considered in detail. In addition to *Tetrabrachium*, these are *Antennarius* Daudin, recognized here as the least derived genus (see Phylogenetic Relationships below) of some eight genera of the Antennariidae (a modification of Schultz 1957; Pietsch in prep.); *Lophichthys*, a monotypic genus recently described by Boeseman (1964) and heretofore not adequately placed within any higher taxonomic category (see Boeseman 1964 and Le Danois 1979); *Brachionichthys* Bleeker (= *Sympterichthys* Gill), containing approximately four southern Australian species, and recognized as constituting an antennarioid family by nearly all authors since Regan (1912); *Chaunax* Lowe, the only genus of the family Chaunacidae; and *Dibranchus* Peters, an underived genus of the Ogcocephalidae (see Bradbury 1967).

[1]Contribution No. 561, College of Fisheries, University of Washington, Seattle, Wash.

[2]College of Fisheries, University of Washington, Seattle, WA 98195.

Manuscript accepted February 1981.
FISHERY BULLETIN: VOL. 79, NO. 3, 1981.

METHODS AND MATERIALS

Standard lengths (SL) are used throughout. All measurements were taken on the left side and rounded to the nearest 0.5 mm. Head length is the distance from the anterior tip of the upper jaw to the posteriormost margin of the preopercle. The illicial bone is the first spinous dorsal ray (Bradbury 1967). Sockets indicating missing teeth in the jaws and on the vomer were included in total tooth counts. The analysis of relationships follows, in a general way, the phylogenetic approach suggested by Hennig (1966) with the exception that not all branching points in the cladogram are formally named. The loss of convenience in discussing individual sister groups by a single epithet is outweighed by the avoidance of adding a multiplicity of new taxonomic categories and names, as well as the necessity of altering names that are well established in the scientific literature. The relative primitiveness of character states is identified by the procedure of outgroup comparison as discussed by Eldredge and Cracraft (1980:63).

The osteology of *Tetrabrachium ocellatum* is based on two specimens (AMS IB.7177, 7178, 56 and 61 mm SL) cleared and stained with alizarin red S following the trypsin digestion technique of Taylor (1967). All additional material examined for comparative purposes is listed in the Appendix. Bone terminology follows Nybelin (1963), Bradbury (1967), and Pietsch (1972). In osteological drawings cartilage is stippled, and where necessary for clarity, open spaces are rendered in solid black.

Material is deposited in the following institutions:

AMS: Australian Museum, Sydney
BMNH: British Museum (Natural History), London
KFRS: Kanudi Fisheries Research Station, Konedobu, Papua, New Guinea
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge
NMV: National Museum of Victoria, Melbourne
RMNH: Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands
USNM: National Museum of Natural History, Washington, D.C.
UW: College of Fisheries, University of Washington, Seattle
WAM: Western Australian Museum, Perth

SYSTEMATICS

Tetrabrachium ocellatum Günther
Figures 1, 2

Tetrabrachium ocellatum Günther 1880:44-45, 78, pl. 19, fig. C (original description, single specimen, 51 mm SL, holotype BMNH 1879.5.14.618, *Challenger* Station 188, south of New Guinea, 9°59′ S, 139°42′ E, 51 m). Gill 1883:551 (after Günther 1880; Pedicalidae of Günther 1880:78 a misprint for Pediculati). Regan 1912:283 (after Günther 1880; Tetrabrachiinae). Fowler 1928:476 (after Günther 1880; Pedicalidae after Günther 1880:78). Gregory 1933:394 (after Günther 1880). Whitley 1934:xxx (second known specimen). Whitley 1935:249 (second and third known specimens; Tetrabrachiidae). Berg 1940:499 (subfamily Tetrabrachiini of Antennariidae). Gregory 1951:224, fig. 9.154C (obliteration of postopercular cleft by branchiostegal membrane). Beaufort and Briggs 1962:222, fig. 50 (description, holotype reexamined). Le Danois 1964:141 (after Günther 1880, Whitley 1935). Norman 1966:590 (in key; Tetrabrachiinae of Antennariidae). Kailola and Wilson 1978:26, 58-59 (additional material, Papua New Guinea).

Material.—Thirty-six specimens, 17-67 mm SL.

Holotype of *T. ocellatum*: BMNH 1879.5.14.618, 51 mm SL, *Challenger* Station 188, south of New Guinea, 9°59′ S, 139°42′ E, 51 m.

Additional nontype material: AMS IB.5836, 64 mm SL, Townsville District, Queensland, 19°16′ S, 146°49′ E, trawled. AMS IA.6003, 17 mm SL, off Hayman Island, Queensland, 20°03′ S, 148°53′ E, 9 m. AMS IA.6136, 27 mm SL, Lindeman Island, Queensland, 1934. AMS IA.6759, 2(20 and 26.5 mm SL), Lindeman Island, Queensland, 20°27′ S, 149°02′ E, trawled. AMS IB.7173-7178, 6(42.5-61 mm SL), Gulf of Carpentaria, Queensland (56 and 61 mm SL specimens cleared and stained). AMS I.15557-281, 7(42-61.5 mm SL), Gulf of Carpentaria, Queensland, 17°29′ S, 140°24′ E, trawled, 5.5 m, 24 November 1963. AMS I.19289-003, 31.5 mm SL, *Alpha Helix*, Arafura Sea, 10°27.5′ S, 136°47.0′ E, trawled on bottom of mud, gravel, and shells, 55 m, 17 March 1975. AMS I.20907-041, 41.5 mm, south of Cooktown, Queensland, 16°01′ S, 145°29′ E, trawled on bottom of mud and shells, 20 m, 6 February 1979.

KFRS 871, 46 mm SL, northwest of Yule Island, Gulf of Papua, New Guinea, March 1963. KFRS 1483, 52 mm SL, Kerema Bay, Gulf of Papua, 5 May 1969. KFRS 2953, 62 mm SL, 6.5-8 km off Kerema Point, Gulf of Papua, prawn trawl, 14.6 m, 9 May 1973. KFRS 3017, 58 mm SL, Kerema Bay, Gulf of Papua, 9-13 m, September-October 1970. KFRS 3023, 61 mm SL, Kerema Bay, Gulf of Papua, 9-13 m, September-October 1970. KFRS 3082, 50 mm SL, FRV *Rossel*, Yule Island, Gulf of Papua, trawl, 18-24 m, January-February 1971.

USNM 177873, 52 mm SL, between Hayman and Magnetic Islands, Queensland, trawl, 18-46 m, May-June 1957.

WAM P.21473-001, 67 mm SL, Vansittart Bay, West Australia, 14°04′ S, 126°17′ E, 26 May 1968. WAM P.26130-001, 2(58 and 67 mm SL), Broome Bay, Napier, West Australia, 14°00′ S, 126°36′ E, 26 November 1968. WAM P.26832-001, 34 mm SL, Wokam and Uru Islands, Indonesia, 5°30′ S, 134°12′ E, 15 June 1970. WAM P.26833-001, 47 mm SL, Aru Island, Indonesia, 5°30′ S, 134°12′ E, 16 June 1971. WAM P.26540-001, 53 mm SL, Mermaid Passage, Dampier Arch, West Australia, 16°25′ S, 123°20′ E, prawn trawl, 8 September 1977. WAM P.26834-001, 35 mm SL, west of Dongara, West Australia, 29°15′ S, 114°01′ E, 20 March 1972.

Diagnosis.—Mouth small, opening dorsally, bones of jaws nearly vertical, nearly completely hidden by folds of skin; lower lip lined with small, cutaneous papillae; eyes small, close-set, protruding from dorsal surface of head; anterior half of frontals separate, posterior half meeting on midline; pterosphenoid present; parietals separated by supraoccipital; mesopterygoid absent; ectopterygoid triradiate, T-shaped; dorsal head of quadrate narrow, less than width of metapterygoid; interhyal with a medial, posterolaterally directed process; interopercle flat, broad; pharyngobranchial I present; epibranchial teeth absent; ceratobranchials toothless; toothed portion of ceratobranchial V expanded; hypohyals II and III bifurcated; ossified basibranchials absent; small basihyal present; neural spines of preural centra 14-22 short, spatulate, not interdigitating with proximal radials of soft dorsal fin; epurals absent; three dorsal fin spines without interconnecting membrane; illicial cavity absent (Bradbury 1967); illicium reduced, without esca, emerging anterior to eyes; second dorsal fin spine covered with cutaneous filaments, emerging from between eyes; third dorsal fin spine nearly completely covered with skin of head, distal tip emerging on posterior margin of cranium; illicial pterygiophore and pterygiophore of third dorsal fin spine with highly compressed, bladelike dorsal expansions, each expansion with a foramen within which lie medially directed prongs of proximal end of respective dorsal fin spine; soft dorsal fin rays 16-17; anal fin rays 11-12; pectoral fin rays 9, divided into dorsal portion of 4 rays interconnected by membrane, ventral portion of 5 interconnected rays, dorsalmost ray attached to lateral surface of body by membrane; pectoral lobe attached to posteriormost ray of pelvic fin by membrane; three pectoral radials; skin naked except for very few microscopic spinules associated with pores of acoustico-lateralis system.

Description (Figure 1).—Body strongly compressed, elongate (greatest depth <50% SL); head compressed, short (<32% SL); cranium strongly oblique in position, posterior end of cranium and anterior vertebrae raised forming a prominent convex hump; mouth small, width <16% SL;

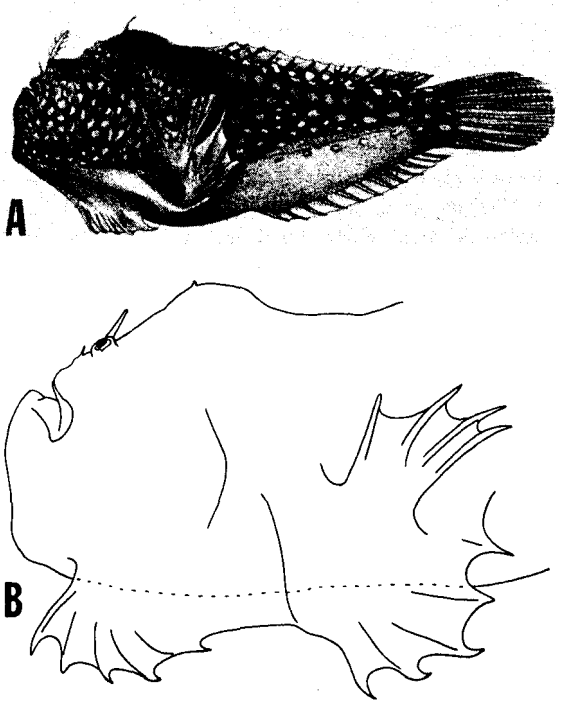

FIGURE 1.—*Tetrabrachium ocellatum*: A. Holotype, BMNH 1879.5.14.618, 51 mm SL, after Günther 1880; B. Diagram showing webbing between lower portion of pectoral fin and body, and between pectoral and pelvic fins.

anterior nostril opening on edge of upper lip, posterior nostril opening approximately half-way between edge of lip and eye; oral valve present lining both upper and lower jaw; gill opening small, situated just below and behind base of pectoral fin lobe; no opening behind fourth gill arch; holobranchs present on ventral half of ceratobranchial I, full length of ceratobranchials II and III, ventral half of epibranchial II, and ventral tip of epibranchial III; hemibranchs present on dorsal half of ceratobranchial IV and ventral tip of epibranchial IV; pseudobranch absent; swim bladder absent; ovaries paired.

Pterygiophore of illicium completely covered with skin of head; illicial bone short (<8% SL) and thin, tapering to a point; bases of soft dorsal and anal fins long (>48% and 42% SL, respectively), rays short; dorsal and anal fin rays enveloped in membrane; in some specimens (7 of 16 specimens examined) distal tips of first 9 rays of soft dorsal fin free, each terminating in a tight ball of tissue, remaining dorsal rays enveloped in membrane; caudal fin long (>30% SL), rounded.

Teeth small, slender, recurved, and depressible; each premaxilla with a single row of 22-25 teeth, each dentary with approximately 35 teeth arranged in two rows; vomerine teeth in two patches, about 25 teeth in each patch; palatine teeth absent; pharyngobranchials II and III and ceratobranchial V toothed.

Color in preservative white on lower half of body to brown on upper half of body, with numerous, small, white spots continuing onto soft dorsal fin, remaining fins white; oral cavity and viscera unpigmented.

Length to 67 mm SL.

Complete counts and measurements of representative material are given in Table 1.

Habitat.—Specific information on the habitat frequented by *T. ocellatum* is available for only two captures: a 31.5 mm SL specimen (AMS I.19289.003) and a 41.5 mm SL specimen (AMS I.20907-041) were trawled off a bottom of mud, gravel, and shell. A number of other specimens were collected in prawn trawls most likely fished over similar, soft-bottom substrates of mud or sand.

Distribution (Figure 2).—*Tetrabrachium ocellatum* is known from 36 specimens collected in shallow water (55 m or less) off the western (as far south as lat. 29° S) and northern coasts of Australia, the southern coast of Papua, New Guinea, and the south Molucca Islands, Indonesia.

Osteology of *Tetrabrachium ocellatum* Figures 3-13

The osteology of lophiiform fishes has been dealt with by numerous authors (Garman 1899; Regan

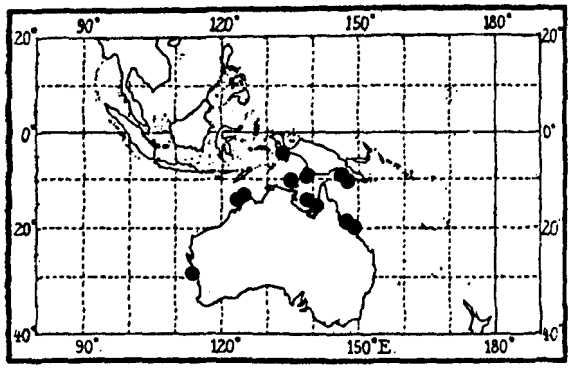

FIGURE 2.—Known distribution of *Tetrabrachium ocellatum*. One symbol may indicate more than one capture.

TABLE 1.—Counts and measurements (in percentage of standard length) of representative specimens of *Tetrabrachium ocellatum*.

	KFRS 3087	UW 20771	AMS IB.7173	KFRS 871	KFRS 3082	USNM 177873	AMS IB.7174	AMS IB.7175	KFRS 3023	KFRS 2953
Standard length, mm	39	39.5	42.5	46	50	50.5	54	56	61	62
Length:										
Head (snout to posteriormost margin of preopercle)	27.7	30.4	25.9	26.1	26.0	23.8	20.4	25.0	23.0	22.6
Snout to emergence of dorsal spine III	22.6	25.3	25.9	25.4	23.2	23.8	25.0	—	23.0	25.0
Illicial bone	7.2	4.6	2.6	4.1	4.0	4.0	3.3	—	—	4.8
Dorsal spine II	7.9	6.3	4.7	8.7	6.8	5.2	4.1	4.6	5.4	4.8
Base of soft dorsal fin	67.9	64.6	49.4	56.5	58.0	63.4	63.0	—	54.9	53.2
Base of anal fin	51.3	51.9	42.3	48.9	51.0	53.5	49.1	—	48.4	48.4
Caudal fin	43.1	36.2	39.3	34.8	32.0	35.6	36.1	36.7	37.7	33.9
Width:										
Between eyes (from center of lens)	11.0	12.4	10.6	11.1	10.4	9.9	9.1	—	10.8	10.3
Least between frontal bones	6.7	6.8	4.9	6.1	5.8	5.5	5.4	—	4.9	5.6
Greatest between sphenotic bones	20.2	19.7	19.8	20.6	19.4	19.2	17.2	17.9	20.5	20.2
Greatest body depth	38.5	43.0	35.3	46.7	46.0	45.5	42.6	37.5	42.6	41.9
Dorsal fin rays	16	17	16	16	16	17	16	16	17	16
Anal fin rays	11	11	11	11	11	12	12	11	12	12

1903, 1912; Gregory 1933; Eaton et al. 1954; Monod 1960; Le Danois 1964, 1974, 1979; Field 1966; Bradbury 1967; Rosen and Patterson 1969; and additional references cited by Pietsch 1972, 1974, 1978, 1979), yet no published osteological information on the genus *Tetrabrachium* is available. In the following account only those comparative aspects that differ from those previously described in other anglerfishes are discussed.

Cranium (Figures 3-6).—The ethmoid cartilage of *T. ocellatum* broadly covers the posterior half of the vomer meeting with the lateral ethmoids laterally and the supraethmoid medially. The supraethmoid forms a narrow, vertical interorbital septum lying between, but well separated from the orbital portions of the frontals. The laterally compressed, ventral end of the supraethmoid meets with the ethmoid cartilage anteriorly and lies within a groove on the dorsal surface of the parasphenoid posteriorly. The dorsal end of the supraethmoid is overlapped on each side by central extensions of the frontals. Each lateral ethmoid has a narrow, cylindrical posterior portion that lies ventral to an anterior extension of the respective frontal, and a larger, ventrally directed, anterior portion that meets with the ethmoid cartilage.

The head of the vomer lies ventral to the ethmoid cartilage. Its anterior margin is indented medially. The ventral surface of the vomer is strongly concave (as seen in anterior view, Figure 6). A laterally compressed, keellike posteromedial process emerges from the ventral surface of this bone and fits within a deep groove on the anteroventral surface of the parasphenoid; the ventral margins of the posteromedial process of the vomer and the anterior end of the parasphenoid are strongly convex (as seen in lateral view, Figure 4). Vomerine teeth are present in two lateral patches, each patch containing approximately 25 teeth arranged in perhaps three irregular rows.

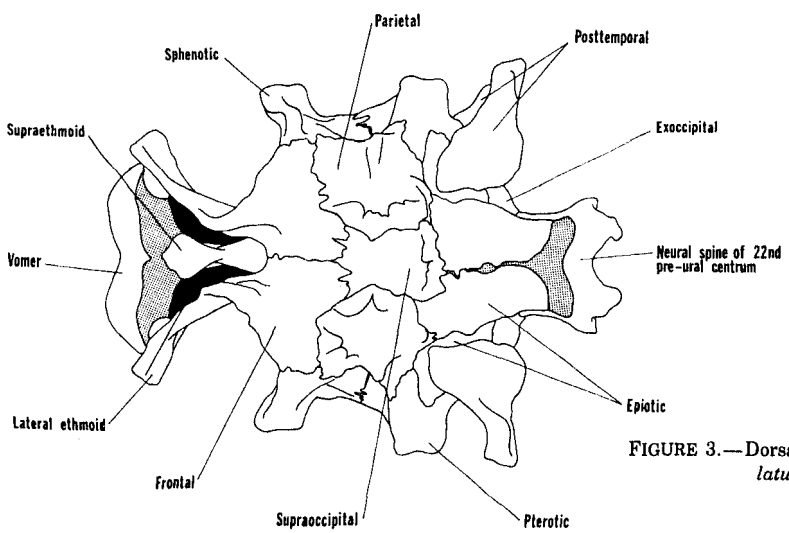

FIGURE 3.—Dorsal view of cranium of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL.

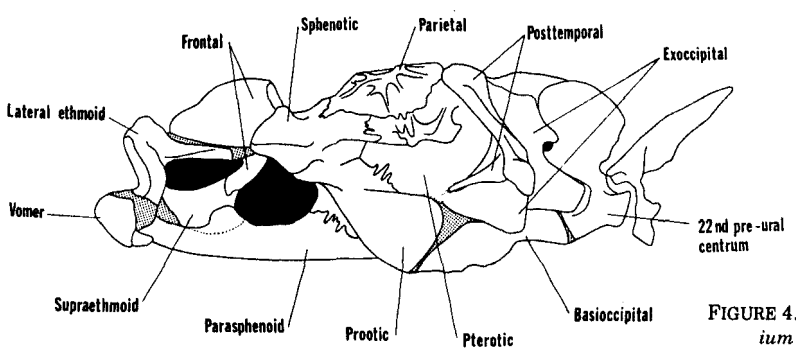

FIGURE 4.—Lateral view of cranium of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL.

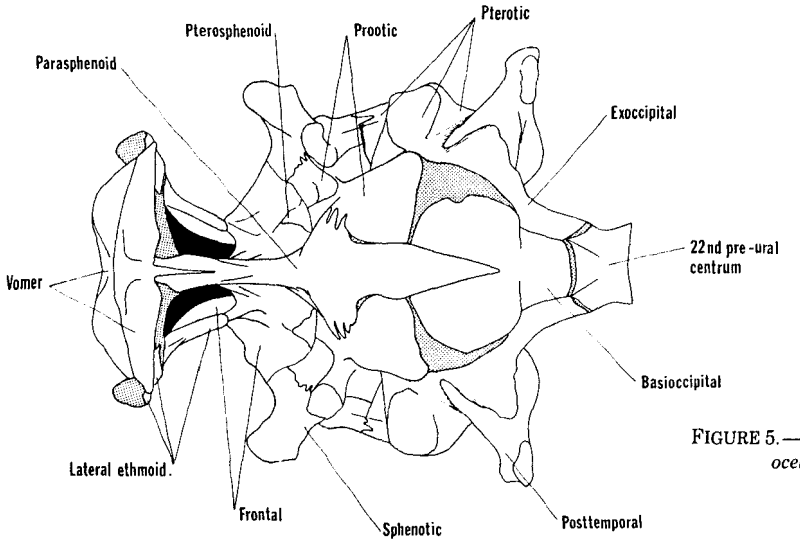

FIGURE 5.—Ventral view of cranium of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL.

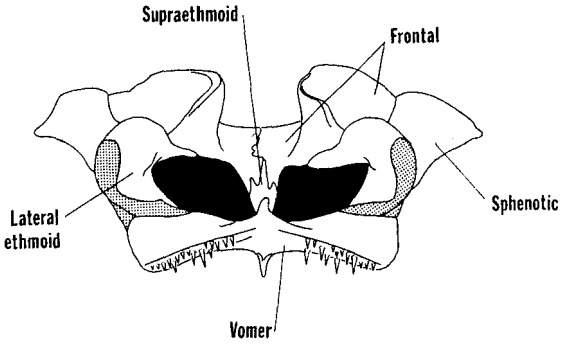

FIGURE 6.—Anterior view of cranium of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL.

The frontals are relatively large and irregular in shape. Each has a laterally compressed, anterior half, well separated from its counterpart of the other side, and a dorsoventrally depressed posterior half that meets its counterpart on the midline. In dorsal view (Figure 3), the frontals form a relatively narrow orbital region to accommodate the closely set, dorsally directed eyes. In lateral view (Figure 4), the depressed posterior half of the frontals form a concavity between the elevated, laterally compressed anterior half of these bones and the posterior half of the cranium.

The parietals are irregularly shaped elements with deeply pitted and grooved external surfaces. They are well separated from each other by the supraoccipital. Each parietal overlaps the respective frontal anteriorly, the sphenotic and pterotic laterally, the supraoccipital medially, and the epiotic posteriorly.

A small pterosphenoid lies on the ventromedial surface of the frontal in contact with the prootic.

The orbitosphenoid and basisphenoid are absent in all lophiiforms.

The parasphenoid is a stout, well-ossified element with a convex ventral margin (Figure 4). Its anterior end is overlapped by the ethmoid cartilage dorsally and by the narrow shaft of the vomer ventrally. Medially, the dorsal surface of this bone forms a deep groove within which lies the laterally compressed, posteroventral part of the supraethmoid. Posteriorly, the parasphenoid is broadly connected with the prootics laterally and the basioccipital medially. At no point does the parasphenoid make contact with the frontals.

Each sphenotic forms a dorsoventrally depressed flange that extends outward in an anterolateral direction, considerably beyond the width of the ethmovomerine region of the cranium (Figure 3).

The remaining elements of the cranium (pterotics, epiotics, prootics, supraoccipital, and exoccipitals) do not differ substantially from those described for other lophiiforms (Regan 1912, fig. 5; Gregory 1933, fig. 265, 267-271; Pietsch 1972, 1974).

Otoliths (Figure 7).—The sagitta of *T. ocellatum* is roughly oval in shape with a length to height ratio of about 1.4:1. The sulcus is only slightly

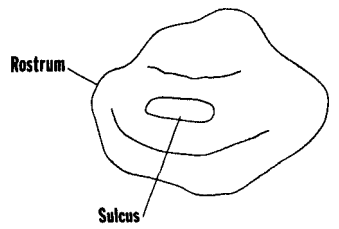

FIGURE 7.—Medial view of right sagitta of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL.

grooved. The rostrum is poorly developed, and an antirostrum is absent.

Mandibular arch (Figures 8, 9).—The premaxillae (Figure 8) are each characterized by having a narrow ascending process, nearly as long as the tapering toothed portion of the bone; a rounded articular process; and an elongate, spatulate postmaxillary process (pmpmx of Rosen and Patterson 1969, fig. 56A). The ascending and articular processes together form an oblique angle with the postmaxillary and toothed processes. The toothed portion of each premaxilla bears a single row of 22 to 25 depressible teeth, the largest at the symphysis, becoming progressively smaller posteriorly.

Each maxilla consists of a broad posterior portion (completely hidden from behind by a thick fold of skin when the mouth is closed), and an expanded anterior head that, in turn, consists of an anterior process that overlaps the respective premaxilla and a medially directed process that is attached by a short ligament to the articular process of the respective premaxilla. The dentaries, articulars, and angulars (Figure 9) are

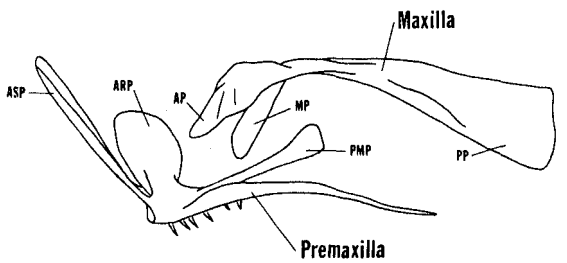

FIGURE 8.—Upper jaw bones of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL. AP = anterior process of maxilla; ARP = articular process of premaxilla; ASP = ascending process of premaxilla; MP = medial process of maxilla; PMP = postmaxillary process of premaxilla; PP = posterior process of maxilla.

similar to those described for other lophiiforms (Gregory 1933, fig. 265, 266, 269-271; Pietsch 1972, 1974). Each dentary bears approximately 35 depressible teeth arranged in two rows.

Palatine arch (Figure 9).—Each metapterygoid is in contact with four other bones: dorsally and posterodorsally with the hyomandibular, posteroventrally with the upper half of the symplectic, and ventrally with the quadrate and ectopterygoid. The ectopterygoid is large and T-shaped, overlapping the medial surface of the metapterygoid dorsally, the quadrate ventrally, and the palatine anteriorly. The mesopterygoid (cartilaginous or ossified) is absent. The palatine is unusually large, approximately twice the length of the ectopterygoid. Palatine teeth are absent.

Hyoid arch (Figures 9, 10).—Dorsally, each hyomandibular is forked forming two heads, both of which articulate with the cranium: an anterior head fits into a concavity formed by the sphenotic and prootic, and a posterior head articulates on the ventrolateral face of the pterotic (Figures 4, 5, 9). The symplectic is separated from the hyomandibular by cartilage dorsally, and lies within a shallow groove on the medial surface of the quadrate ventrally. The dorsal head of the quadrate is narrow, considerably less than the width of the metapterygoid. The interhyal bears a prominent medial, posterolaterally directed process that wraps around the posterior margin of the respective preopercle when the interhyal rotates upward (e.g., during a feeding event). This contact between the interhyal and the preopercle limits the dorsal rotation of the interhyal and, in turn, limits the extent of abduction of the lower jaw via ligamentous connections to the respective interopercle.

The epihyal and ceratohyal do not differ substantially from those described for other lophiiforms (Pietsch 1974, 1979). There are two hypohyals on each side (Figure 10), both of which are connected to the ceratohyal by a posteriorly directed strut. The dorsal hypohyal is further connected to an anterodorsal extension of the ceratohyal by a cylindrical piece of cartilage.

There are six branchiostegal rays all borne on the ceratohyal (Figure 10); the two anteriormost rays articulate on the medial surface, the four posterior rays on the lateral surface. Branchiostegal rays 3 and 4 are curved in an anteroventral direction, in contrast to the posterodorsal direc-

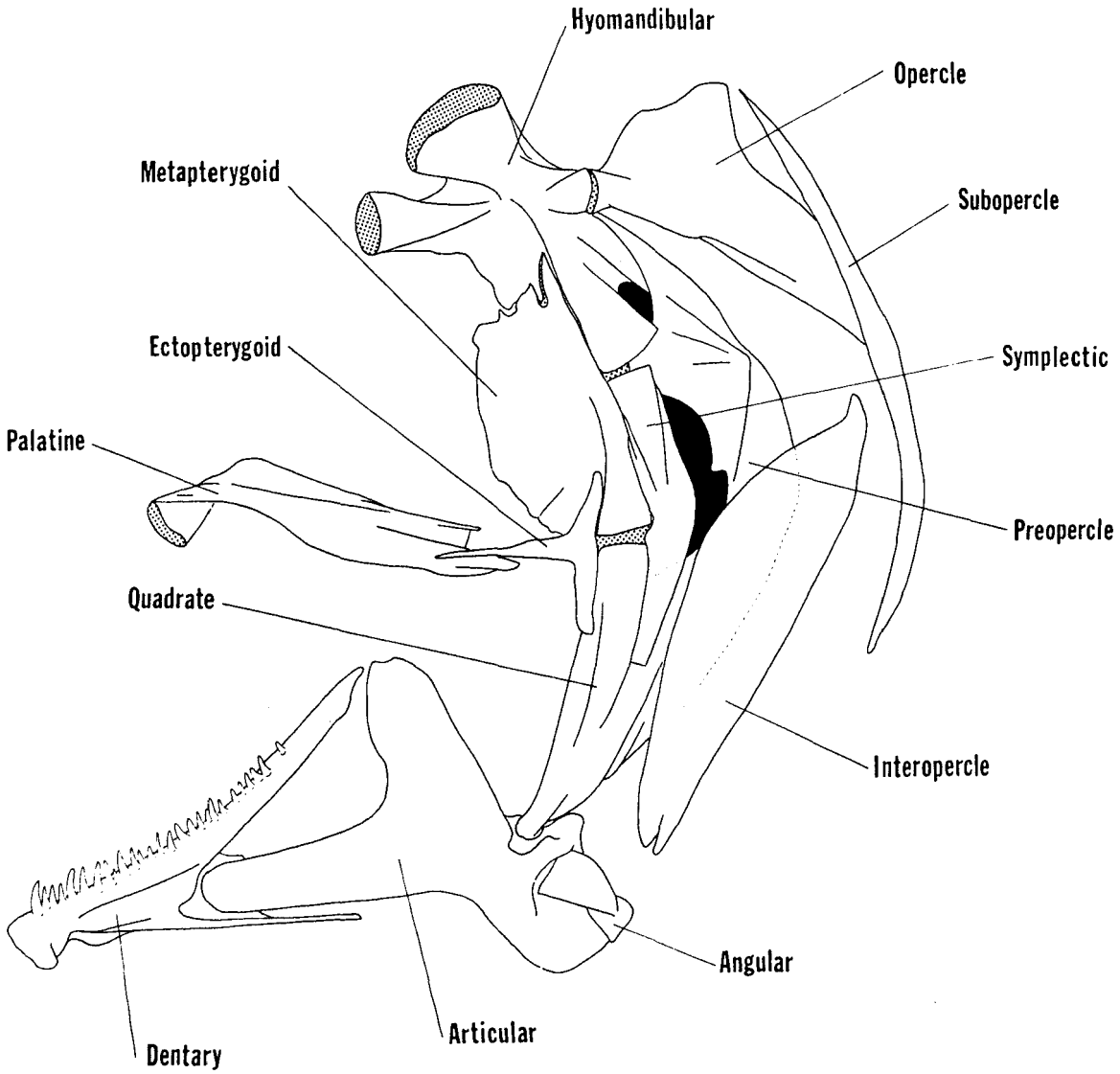

FIGURE 9.—Medial view of lower jaw, suspensorium, interhyal, and opercular apparatus of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL, right side.

tion of the remaining rays. On the left ceratohyal of the 61 mm cleared and stained specimen of *T. ocellatum* (Figure 10), the fifth branchiostegal ray is bifurcated at midlength, giving the impression of having seven total rays.

A small, triangular basihyal is present (Figure 10). The urohyal is absent in all lophiiforms.

Opercular apparatus (Figure 9).—The opercle is triangular in shape with a slightly concave posterior margin. An elongate, crescent-shaped subopercle lies medial to the ventral tip of the opercle. A subopercular spine is absent. The interopercle is large, flat, and broad. The crescent-shaped preopercle is also large, strengthening the entire length of the suspensorium.

Branchial arches (Figure 11).—There are three pharyngobranchials. That of the first arch is a small, toothless, suspensory pharyngobranchial; those of the second and third arches are considerably larger, tooth-bearing elements closely at-

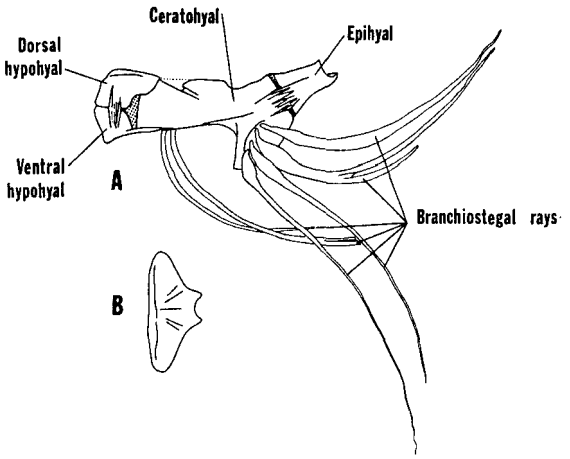

FIGURE 10.—Hyoid apparatus of *Tetrabrachium ocellatum*: A. AMS IB.7178, 61 mm SL, left lateral view; B. Basihyal, AMS IB.7177, 56 mm SL, ventral view, anterior to the left.

tached to each other and to the dorsal end of epibranchials II through IV. Epibranchial I is triradiate in shape, articulating with ceratobranchial I proximally, bearing pharyngobranchial I distally, and attached by a short ligament to the proximal end of epibranchial II medially. Ceratobranchials I through IV are toothless. The expanded, proximal end of each ceratobranchial V bears about 19 to 21 depressible teeth arranged in two rows. Hypobranchial I is a simple, rod-shaped

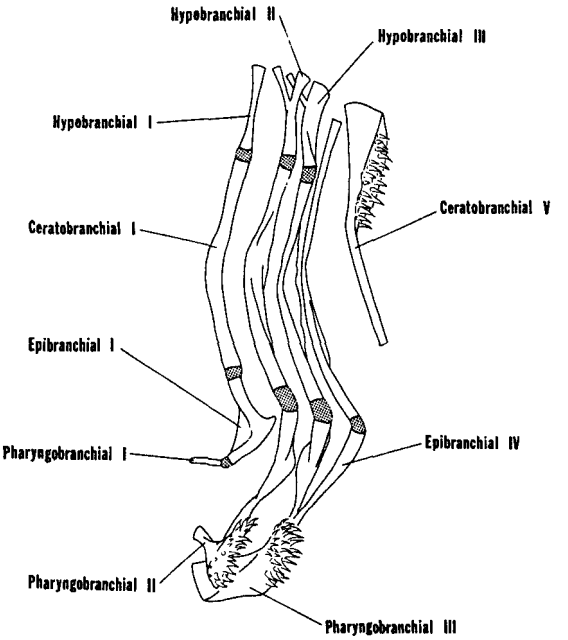

FIGURE 11.—Branchial arches of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL. The ventral portion of the branchial basket is shown in dorsal view, the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view.

element. Hypobranchials II and III are bifurcated proximally. Ossified basibranchials are absent.

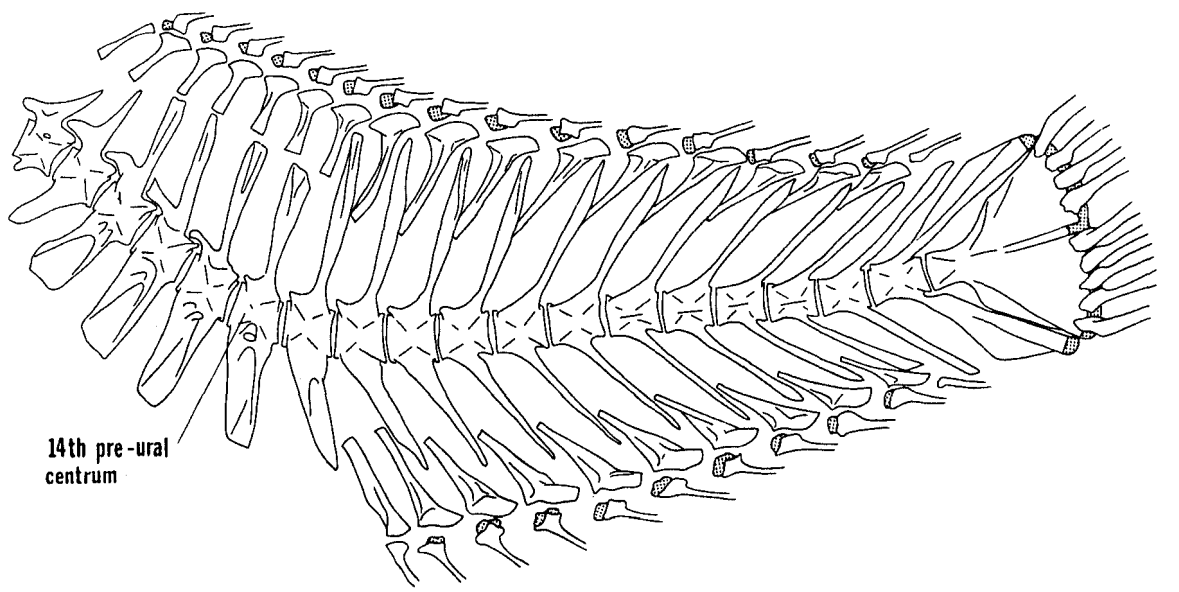

FIGURE 12.—Vertebrae, caudal skeleton, and median fins of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL.

Vertebrae and caudal skeleton (Figure 12).—In the two cleared and stained specimens of *T. ocellatum* examined, there are 22 vertebrae (including the last centrum to which is fused the hypural plate; Pietsch 1972:38). Preural centra 2 through 18 bear complete haemal arches and are considered caudal vertebrae. The neural spines of preural centra 14 through 22 are considerably shorter than those of the more posterior centra; correspondingly, the seven anteriormost proximal radials of the soft dorsal fin are also short so that they do not interdigitate with the respective neural spines. Further, there appears to be little if any connective tissue between the elements of the soft dorsal fin and the vertebral column in this region allowing for independent movement of the anterior portion of the fin relative to the axial skeleton. The haemal spines of preural centra 14 through 17 are unusually broad and laterally compressed.

The hypural plate, slightly notched posteriorly, bears the overlapping bases of nine principle caudal rays. The central seven caudal rays are bifurcated distally. There are no epurals.

Median fins and illicial apparatus (Figures 12, 13).—The spinous dorsal fin consists of three spines. The anteriormost two are supported by a single, elongate, horizontally situated pterygiophore (Figure 13) that is loosely attached to the dorsal surface of the cranium between the anterior halves of the frontal bones by three pairs of extrinsic illicial muscles (Bertelsen 1951:18, fig. 4; Bradbury 1967, fig. 2; Winterbottom 1974:284, fig. 44). The illicial bone (Bradbury 1967:401) is considerably reduced in size relative to other lophiiforms (Gregory 1933, fig. 265, 266, 267; Pietsch 1972, 1974, 1979). The second spine is considerably thicker and approximately three times longer than the first. The third spine, slightly longer and thicker than the second, is supported by a second, elongate, and horizontally placed, cephalic pterygiophore that is tightly connected to the posterior, dorsomedial surface of the supraoccipital and anterior, dorsomedial margins of the epiotics. The proximal end of each spine is bifurcated, each fork bearing a small, medially directed prong; the prongs of each spine fit within a large, rounded foramen located on a highly compressed, bladelike dorsal expansion of the respective pterygiophore.

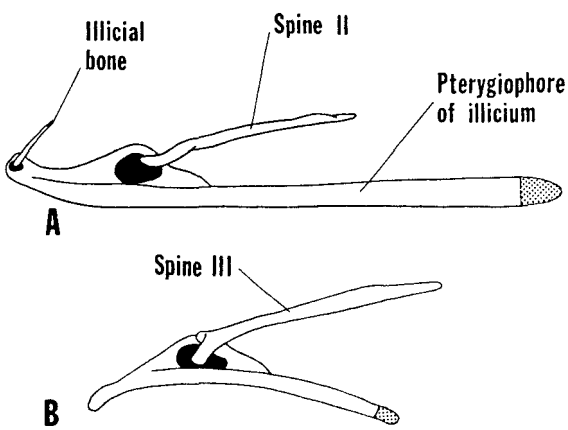

FIGURE 13.—Spinous dorsal fin of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL: A. Illicial apparatus, second dorsal spine, and common pterygiophore; B. Third dorsal spine and pterygiophore.

The soft dorsal fin consists of 16 biserial, segmented, and unbranched rays, each supported by a cartilaginous distal radial and an ossified proximal radial. The proximal end of the anteriormost proximal radial lies above the neural spine of the 19th preural centrum, while the proximal end of the last proximal radial lies between the neural spines of the fourth and fifth preural centra.

The anal fin consists of 11 biserial, segmented, and unbranched rays. The first two rays share a single supporting radial. The remaining rays are each supported by a small, cartilaginous distal radial and an elongate, ossified proximal radial. The proximal ends of the two anteriormost proximal radials lie between the haemal spines of the 12th and 13th preural centra. The proximal radials of the nine remaining anal fin rays have a one-to-one correspondence with the haemal spines, so that the radial of the last anal ray lies between the haemal spines of the fourth and fifth preural centra. The posteriormost rays of the dorsal and anal fins are broadly connected by a membrane to the dorsal and ventral margins of the caudal fin so that a caudal peduncle is absent.

Pectoral and pelvic girdles and fins (Figure 14).—The posttemporal is unusually large and connected to the posterolateral corner of the cranium in such a way as to allow for considerable movement (relative to the cranium) in an anterodorsal-posteroventral plane. The bone consists of a broad, dorsal flange that overlaps the dorsolateral surface of the epiotic, pterotic, and exoccipital. A large ligament originates on the posterodorsal margin of the prootic and inserts on the tip of

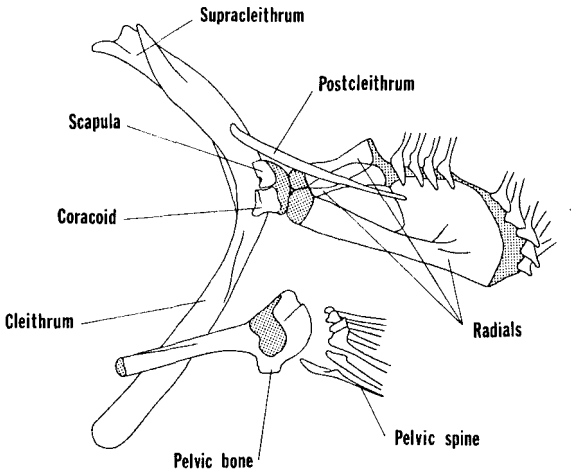

FIGURE 14.—Medial view of right pectoral girdle, and pectoral and pelvic fins of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL. Cartilaginous radials supporting pelvic fin rays and cartilaginous distal radials supporting pectoral fin rays not shown; see text.

an elongate, ventromedially directed extension of the posttemporal.

The supracleithrum, cleithrum, coracoid, and scapula (Figure 14) are similar to those described for other lophiiforms (Gregory 1933, fig. 265; Pietsch 1972, 1974). A cleithral spine is absent. There is a single rodlike postcleithrum.

The pectoral fin is supported by three pectoral radials (Figure 14). The two dorsalmost radials are similar in size and shape. The third or ventralmost radial is considerably larger; its expanded distal portion bears the bases of nine unbranched, pectoral fin rays (each ray associated with a small, cartilaginous distal radial; not shown in Figure 14). The pectoral fin itself is divided into two portions: a dorsal portion consisting of four rays that are interconnected by a membrane, and a ventral portion consisting of five rays that are similarly connected to each other, but also to the lateral surface of the body. In a similar way, the pectoral fin lobe is connected by a membrane to the rays of the respective pelvic fin (Figure 1B). The pelvic bone, nearly as long as the ventralmost pectoral radial, bears on its expanded distal end a single spine and five unbranched pelvic fin rays (each ray associated with a small, cartilaginous radial; not shown in Figure 14).

Skin spines.—Dermal spines are absent except for the very rare occurrence of a tiny, crescent-shaped spinule associated with an individual pore of the acoustico-lateralis system of the head and trunk.

COMPARATIVE OSTEOLOGY OF ANTENNARIOID FAMILIES

The following discussion is based primarily on an osteological comparison of a representative of each of six major subgroups of the Antennarioidei (here recognized as families; see Phylogenetic Relationships and Appendix below): *Antennarius* Daudin, thought to be the least derived genus of the Antennariidae (see Phylogenetic Relationships below); *Tetrabrachium* Günther, the only genus of the Tetrabrachiidae; *Lophichthys* Boeseman, the only genus of the Lophichthyidae; *Brachionichthys* Bleeker, the only extant genus of the Brachionichthyidae (see p. 416); *Chaunax* Lowe, the only genus of the Chaunacidae; and *Dibranchus* Peters, an underived genus of the Ogcocephalidae (see Bradbury 1967). Only those comparative aspects that might have a bearing on the phylogenetic interrelationships of these taxa are discussed.

Cranium (Figures 3-6, 15-19).—In *Tetrabrachium* and *Antennarius* the ventral surface of the vomer is strongly concave (as seen in anterior view, Figure 6). A laterally compressed, keellike posteromedial process emerges from the ventral surface of this bone and fits within a deep groove on the anteroventral surface of the parasphenoid; the ventral margins of the posteromedial process of the vomer and the anterior end of the parasphenoid are strongly convex (as seen in lateral view, Figure 4). In all other antennarioids examined the posteromedial process of the vomer is flush with the more or less flat ventral surface of this bone; the ventral margins of the vomer and anterior end of the parasphenoid (as seen in lateral view) are straight to slightly concave.

Other osteological variation in the crania of antennarioids occurs primarily in the shape and relative position of the frontal bones. In *Antennarius*, *Lophichthys*, *Brachionichthys*, and *Dibranchus* (Figures 15-17, 19) the frontals are broad and roughly triangular in shape, well separated from each other anteriorly, but meeting on the midline posteriorly. The narrow interorbital space formed by these elements in *Tetrabrachium* is absent (compare Figures 3 and 15). The anterior ends of the frontals of *Lophichthys* are exceptionally narrow, gradually tapering to a point (Figure

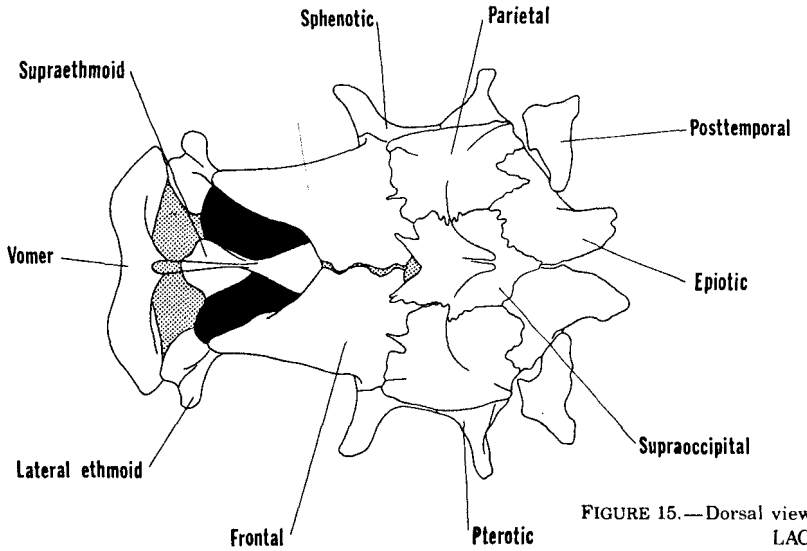

FIGURE 15.—Dorsal view of cranium of *Antennarius sanguineus*, LACM 8125, 76 mm SL.

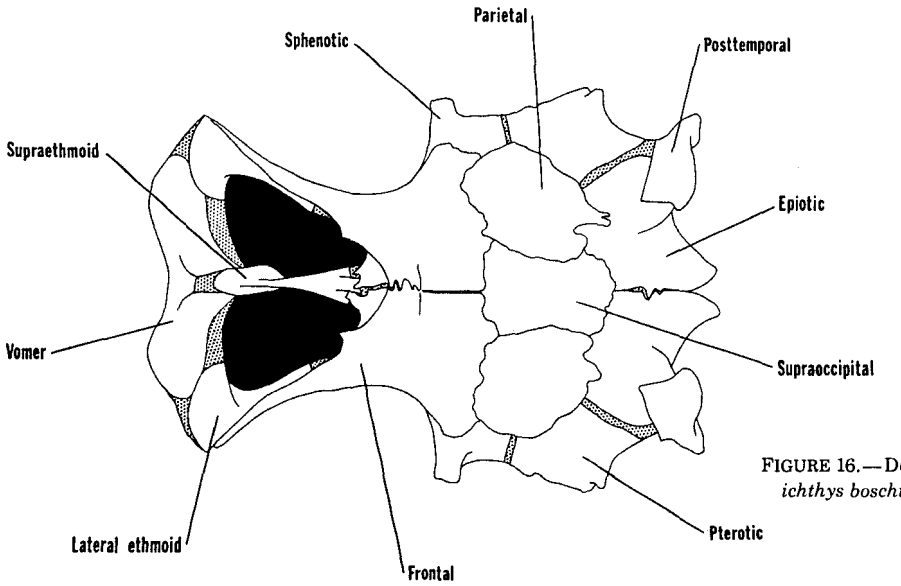

FIGURE 16.—Dorsal view of cranium of *Lophichthys boschimai*, UW 20773, 47 mm SL.

16); they diverge laterally to a much greater extent than in the other genera examined in response to a much wider vomer and laterally expanded lateral ethmoids.

In contrast to all other antennarioids examined, the frontals of *Chaunax* (Figure 18) are elongate and narrow, meeting on the midline for their entire length. The lateral ethmoids of this genus are also unusually long and narrow.

In *Antennarius*, *Lophichthys*, *Tetrabrachium*, *Chaunax*, and *Dibranchus* the parietals are well separated from each other by the supraoccipital. In *Brachionichthys*, however (Figure 17), these elements approach each other above the supraoccipital and meet on the midline, roofing over a small longitudinal passageway within which lies the posterior tip of the pterygiophore of the third dorsal fin spine.

Mandibular arch (Figures 8, 9, 20-25).—The premaxilla of *Antennarius* is very similar to that of *Tetrabrachium* (Figures 8, 20A); both genera

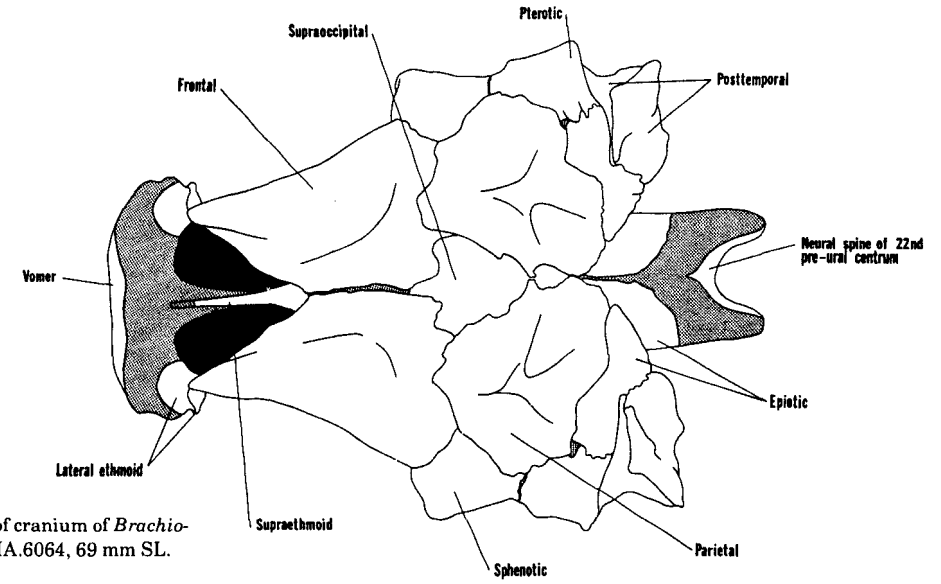

FIGURE 17.—Dorsal view of cranium of *Brachionichthys hirsutus*, AMS IA.6064, 69 mm SL.

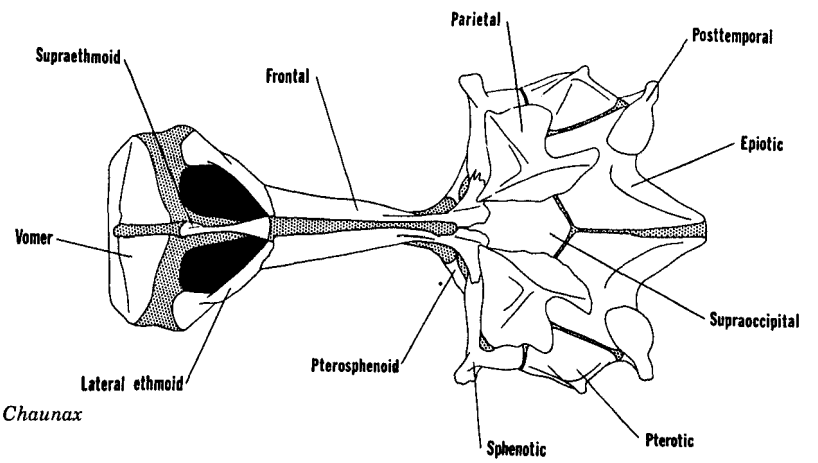

FIGURE 18.—Dorsal view of cranium of *Chaunax pictus*, UW 20770, 90 mm SL.

are characterized by having a spatulate postmaxillary process. The premaxilla of *Lophichthys* is also quite similar but bears a narrow, tapering postmaxillary process (Figure 20B). The premaxillae of the remaining antennarioid taxa examined are each somewhat different from these and from each other. In *Brachionichthys* (Figure 20C), the ascending and articular processes are at right angles to the toothed portion of the bone; the toothed portion is unusually short, about as long as the postmaxillary process and considerably shorter than the ascending process. In *Chaunax* (Figure 20D), the shape and relative proportions of the ascending, articular, and toothed processes of the premaxilla are similar to those of *Antennarius* and *Tetrabrachium*; the postmaxillary process, however, is represented by a large flange of bone, broadly connected to the toothed process. In *Dibranchus* (Figure 20E), the ascending and articular processes together form an acute angle with the postmaxillary and toothed processes; the articular process is nearly as long as the ascending process; and the postmaxillary process is connected by bone to the toothed process of the premaxilla for about half its length.

Palatine arch (Figures 9, 21-25).—A mesopterygoid is present in *Antennarius*, *Chaunax*, and

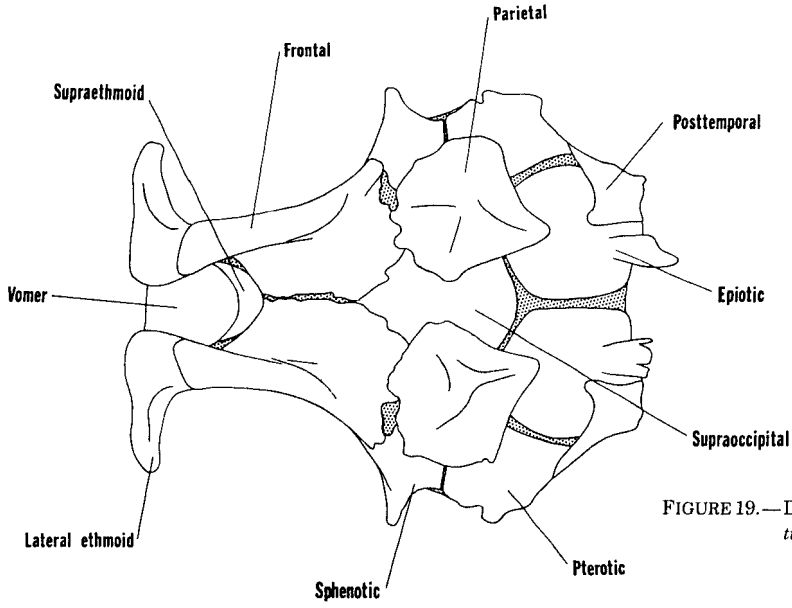

FIGURE 19.—Dorsal view of cranium of *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

Dibranchus (Figures 21, 24, 25), but absent in *Tetrabrachium*, *Lophichthys*, and *Brachionichthys* (Figures 9, 22, 23). The triradiate ectopterygoid of *Antennarius*, *Tetrabrachium*, and *Lophichthys* (T-shaped in *Tetrabrachium* and *Antennarius*, Figures 9, 21, but Y-shaped in *Lophichthys*, Figure 22) overlaps the medial surface of the metapterygoid dorsally; in *Chaunax* and *Dibranchus* the ectopterygoid is crescent-shaped and makes no contact with the metapterygoid. An ectopterygoid is absent in the larger (69 mm SL) specimen of *Brachionichthys* examined (Figure 23A) but represented by a small, weakly ossified remnant in the smaller specimen (42 mm SL) (Figure 23B).

The palatine is well toothed in *Antennarius*, *Lophichthys*, and *Chaunax*, but toothless in *Tetrabrachium* and in the single cleared and stained specimen of *Dibranchus* examined (palatine teeth are present in some ogcocephalid genera and sometimes in *Dibranchus*; Bradbury 1967: 409). In the absence of a mesopterygoid and reduced (or absent) ectopterygoid, the toothless palatine bone of *Brachionichthys* is widely separated from the suspensorium (Figure 23).

Hyoid arch (Figures 9, 10, 21-27).—In *Tetrabrachium* and *Antennarius* (Figures 9, 21) the dorsal head of the quadrate is relatively narrow, somewhat less than the width of the ventral head of the metapterygoid. In contrast, the quadrate of *Lophichthys*, *Brachionichthys*, *Chaunax*, and *Dibranchus* (Figures 22-25) is broad, making a much broader contact with an expanded metapterygoid. In *Dibranchus* the quadrate is exceptionally broad, the anterior half of the dorsal margin coming into contact with the mesopterygoid (Figure 25).

The interhyal of *Antennarius*, *Lophichthys*, and *Brachionichthys* is similar to that of *Tetrabrachium* (but in contrast to that of *Chaunax* and *Dibranchus*; Figures 24, 25) in having a prominent, medial, posterolaterally directed process that wraps around the posterior margin of the respective preopercle when the interhyal rotates upward (Figure 26). This contact between the interhyal and preopercle limits the dorsal rotation of the interhyal and, in turn, limits the extent of abduction of the lower jaw via ligamentous connections with the respective interopercle.

In shape and relative proportions, the branchiostegal rays of *Antennarius*, *Lophichthys*, and *Brachionichthys* are similar to those of *Tetrabrachium*; *Brachionichthys*, however, has lost the anteriormost element in this series (Table 2). In *Chaunax* and *Dibranchus* (Figure 27) the posteriormost branchiostegal ray is greatly enlarged, becoming ankylosed to the ventromedial margin of the subopercle in the later genus.

A small basihyal is present in *Antennarius*, *Tetrabrachium*, *Lophichthys*, and *Chaunax*, but absent in *Brachionichthys* and *Dibranchus*.

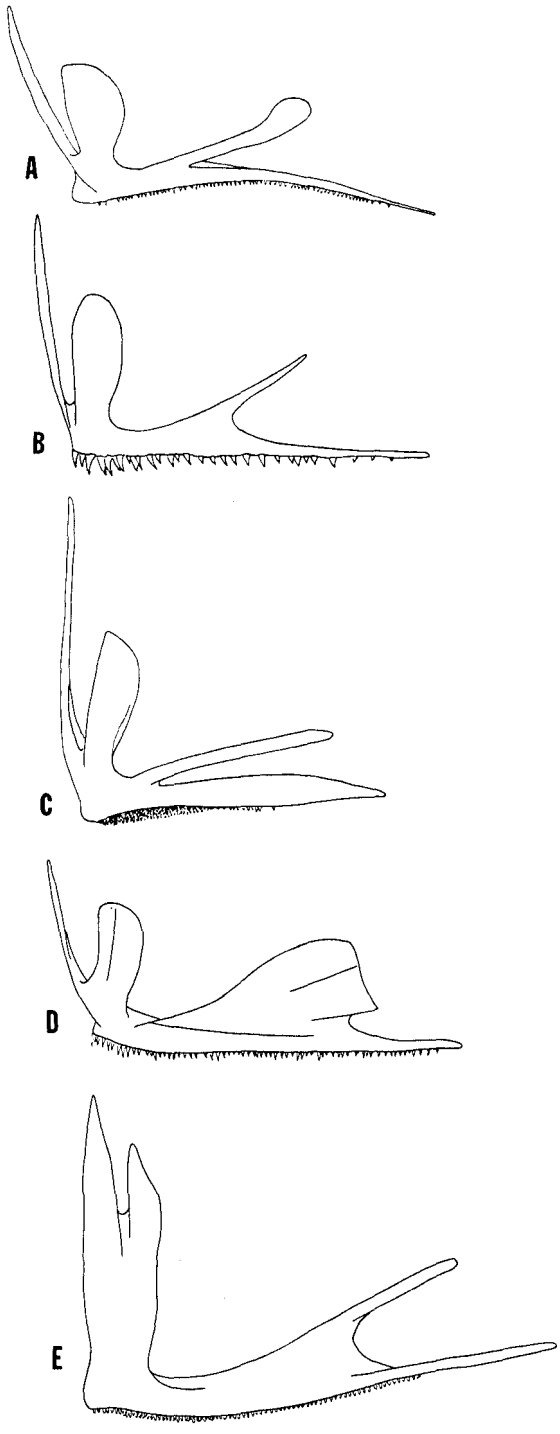

FIGURE 20.—Premaxillae, left lateral views: A. *Antennarius sanguineus*, LACM 8125, 76 mm SL; B. *Lophichthys boschmai*, UW 20773, 47 mm SL; C. *Brachionichthys hirsutus*, AMS IA.6064, 69 mm SL; D. *Chaunax pictus*, UW 20770, 90 mm SL; E. *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

Opercular apparatus (Figures 9, 21-25).—The opercle and subopercle of *Antennarius*, *Tetrabrachium*, and *Brachionichthys* are similar except in the following details: both elements are considerably reduced in size in *Tetrabrachium* and *Antennarius* (Figures 9, 21); in contrast to the smooth, slightly concave (sometimes deeply incised), posterior margin of the opercle of *Antennarius*, *Tetrabrachium*, and *Lophichthys*, the posterior margin of this bone in *Brachionichthys* is broken into numerous, weakly ossified, bony filaments (Figure 23A); in contrast to the relatively broad, spined subopercle of *Antennarius* and *Lophichthys*, the subopercle of *Tetrabrachium* and *Brachionichthys* (Figures 9, 23A) is a narrow, crescent-shaped element lacking a subopercular spine.

In contrast to the small opercle and subopercle of *Antennarius*, *Tetrabrachium*, *Lophichthys*, and *Brachionichthys*, those of *Chaunax* and *Dibranchus* (Figures 24, 25) are greatly enlarged and expanded posteriorly. A well-developed subopercular spine is present in *Chaunax*, but absent in *Dibranchus*.

The interopercle of *Antennarius*, *Lophichthys*, and *Brachionichthys* (Figures 21-23) is similar to that of *Tetrabrachium*; the interopercle of *Chaunax* and *Dibranchus* (Figures 24, 25) is much more slender and elongate.

Branchial arches (Figures 11, 28-32).—Pharyngobranchial I is represented by a simple, rod-shaped element in *Tetrabrachium*, *Antennarius*, and *Lophichthys* (Figures 11, 28, 29). In the single specimen of *Chaunax* examined pharyngobranchial I is Y-shaped (Figure 31). This element is toothless in *Antennarius*, *Tetrabrachium*, and *Chaunax*, but bears a series of approximately eight small teeth in *Lophichthys* (Figure 29). Pharyngobranchial I is absent in *Brachionichthys* and *Dibranchus*. Pharyngobranchial IV is absent in all antennarioids.

In *Tetrabrachium*, *Antennarius*, and *Lophichthys* (Figures 11, 28, 29), epibranchial I is triradiate in shape, toothless in *Antennarius* and *Tetrabrachium*, but bearing a single row of about 13 small teeth in *Lophichthys* (Figure 29). A similarly shaped epibranchial I, associated with three and two tooth plates is present in *Chaunax* and *Dibranchus*, respectively (Figures 31, 32). An L-shaped epibranchial I, associated with a single tooth plate, is present in *Brachionichthys* (Figure

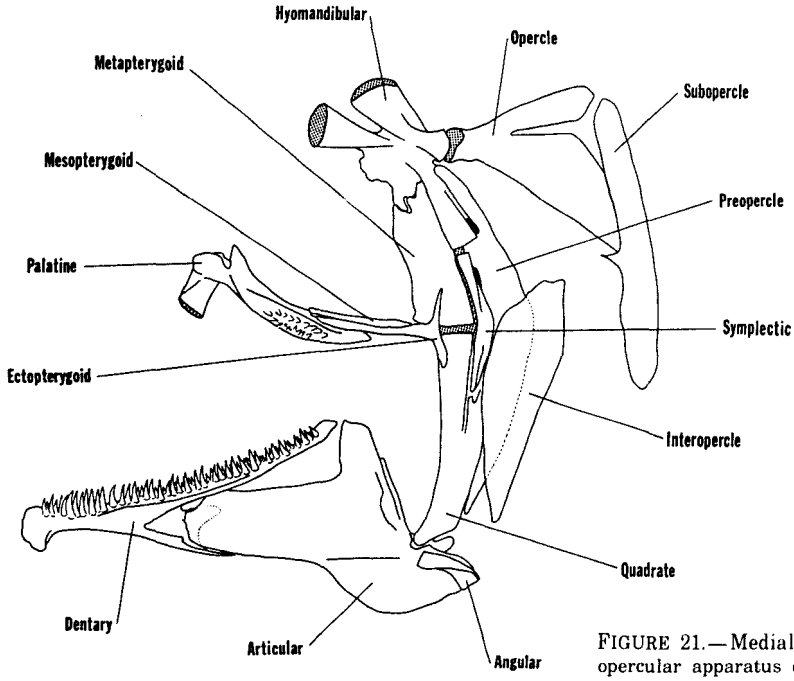

FIGURE 21.—Medial view of lower jaw, suspensorium, and opercular apparatus of *Antennarius sanguineus*, LACM 8125, 76 mm SL.

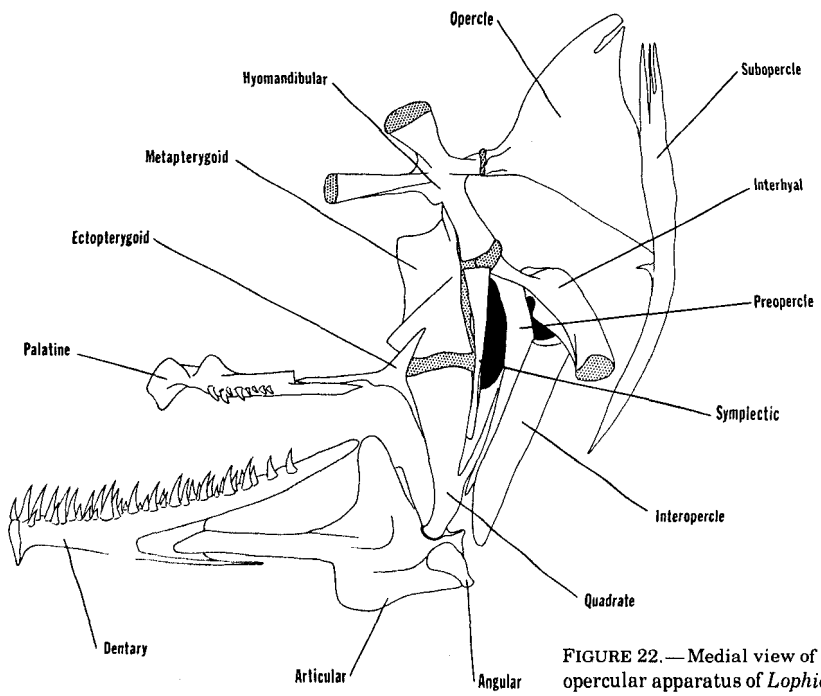

FIGURE 22.—Medial view of lower jaw, suspensorium, interhyal, and opercular apparatus of *Lophichthys boschmai*, UW 20773, 47 mm SL.

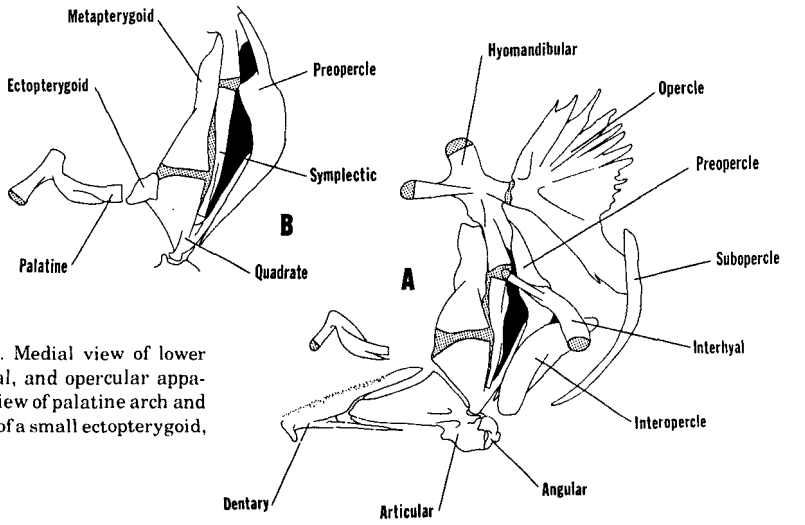

FIGURE 23.—*Brachionichthys hirsutus*: A. Medial view of lower jaw, palatine bone, suspensorium, interhyal, and opercular apparatus, AMS IA.6064, 69 mm SL; B. Medial view of palatine arch and suspensorium, right side, showing presence of a small ectopterygoid, UW 20769, 42 mm SL.

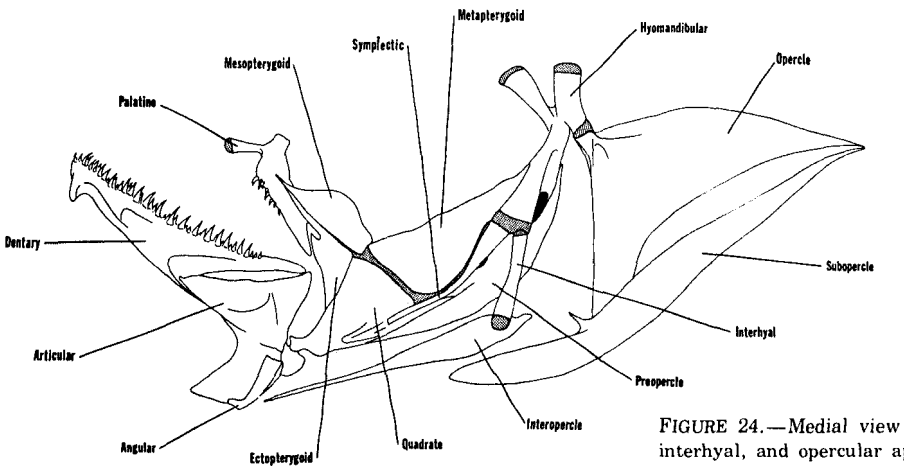

FIGURE 24.—Medial view of lower jaw, suspensorium, interhyal, and opercular apparatus of *Chaunax pictus*, UW 20770, 90 mm SL.

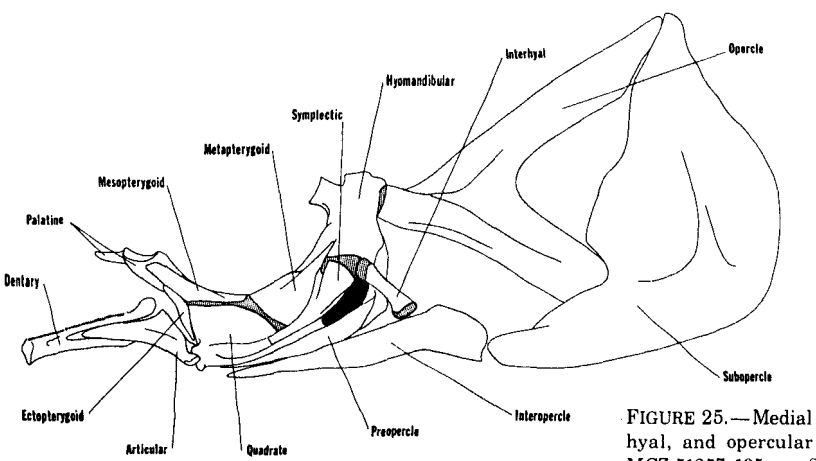

FIGURE 25.—Medial view of lower jaw, suspensorium, interhyal, and opercular apparatus of *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

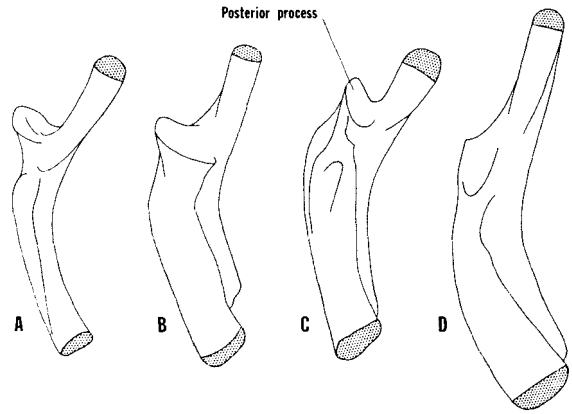

FIGURE 26.—Lateral view of interhyal, right side: A. *Antennarius sanguineus*, LACM 8125, 76 mm SL; B. *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL; C. *Lophichthys boschmai*, UW 20773, 47 mm SL; D. *Brachionichthys hirsutus*, AMS IA.6064, 69 mm SL.

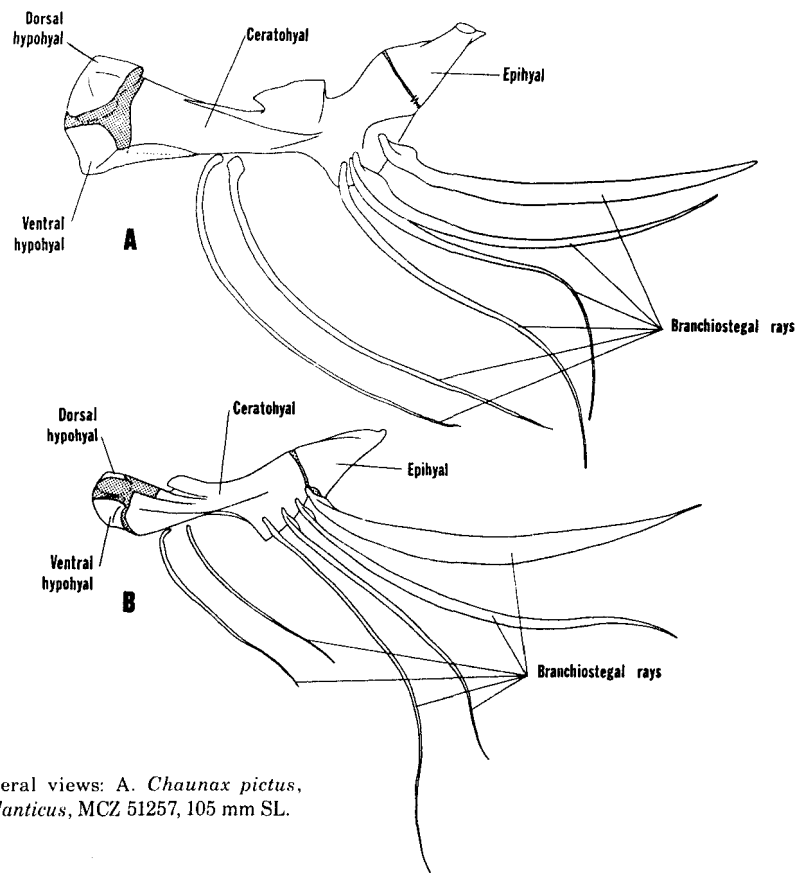

FIGURE 27.—Hyoid apparatus, left lateral views: A. *Chaunax pictus*, UW 20770, 90 mm SL; B. *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

TABLE 2.—Characters of representative genera of the major subgroups of the Antennarioidei.

Item	*Antennarius*	*Tetrabrachium*	*Lophichthys*	*Brachionichthys*	*Chaunax*	*Dibranchus*
Branchiostegal rays	2+4	2+4	2+4	1+4	2+4	2+4
Pharyngobranchial I	rod shaped (toothless)	rod shaped (toothless)	rod shaped (toothed)	absent	forked (toothless)	absent
Palatine teeth	present	absent	present	absent	present	absent
Epibranchial teeth						
Arch I	absent	absent	single row	1 plate	3 plates	2 plates
Arch III	absent	absent	absent	absent	absent	1 plate
Ceratobranchial teeth						
Arch I	absent	absent	absent	2 plates	present	present
Arch II	absent	absent	absent	1 plate	present	present
Arch III	absent	absent	absent	1 plate	present	present
Arch IV	absent	absent	absent	absent	present	present or absent
Hypobranchial II	bifurcated	bifurcated	bifurcated	simple	simple	absent
Hypobranchial III	bifurcated	bifurcated	bifurcated	simple	simple	absent
Pseudobranch	present	absent	absent	absent	absent	absent
Swim bladder	present	absent	absent	absent	absent	absent
Basihyal	present	present	present	absent	present	absent
Vertebrae (precaudal)	19(4)	22(4)	19(4)	22(4)	19(4)	19(6)
Epural	1	0	remnant present or absent	0	1	1
Dorsal fin rays	11-15	16-17	12-13	17	12	5
Anal fin rays	6-9	11-12	9	7	7	4
Pectoral fin radials	3	3	3	2	3	3
Pectoral fin rays	7-14	4+5	7	8	14	14
Pelvic fin rays	I+5	I+5	I+5	I+4	I+4	I+5

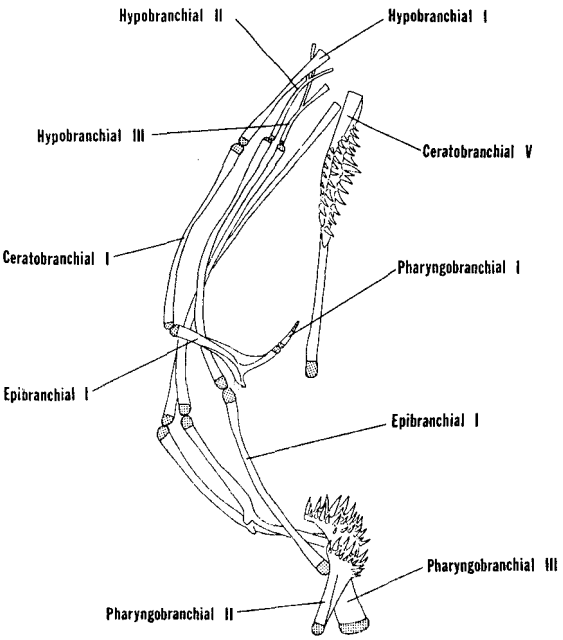

FIGURE 28.—Branchial arches of *Antennarius sanguineus*, LACM 8125, 76 mm SL. The ventral portion of the branchial basket is shown in dorsal view, the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view.

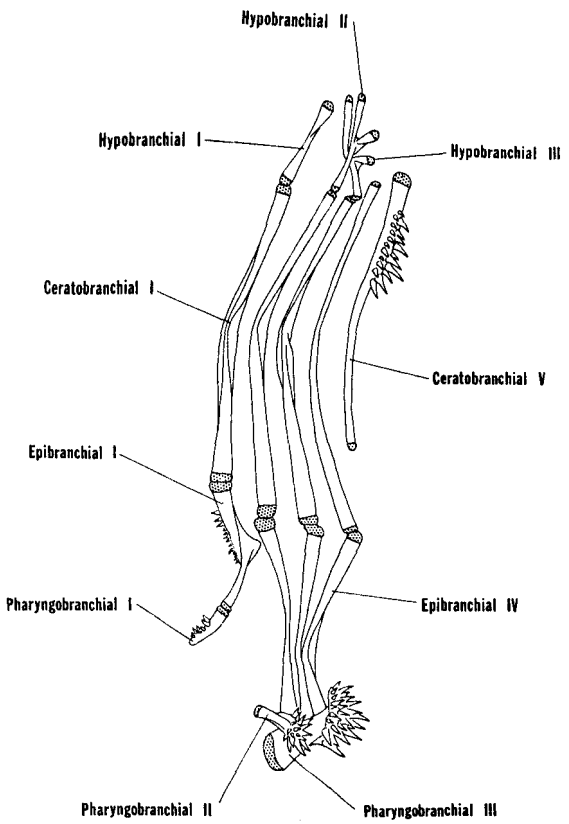

FIGURE 29.—Branchial arches of *Lophichthys boschmai*, UW 20773, 47 mm SL. The ventral portion of the branchial basket is shown in dorsal view, the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view.

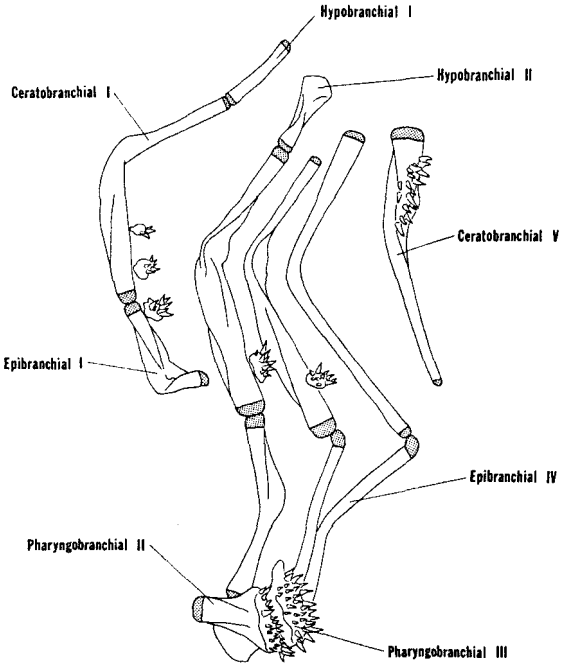

FIGURE 30.—Branchial arches of *Brachionichthys hirsutus*, AMS IA.6064, 69 mm SL. The ventral portion of the branchial basket is shown in dorsal view, the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view.

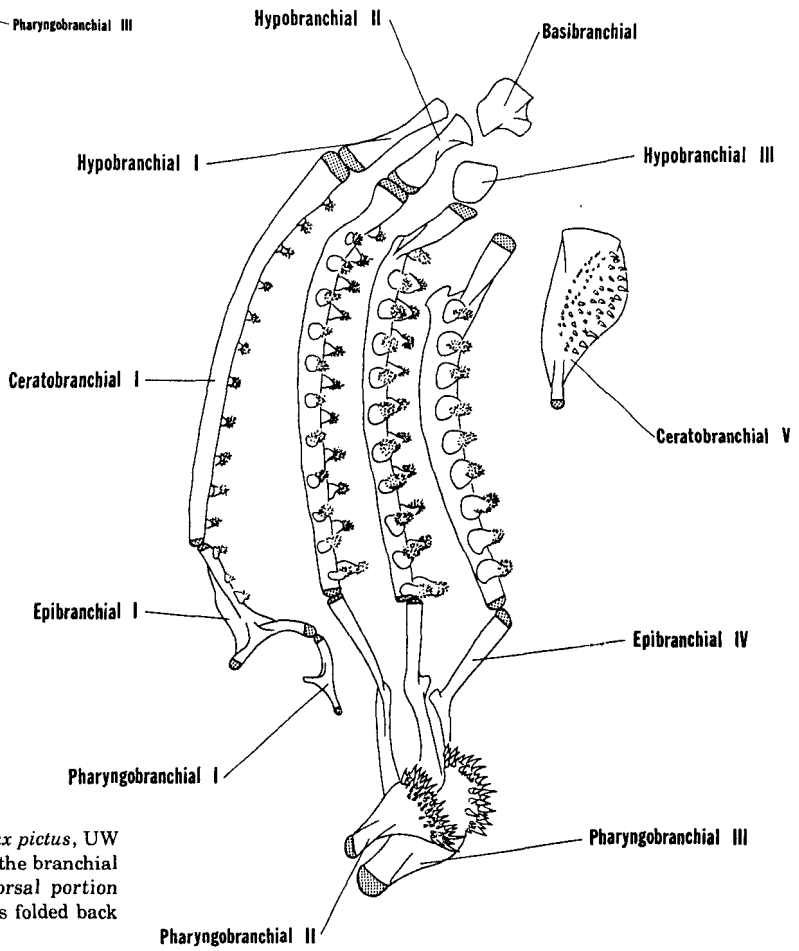

FIGURE 31.—Branchial arches of *Chaunax pictus*, UW 20770, 90 mm SL. The ventral portion of the branchial basket is shown in dorsal view, the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view.

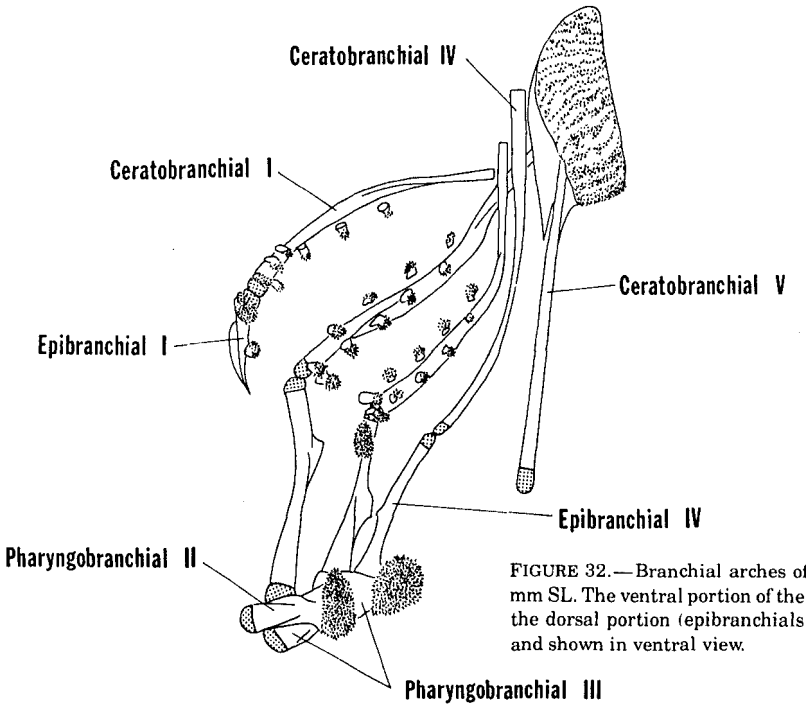

FIGURE 32.—Branchial arches of *Dibranchus atlanticus*, MCZ 51257, 105 mm SL. The ventral portion of the branchial basket is shown in dorsal view, the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view.

30). Epibranchial III is toothless in all antennarioids examined except in *Dibranchus* (Figure 32) where this bone is associated with a single tooth plate.

Ceratobranchials I through IV are toothless in *Tetrabrachium*, *Antennarius*, and *Lophichthys* (Figures 11, 28, 29). In *Brachionichthys* (Figure 30), one to three tooth plates are present on ceratobranchials I through III; in *Chaunax* (Figure 31), tooth plates are present on ceratobranchials I through IV; in *Dibranchus* (Figure 32), tooth plates are present on ceratobranchials I through III (but also sometimes present on ceratobranchial IV, see Bradbury 1967:408) (Table 2).

In contrast to the separate, individual teeth present on pharyngobranchial I and epibranchial I of *Lophichthys* (Figure 29), those present on epibranchial I and ceratobranchials I through IV of *Brachionichthys*, *Chaunax*, and *Dibranchus* (Figures 30-32) are born in clusters on individual tooth plates. The tooth plates of *Chaunax* and *Dibranchus* (Figures 31, 32) (and a number of other ogcocephalid taxa, see Bradbury 1967) differ from those of *Brachionichthys* (Figure 30) and from those of all other lophiiforms in being raised, pedicallike structures bearing a cluster of numerous, tiny teeth at the apex (but see Bradbury 1967, fig. 7, for other forms of gill teeth in ogcocephalids).

Ceratobranchial V is well toothed in all antennarioids examined. In *Tetrabrachium*, *Antennarius*, *Lophichthys*, and *Brachionichthys* (Figures 11, 28-30), this bone consists of a narrow, toothed proximal portion and a tapering, cylindrical distal portion; in *Chaunax* (Figure 31) only a triangular, toothed portion is present. In *Dibranchus* (Figure 32), ceratobranchial V is greatly enlarged, consisting of a finely toothed, expanded proximal portion and a long, cylindrical distal shaft.

Hypobranchial I of *Tetrabrachium*, *Antennarius*, *Lophichthys*, *Brachionichthys*, and *Chaunax* (Figures 11, 28-31) and hypobranchial II of *Brachionichthys* and *Chaunax* (Figures 30, 31) are simple, rod-shaped bones. Hypobranchials II and III of *Tetrabrachium*, *Antennarius*, and *Lophichthys* (Figures 11, 28, 29) are bifurcated proximally (this feature is probably plesiomorphic for lophiiforms since a similar situation is present in all batrachoidids examined). Hypobranchial III is absent in *Brachionichthys* (Figure 30), but represented by a semicircular ossification in *Chaunax* (Figure 31). There are no ossified hypobranchials in the single specimen of *Dibranchus* examined (Figure 32, Table 2).

Basibranchials are represented by a single ossification in *Chaunax* (Figure 31), but are absent in *Antennarius*, *Tetrabrachium*, *Lophichthys*, *Brachionichthys*, and *Dibranchus*.

Gill filaments are absent on arch I of *Chaunax* and *Dibranchus*. Filaments are present as holobranchs on arch I of *Antennarius*, *Tetrabrachium*, *Lophichthys*, and *Brachionichthys*, and on arches II and III of all antennarioids examined. Hemibranchs are present on arch IV of all antennarioids examined (filaments may sometimes be absent on arch IV of *Dibranchus*; Bradbury 1967:408).

A small pseudobranch is present in *Antennarius*, but absent in all other antennarioids examined.

Vertebrae and caudal skeleton (Figures 12, 33-35).—The vertebral column of *Antennarius*, *Lophichthys*, and *Brachionichthys* (Figures 33, 34A) is similar to that of *Tetrabrachium* (Figure 12) in having the neural spines of three to four anterior vertebrae (preural centra 11-13 in *Antennarius*, Figure 33; 14-17 in *Tetrabrachium*, Figure 12; 12-14 in *Lophichthys*, Figure 34A; and 15-18 in *Brachionichthys*) short (spatulate in all antennarioids examined except for *Lophichthys*, *Chaunax*, *Dibranchus*, and a few specialized antennariid genera, i.e., *Echinophryne*, *Trichophryne*, and *Rhycherus*; see Appendix) and not interdigitating with the corresponding proximal radials of the overlying soft dorsal fin (this feature appears to be plesiomorphic for the Lophiiformes being more or less developed in nearly all taxa).

In *Chaunax* (Figure 35A), the neural spines are similar throughout the length of the axial skeleton. In *Dibranchus* (Figure 35B), the vertebral column and caudal skeleton are strongly modified for a benthic life-style. The neural and haemal spines of all centra are short and broad. Preural centra 14 through 18 are considerably more elongate than the remaining centra; the neural spines of these centra are expanded anteroposteriorly and compressed laterally to form a solid bony partition along the dorsal midline. Mobility in this region of the axial skeleton is severely reduced due to large, overlapping prezygapophyses (considerable movement is retained, however, between the two anteriormost centra, preural centra 18 and 19).

In both specimens of *Lophichthys* examined a peculiar bridging of bone is present between the distal tips of the haemal spines of the 14th through the 16th preural centra (Figure 34A). This kind of ossification has not been described for any other lophiiform.

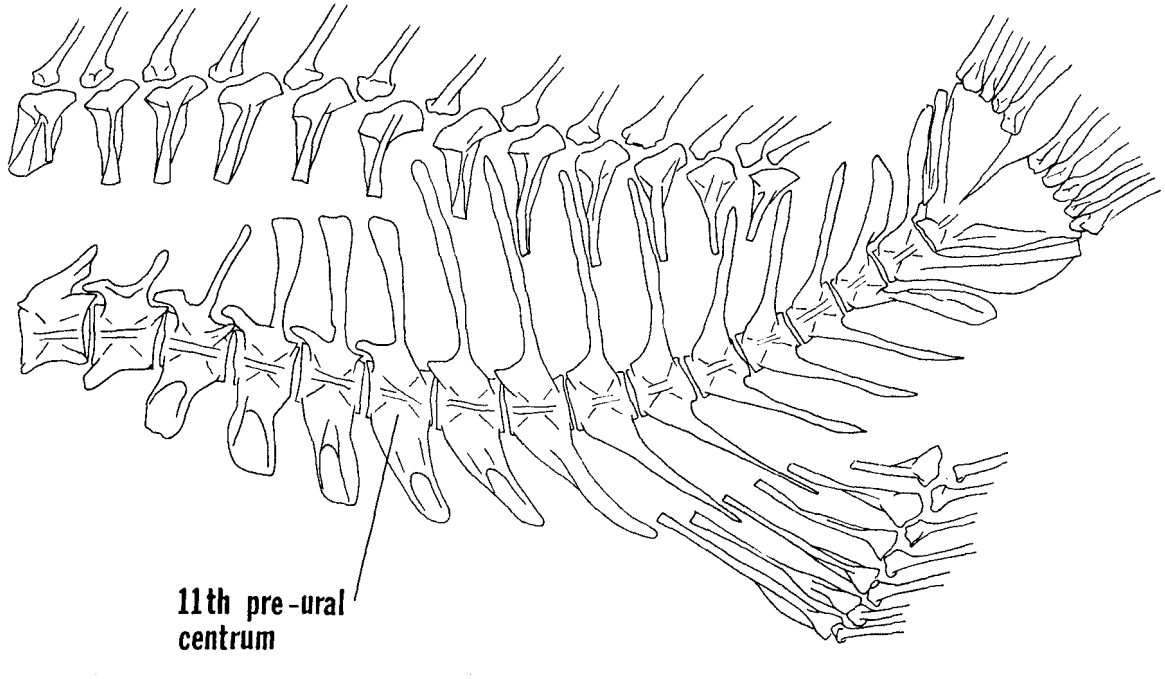

FIGURE 33.—Vertebrae, caudal skeleton, and median fins of *Antennarius sanguineus*, LACM 8125, 76 mm SL.

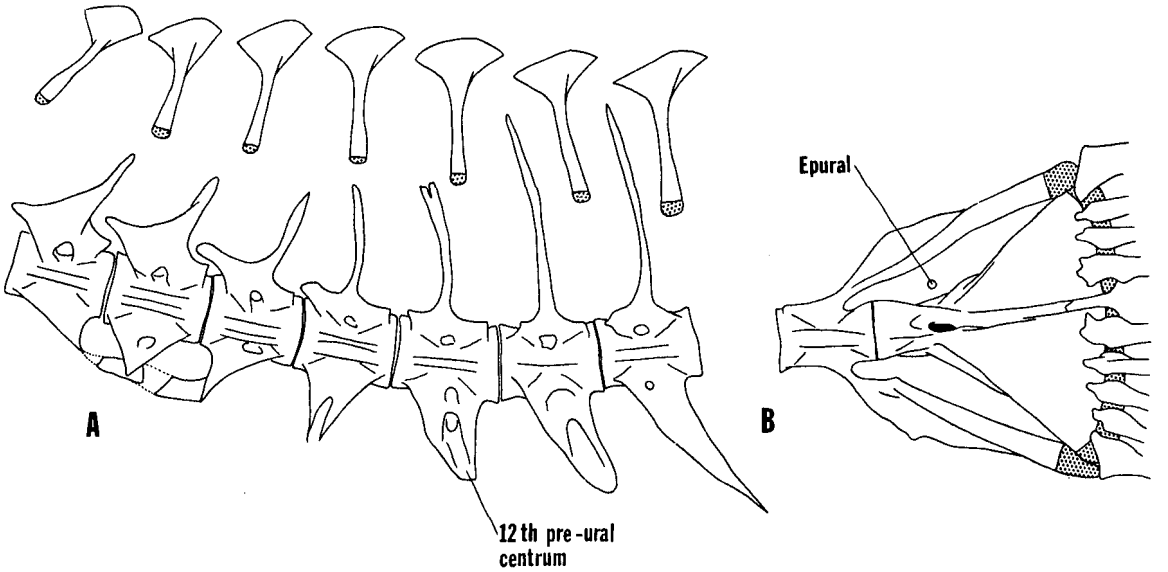

FIGURE 34.—*Lophichthys boschmai*, UW 20773, 47 mm SL: A. Preural centra 12 through 16, showing partially ossified connection between distal tips of haemal spines of preural centra 14 through 16; B. Caudal skeleton showing remnant of epural.

A single epural is present in *Antennarius*, *Chaunax*, and *Dibranchus* (Figures 33, 35) (oval and laterally compressed in the later genus). In the larger (47 mm) of the two specimens of *Lophichthys* (Figure 34B) examined, the epural is represented by a tiny circular ossification. No trace of this element is present in the smaller (44 mm) individual of *Lophichthys*, or in any other antennarioid examined.

Axial skeletal elements of the antennarioid taxa examined are compared in Table 2.

Medial fins and illicial apparatus (Figures 13, 36-39).—The spinous dorsal fin of *Tetrabrachium*,

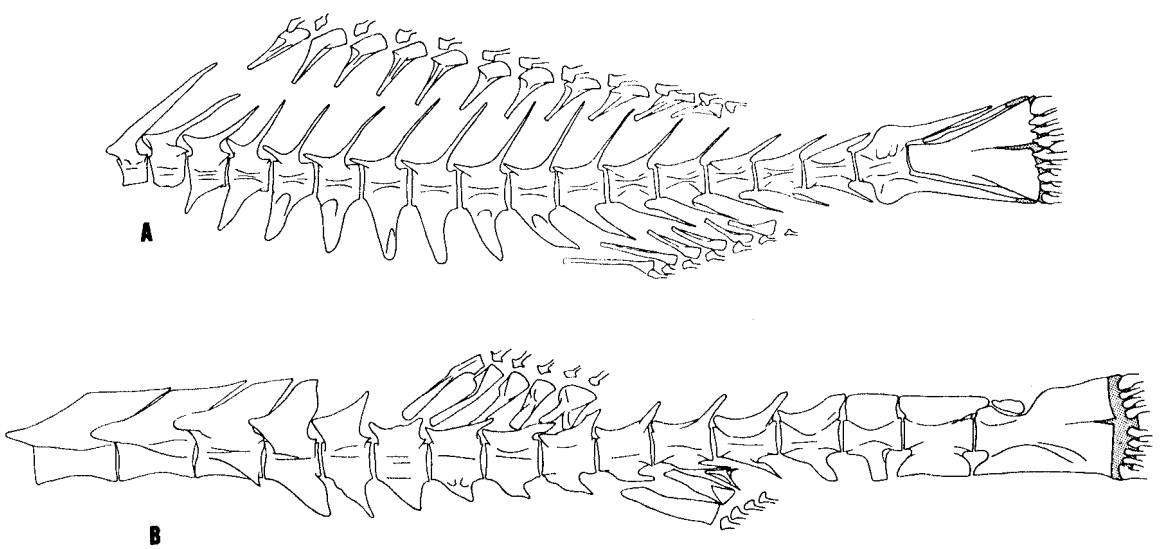

FIGURE 35.—Vertebrae, caudal skeleton, and median fins: A. *Chaunax pictus*, UW 20770, 90 mm SL; B. *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

Antennarius, *Brachionichthys*, *Lophichthys*, and *Chaunax* consists of three spines. In *Antennarius*, *Brachionichthys*, and *Lophichthys* (Figures 36, 37) all three spines are well developed, extending above the skin of the head. In many species of *Antennarius* spines II and III are membranously attached posteriorly to the head; in *Brachionichthys*, and in some forms of *Antennarius* (e.g. *A. pauciradiatus* Schultz 1957:100, fig. 7; *A. randalli* Allen 1970:518, fig. 1, 2a), spine II is membranously attached to the full length of spine III, and spine III is, in turn, membranously attached posteriorly to the head.

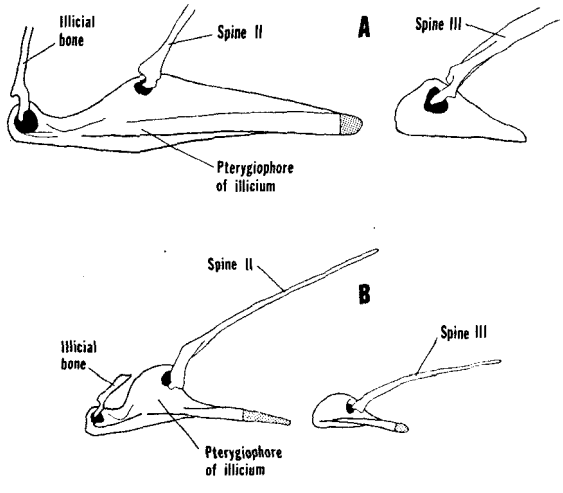

FIGURE 36.—Spinous dorsal fin, left lateral view: A. *Antennarius sanguineus*, LACM 8125, 76 mm SL; B. *Brachionichthys hirsutus*, AMS IA.6064, 69 mm SL.

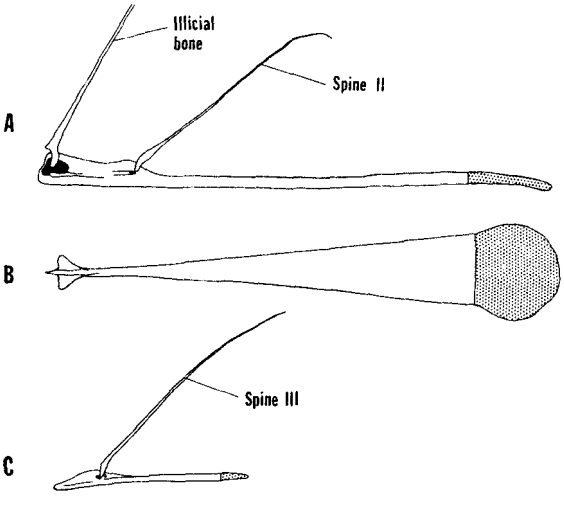

FIGURE 37.—Elements of spinous dorsal fin of *Lophichthys boschmai*, UW 20773, 47 mm SL: A. Anteriormost pterygiophore bearing illicial bone and dorsal spine II, left lateral view; B. Anteriormost pterygiophore, ventral view; C. Second pterygiophore bearing dorsal spine III, left lateral view.

In *Tetrabrachium* (Figure 13), all three dorsal fin spines are evident externally, but all are reduced in size; the greater part of spine III is covered by skin of the head, only the tip emerging. In *Chaunax* (Figure 38A), all three dorsal fin spines are relatively well developed, but spines II and III are laid back on the surface of the cranium completely covered by skin and apparently nonfunctional (a similar situation is found in *Histiophryne*, a highly specialized genus of the Antennariidae). The illicial bone (dorsal spine I), when retracted, comes to lie within an aperture on the face between the nostrils and eyes, called the illicial cavity (Figure 39A; Bradbury 1967).

In *Dibranchus* (Figure 38B), dorsal spine III and its pterygiophore are absent. Spine II is reduced to a small vestige of bone (the "H-shaped" bone of Bradbury 1967:402, fig. 1) lying on, or often fused to the anteriormost pterygiophore just behind the articulation of the pterygiophore and the illicial bone. As in *Chaunax*, the illicial bone, when retracted, comes to lie within an illicial cavity (Figure 39B, C).

In *Tetrabrachium*, *Antennarius*, *Lophichthys*, and *Brachionighthys* (Figures 13, 36-37), the anteriormost pterygiophore that supports the illicial bone and dorsal spine II, and the second pterygiophore that supports dorsal spine III have highly compressed, bladelike dorsal expansions. Each

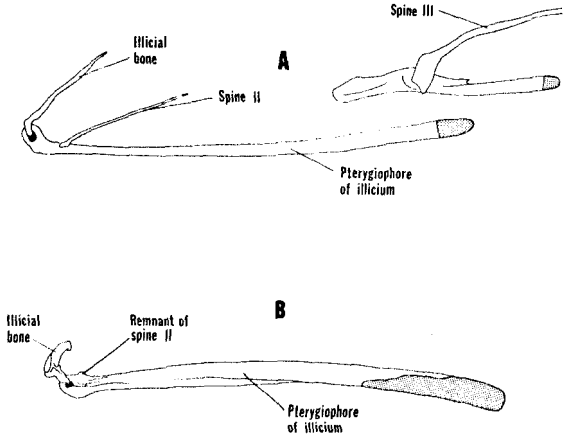

FIGURE 38.—Spinous dorsal fin, left lateral views: A. *Chaunax pictus*, UW 20770, 90 mm SL; B. *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

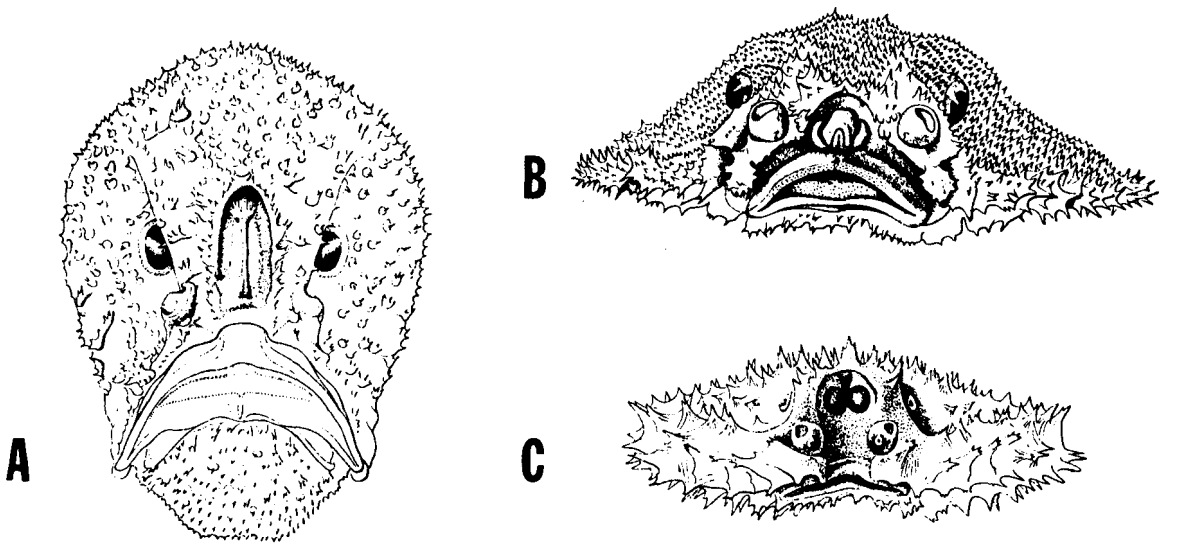

FIGURE 39.—Anterior views showing illicial cavity within which the illicial bone, when fully retracted, comes to lie: A. *Chaunax coloratus* Garman; B. *Dibranchus spinosa* (Garman); C. *Halieutopsis tumifrons* (Garman). After Garman (1899).

expansion is pierced by a large, circular foramen within which fits the bifurcated proximal end of the respective dorsal fin spine. The anteriormost pterygiophore of *Lophichthys* (Figure 37A, B) is unique among the antennarioids examined in being much more elongate, and in becoming greatly depressed and laterally expanded posteriorly. In *Chaunax* and *Dibranchus* (Figure 38), the pterygiophores of the dorsal fin spines are cylindrical in cross section along their entire length.

Dorsal and anal fin ray counts of the antennarioids examined are compared in Table 2.

Pectoral and pelvic girdles and fins (Figures 14, 40).—The posttemporal of *Antennarius*, *Lophichthys*, *Brachionichthys*, and *Chaunax* is similar to that of *Tetrabrachium*, attached to the cranium in such a way that considerable movement in an anterodorsal-posteroventral plane is possible. In contrast, the posttemporal of *Dibranchus* is fused to the cranium.

The number and length of the pectoral fin radials varies somewhat among the antennarioids examined. There are three relatively short pectoral radials in *Tetrabrachium*, and *Antennarius* (Figures 14, 40A). The three radials of *Lophichthys* (Figure 40B) are exceptionally long and narrow; the second radial is reduced, tapering proximally to a slender filament. *Brachionichthys* (Figure 40C) has two, somewhat elongate pectoral

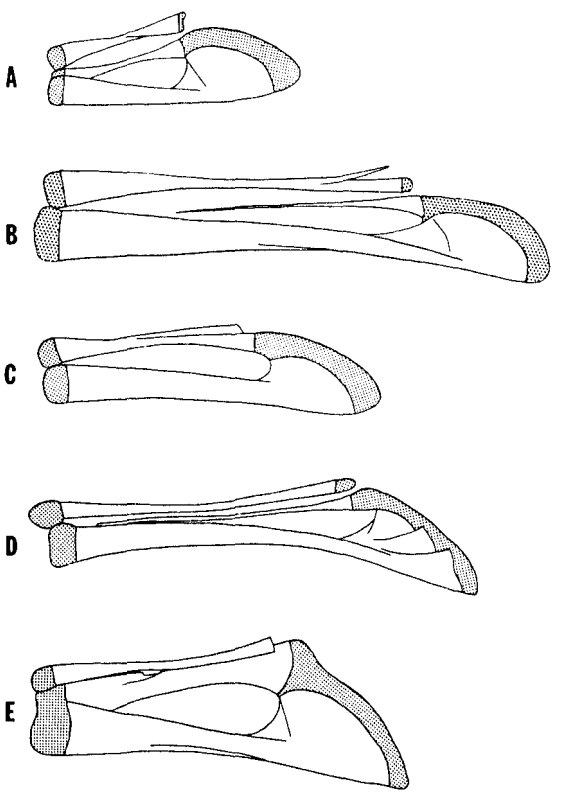

FIGURE 40.—Pectoral radials, lateral view, left side: A. *Antennarius striatus*, UW 20768, 67 mm SL; B. *Lophichthys boschmai*, UW 20773, 47 mm SL; C. *Brachionichthys hirsutus*, AMS IA.6064, 69 mm SL; D. *Chaunax pictus*, UW 20770, 90 mm SL; E. *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

radials. In the single osteological preparation of *Chaunax* examined (Figure 40D), there are three separate, relatively long radials, but the ventralmost element appears to be the result of fusion of three, perhaps indicating the presence of a total of five radials. In *Dibranchus* (Figure 40E) there are three, relatively short radials, the dorsalmost two lying side-by-side and fused to one another at their proximal and distal ends.

Skin spines.—Numerous, close-set dermal spines cover the head and body of *Antennarius*, *Lophichthys*, *Brachionichthys*, and *Chaunax*; the spines are bifurcated in *Antennarius*, but simple in *Lophichthys*, *Brachionichthys*, and *Chaunax*. Dermal spines are absent in *Tetrabrachium*, except for the occasional presence of a spinule associated with an individual pore of the acoustico-lateralis system. The head and body of *Dibranchus* are nearly totally enclosed in a covering of thick, nonoverlapping tubercles (Bradbury 1967:404).

PHYLOGENETIC RELATIONSHIPS

The order Lophiiformes is an assemblage of 18 families, 59 genera, and approximately 255 living species of marine teleosts, the monophyletic origin of which seems certain based on the following list of synapomorphic features:

1) Spinous dorsal fin primitively of six spines, the anteriormost three of which are cephalic in position and modified to serve as a luring apparatus (involving numerous associated specializations, e.g., a medial depression of the anterior portion of the cranium, loss of the nasal bones [nasal of Rosen and Patterson 1969 = lateral ethmoid] and supraoccipital lateral-line commissure, and modifications of associated musculature and innervation);
2) Epiotics separated from parietals and meeting on the midline posterior to the supraoccipital;
3) Gill opening restricted to a small, elongate tubelike opening situated immediately dorsal to, posterior to, or ventral to (rarely partly anterior to) pectoral fin base;
4) Second ural centrum fused with the first ural and first preural centra to form a single hypural plate (sometimes deeply notched posteriorly) that emanates from a single, complex half-centrum (Rosen and Patterson 1969:441, text fig. 4E, 60);
5) Pectoral radials narrow and elongate, the ventralmost radial considerably expanded distally;
6) Eggs spawned in a double, scroll-shaped mucous sheath (Rasquin 1958).

Since Regan (1912), three major lophiiform taxa of equal rank have been recognized by nearly all authors. These taxa, together with their currently recognized families (the 11 families of the bathypelagic Ceratioidei excluded), are:

Suborder Lophioidei
  Family Lophiidae
Suborder Antennarioidei
  Family Antennariidae
  Family Brachionichthyidae
  Family Chaunacidae
  Family Ogcocephalidae
Suborder Ceratioidei

In attempting to place *Tetrabrachium* within the framework of this classification it became apparent that not all of the relationships expressed can be supported by an adherence to cladistic methodology. Although never questioned by any subsequent author, the monophyly of each of Regan's (1912) three major lophiiform taxa has not been established. Serious problems lie within the Antennarioidei: a number of synapomorphic features support a sister-group relationship between the Antennariidae and Brachionichthyidae (see below), and between the Chaunacidae and Ogcocephalidae, but no convincing synapomorphy is known at the present time that will link these two larger subgroups. Thus, the problems of interpreting the interrelationships of higher taxonomic categories within the Antennarioidei, and the relationships of this suborder to the Lophioidei and Ceratioidei are postponed. The following discussion is limited for the most part to *Tetrabrachium* and its relationship to the Antennariidae, to *Lophichthys* (here given familial rank as suggested by Boeseman 1964), and to the Brachionichthyidae. Synapomorphic features that establish monophyly for a group containing the Chaunacidae and Ogcocephalidae are also enumerated. The relative primitiveness of the character states utilized below was determined by examining their distribution among all available lophiiform material (47 of the 59 currently recognized genera;

material unavailable for comparison includes the lophioid genus *Sladenia* Regan, seven of the nine ogcocephalidid genera, and a number of rare and highly derived ceratioid genera), as well as representative taxa of the Batrachoidiformes (3 of the 12 nominal genera), the only group bearing evidence of sister-group relationship with the Lophiiformes (Regan 1912; Gregory 1933; Rosen and Patterson 1967) (see Appendix).

Antennarius, used here as the representative taxa of the Antennariidae, is recognized as the least derived genus of the family based on a comparative anatomical study of some eight nominal antennariid genera (Pietsch in prep., see Appendix). Except for synapomorphies that establish monophyly for *Antennarius*, all known characters of taxonomic importance found among the eight genera are present in *Antennarius* in the primitive state. For example, a mesopterygoid and an epural are present in *Antennarius* but absent in all other genera except *Histrio*; *Histrio* is clearly derived relative to *Antennarius* in having enlarged pelvic fins, a pectoral fin lobe that is detached from the body along most of its length, absence of skin spines, and a unique pelagic habitat in sargassum weed. Similarly, each of the remaining six antennariid genera possesses a number of autapomorphic features that indicate its derived nature relative to *Antennarius*. Although these and other data support the least derived position of *Antennarius*, this verification is not basic to the subsequent discussion of relationships since the synapomorphic features used to establish the sister groups proposed below are synapomorphic for all eight antennariid genera.

Tetrabrachium is most closely related cladistically to *Antennarius*, and is here classified on this basis as a sister-family, the Tetrabrachiidae (first proposed by Whitley 1935), of the Antennariidae (Figure 41). This hypothesis of relationship is supported by three synapomorphies:

1) Posteromedial process of vomer emerging from ventral surface as a laterally compressed, keellike structure, its ventral margin (as seen in lateral view) strongly convex (this character state is present in *Tetrabrachium* and in all antennariid taxa examined; in the batrachoidids and other lophiiforms examined the posteromedial process is flush with the ventral surface of the vomer, its ventral margin straight to slightly concave);
2) Postmaxillary process of premaxilla spatulate (this character state is present in *Tetrabrachium* and in all antennariid taxa examined; in the batrachoidids and other lophiiforms examined the postmaxillary process of the premaxilla is connected to the toothed portion of this element by bone, represented by a narrow, tapering structure, or absent);
3) Opercle similarly reduced in size (in *Tetrabrachium* and all antennariid taxa examined the width of the opercle is approximately $\leq 25\%$ the length of the suspensorium; in the batrachoidids and other lophiiforms examined this distance is $>40\%$).

Although the classification of taxa presented here is based on recency of common descent, the amount and nature of evolutionary change between the Antennariidae and the Tetrabrachiidae is an important part of their evolutionary histories. That the Tetrabrachiidae has entered a "new adaptive zone" relative to the Antennariidae is evidenced morphologically by a number of unique, derived features: eyes small, close set, protruding from the dorsal surface of the head; mouth small, superior, lower lip fringed with small cutaneous papillae; illicial apparatus reduced; pectoral fin double, the ventral portion membranously attached to the side of the body; and pectoral fin lobe membranously attached to the rays of the pelvic fin. The webbing between the pectoral fin and the body, and between the pectoral and pelvic fins is apparently used to remove soft-bottom substrate (fine sand or mud) from beneath by scooping material away in a lateral direction and simultaneously throwing material up and over to cover the animal; the fringed lip allows for intake of water while helping to prevent particles from entering the pharyngeal cavity. These and other characters listed above reflect a life style similar to that of a uranoscopid or synanceiid, lying for long periods of time buried up to the eyes in sand or mud, a mode of existence unlike that of any other antennarioid.

The results of this study further show that the Antennariidae and Tetrabrachiidae together form the primitive sister group of the Lophichthyidae and that these three taxa together form the primitive sister group of the Brachionichthyidae (Figure 41). The monophyly of a group including the Antennariidae, Tetrabrachiidae, and Lophichthyidae is supported by a single synapomorphy:

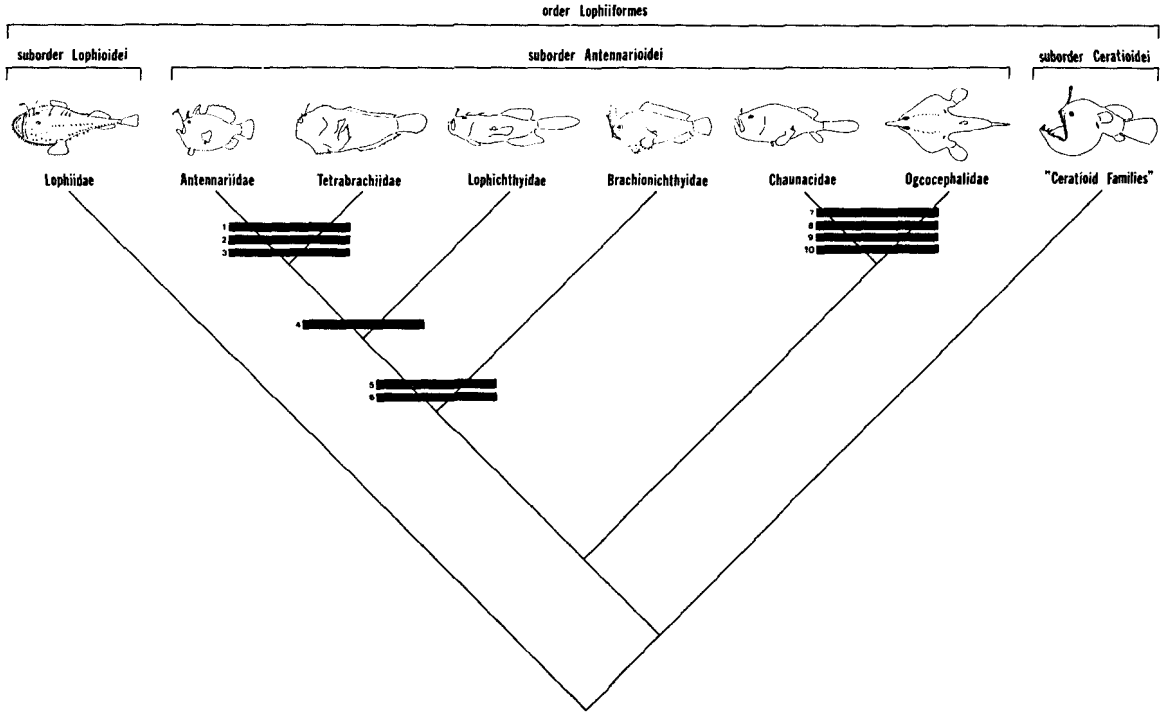

FIGURE 41.—Cladogram showing proposed phylogenetic relationships of major subgroups of the Lophiiformes. Note that not all sister-group relationships are supported by sufficient data. Black bars and numbers refer to synapomorphic features discussed in the text: 1) Posteromedial process of vomer emerging from ventral surface as a laterally compressed, keellike structure; 2) Postmaxillary process of premaxilla spatulate; 3) Opercle reduced; 4) Ectopterygoid triradiate; 5) Interhyal with a medial, posterolaterally directed process; 6) Illicial pterygiophore and pterygiophore of third dorsal fin spine with highly compressed, bladelike dorsal expansions; 7) Posterior-most branchiostegal ray exceptionally large; 8) Gill teeth tiny, arranged in a tight cluster at apex of pedicellike tooth plates; 9) Gill filaments of gill arch I absent; 10) Illicial bone, when retracted, lying within an illicial cavity. Drawings courtesy of The American Museum of Natural History.

4) Ectopterygoid triradiate, a dorsal process overlapping the medial surface of the metapterygoid (this character state is present in *Tetrabrachium*, *Lophichthys*, and all antennariids examined; in the batrachoidids and other lophiiforms examined this element is crescent shaped, making no contact with the metapterygoid).

That the Antennariidae, Tetrabrachiidae, Lophichthyidae, and Brachionichthyidae constitute a monophyletic group is supported by two synapomorphies:

5) Interhyal with a medial, posterolaterally directed process that comes into contact with the respective preopercle (this character state is present in *Tetrabrachium*, *Lophichthys*, *Brachionichthys*, and all antennariids examined; in the batrachoidids and all other lophiiforms examined this interhyal process is absent);
6) Illicial pterygiophore and pterygiophore of the third dorsal fin spine with highly compressed, bladelike dorsal expansions (this character state is present in *Tetrabrachium*, *Lophichthys*, *Brachionichthys*, and all antennariids examined; in other lophiiforms examined these dorsal expansions are absent; this character does not extend to batrachoidids).

Gregory (1933:388, fig. 264) speculated that the membranous connection between the spines of the dorsal fin of *Brachionichthys* represents a primitive feature: "This is the most primitive condition among the typical pediculates" (= lophiiforms). On this assumption, in addition to a statement that the skeleton of *Brachionichthys* is relatively primitive in appearance, Gregory (1933:387) concluded that "...*Brachionichthys* is much less spe-

cialized [relative to antennariids and lophiids] and in fact seems to give several clues to the origin of the entire order." On the contrary, all evidence indicates that a membranous connection between the dorsal fin spines is apomorphic for anglerfishes; of the approximately 255 living species of the order this feature is present in the four nominal species of *Brachionichthys* and in two of the most derived species of the genus *Antennarius* (*A. pauciradiatus* and *A. randalli*; Pietsch in prep.). Besides this character, *Brachionichthys* possesses a set of autapomorphic features that clearly remove it from consideration as "the most primitive lophiiform." In addition to those autapomorphies listed in the analytical key below, Winterbottom (1974:284) has identified an apparently unique derived condition of the inclinator dorsales muscle of the second dorsal fin spine of *Brachionichthys*.

Although strikingly dissimilar at first glance, a number of synapomorphies support a hypothesis of sister-group relationship between the families Chaunacidae and Ogcocephalidae (Figure 41):

7) Posteriormost branchiostegal ray exceptionally large (in batrachoidids and all other lophiiforms examined the size of the posteriormost branchiostegal does not differ significantly from the adjacent branchiostegal);
8) Gill teeth tiny, arranged in a tight cluster at apex of pedicellike tooth plates (in batrachoidids and other lophiiforms examined the gill teeth are relatively large, and either single, or associated with a flat, rounded tooth plate);
9) Gill filaments of gill arch I absent (in batrachoidids and all other lophiiforms examined gill filaments are present on arch I);
10) Illicial bone, when retracted, lying within an illicial cavity (an illicial cavity is absent in all other lophiiforms examined; this character does not extend to batrachoidids).

Historically, chaunacids and ogcocephalids have been classified with antennariids and brachionichthyids by aspects of general similarity (i.e., they neither look like lophioids or ceratioids). Nearly all of these similarities are easily identified as character states that are plesiomorphic for antennarioids (or for lophiiforms as a whole); the synapomorphic nature of the few remaining similarities is unresolvable. Thus, despite a thorough osteological search, this study has failed to identify the sister group of a group including the Chaunacidae and Ogcocephalidae among the known members of the Lophiiformes. In the absence of any evidence for or against, these taxa are tentatively retained within the Antennarioidei (Figure 41).

Of the possible cladograms that could be constructed on the basis of the data provided in this study, the one shown in Figure 41 involves the least number of convergences. The preferred phylogeny requires four cases of convergence (Table 2), all of which, however, are loss characters that extend to other lophiiform taxa:

1) the independent loss of palatine teeth in the Tetrabrachiidae and Brachionichthyidae [also absent in some ogcocephalids (see Bradbury 1967:409) and in all ceratioids];
2) the independent loss of a pseudobranch in the Tetrabrachiidae, Lophichthyidae, and Brachionichthyidae (also absent in chaunacids, ogcocephalids, and all ceratioids);
3) the independent loss of the swim bladder in the Tetrabrachiidae, Lophichthyidae, and Brachionichthyidae (also absent in lophioids, chaunacids, ogcocephalids, and ceratioids);
4) the independent loss of the epural in the Tetrabrachiidae and Brachionichthyidae also absent in all antennariid genera examined except *Antennarius*, *Antennatus*, and *Histrio*; [although present in the Caulophrynidae (Pietsch 1979, fig. 11), the epural is absent in all other ceratioids].

Plesiomorphic and autapomorphic features of the major subgroups of the Antennarioidei are incorporated into the following analytical key:

1A. Spinous dorsal of three spines, emerging from dorsal surface of cranium, illicium not retractable within an illicial cavity; ectopterygoid present or absent, interopercle flat and broad 2
1B. Spinous dorsal of one spine (spines II and III reduced and embedded beneath skin of head or lost), illicium retractable within an illicial cavity; ectopterygoid present, crescent shaped; interopercle elongate and narrow 5
2A. Parietals well separated by supraoccipital; ectopterygoid triradiate; ceratobranchials I through IV toothless; hypobranchials II and III bifurcated prox-

imally; three pectoral radials; pelvic fin of one spine and five rays 3

2B. Parietals meeting on the midline dorsal to supraoccipital; ectopterygoid roughly oval in shape or absent; ceratobranchials I through III with one or more tooth plates; hypobranchial II simple, hypobranchial III absent; two pectoral radials; pelvic fin of one spine and four rays ..... Brachionichthyidae

3A. Vomer narrow, width between lateral ethmoids considerably less than between lateral margins of sphenotics; dorsal head of quadrate narrow, width less than that of metapterygoid; postmaxillary process of premaxilla spatulate; opercle reduced in size; pharyngobranchial and epibranchial of first arch toothless; bony connection between tips of haemal spines absent; pterygiophore of illicium short, posterior end cylindrical 4

3B. Vomer wide, width between lateral ethmoids nearly as great as between lateral margins of sphenotics; dorsal head of quadrate broad, width equal to or greater than that of metapterygoid; postmaxillary process of premaxilla tapering to a point; opercle expanded posteriorly; pharyngobranchial and epibranchial of arch I toothed; bony connection between tips of haemal spines of 14th through 16th preural centra; pterygiophore of illicium elongate, greatly depressed and laterally expanded posteriorly ..... Lophichthyidae

4A. Eyes lateral, dorsal fin spines well developed; mouth large; pectoral fin single, rays not membranously attached to side of body; pectoral fin lobe not membranously attached to rays of pelvic fin; soft dorsal fin rays 11 to 15, anal fin rays 6 to 9 ..... Antennariidae

4B. Eyes dorsal; dorsal fin spines reduced; mouth small; pectoral fin double, dorsalmost ray of ventral portion membranously attached to side of body; pectoral fin lobe membranously attached to rays of pelvic fin; soft dorsal fin rays 16 or 17, anal fin rays 11 or 12 ..... Tetrabrachiidae

5A. Body slightly compressed laterally; cleft of mouth nearly vertical; frontal bones narrow, meeting each other on the midline along their entire length; lateral ethmoids long and narrow; posteriormost branchiostegal ray free; dorsal fin spines II and III present, embedded beneath skin of head; pelvic fin of one spine and four rays; soft dorsal fin rays 11 to 13; anal fin rays 5 to 7 ..... Chaunacidae

5B. Body strongly depressed dorsoventrally; cleft of mouth horizontal; frontal bones triangular in shape, only their posterior halves meeting on the midline; lateral ethmoids short and stout; posteriormost branchiostegal ray ankylosed to ventromedial margin of subopercle; dorsal fin spine III absent, spine II reduced to a small remnant embedded beneath skin and lying on, or fused to, dorsal surface of pterygiophore just behind base of illicial bone; pelvic fin of one spine and five rays; soft dorsal fin rays 4 or 5; anal fin rays 4 ..... Ogcocephalidae

Although not all of the sister groups suggested are supported by sufficient data at this time, the following classification of the Lophiiformes is proposed. While the ranking of taxa is not dichotomous (see Methods), internested sets of vertical lines are used to indicate sister-group relationships:

Order Lophiiformes
- Suborder Lophioidei
- Suborder Antennarioidei
  - Family Antennariidae
  - Family Tetrabrachiidae
  - Family Lophichthyidae
  - Family Brachionichthyidae
  - Family Chaunacidae
  - Family Ogcocephalidae
- Suborder Ceratioidei

As a final note, the genus *Histionotophorus*, based on a single species, *H. bassani* (Zigno 1887) from the Eocene of Monte Bolca, Italy, should be mentioned. From the available fossil evidence, this genus does not appear to differ substantially from *Brachionichthys*, and probably should be synonymized with the latter (Rosen and Patterson 1969:442). Reconstructions and photographs of the few known specimens (Eastman 1904, text fig. C, pl. 1, fig. 1-3; Gill 1904; Le Danois 1964:141, fig. 75, 76) show the following brachionichthyid features: mouth horizontal; mesopterygoid greatly reduced or absent (?); ectopterygoid absent (?); 22 vertebral

centra; epural absent; dorsal of three well-developed cephalic spines; membrane between dorsal spines II and III (?); caudal fin rays elongate; two elongate pectoral radials.

ACKNOWLEDGMENTS

I thank the following individuals and their institutions for providing material and specimen data: J. R. Paxton (AMS), G. R. Allen (WAM), S. Karnella (USNM), A. Wheeler (BMNH), P. Kailola and M. A. Wilson (formerly of KFRS), B. R. Smith (KFRS), K. Hartel (MCZ), R. J. Lavenberg and J. W. Neumann (LACM), M. F. Gomon (NMV), and M. Boeseman (RMNH). Special thanks are extended to Patricia Kailola for providing specimens of *Lophichthys boschmai*, and to two referees who helped to greatly improve the final draft of this paper. An earlier version of the manuscript was critically reviewed by K. M. Howe and S. L. Leipertz, College of Fisheries, University of Washington.

The work was supported by National Science Foundation Grants DEB 76-82279, DEB 78-26540, and DEB 80-05064, the National Geographic Society, and PHS Biomedical Research Support Grant No. RR-07096 administered through the Graduate School Research Fund of the University of Washington.

LITERATURE CITED

ALLEN, G. R.
1970. Two new species of frogfishes (Antennariidae) from Easter Island. Pac. Sci. 24:517-522.

BEAUFORT, L. F. DE, AND J. C. BRIGGS.
1962. The fishes of the Indo-Australian Archipelago XI. Scleroparei, Hypostomides, Pediculati, Plectognathi, Opisthomi, Discocephali, Xenopterygii. Brill, Leiden, Neth.

BERG, L. S.
1940. Classification of fishes, both recent and fossil. Trav. Zool. Inst. Akad. Nauk SSSR 5:87-517 (reprint, J. W. Edwards, Ann Arbor, Mich., 1947).

BERTELSEN, E.
1951. The ceratioid fishes. Ontogeny, taxonomy, distribution and biology. Dana Rep., Carlsberg Found. 7(39), 276 p.

BOESEMAN, M.
1964. Notes on the fishes of western New Guinea II. *Lophichthys boschmai*, a new genus and species from the Arafoera Sea. Zool. Meded. (Leiden) 39:12-18.

BRADBURY, M. G.
1967. The genera of batfishes (family Ogcocephalidae). Copeia 1967:399-422.

EASTMAN, C. R.
1904. Descriptions of Bolca fishes. Bull. Mus. Comp. Zool. Harv. Coll. 46:1-36.

EATON, T. H., JR., C. A. EDWARDS, M. A. MCINTOSH, AND J. P. ROWLAND.
1954. Structure and relationships of the anglerfish, *Lophius americanus*. J. Elisha Mitchell Sci. Soc. 70: 205-218.

ELDREDGE, N., AND J. CRACRAFT.
1980. Phylogenetic patterns and the evolutionary process. Columbia Univ. Press, N.Y., 349 p.

FIELD, J. G.
1966. Contributions to the functional morphology of fishes. Part II. The feeding mechanism of the anglerfish, *Lophius piscatorius* Linnaeus. Zool. Afr. 2:45-67.

FOWLER, H. W.
1928. The fishes of Oceania. Mem. Bernice P. Bishop Mus. 10, 540 p.

GARMAN, S.
1899. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer "Albatross," during 1891, Lieut. Commander Z. L. Tanner, U.S.N., commanding. XXVI. The fishes. Mem. Harvard Mus. Comp. Zool., Harv. Coll. 24, 431 p.

GILL, T. N.
1882. Supplementary note on the Pediculati. Proc. U.S. Natl. Mus. 5:551-556.
1904. Extinct pediculate and other fishes. Science (Wash., D.C.) 20:845-846.

GREGORY, W. K.
1933. Fish skulls. A study of the evolution of natural mechanisms. Trans. Am. Philos. Soc. 23:75-481.
1951. Evolution emerging. A survey of changing patterns from primeval life to man. Vol. 1, 704 p. Macmillan, N.Y.

GÜNTHER, A.
1880. Report on the shore fishes procured during the voyage of H.M.S. Ch...lenger in the years 1873-1876. Rep. Sci. Res. Voy. Challenger. Zool. 1(6), 82 p.

HENNIG, W.
1966. Phylogenetic systematics. Univ. Ill. Press, Urbana, 263 p.

KAILOLA, P. J., AND M. A. WILSON.
1978. The trawl fisheries of the Gulf of Papua. Papua New Guinea, Dep. Primary Ind., Fish. Res. Bull. 20:1-85.

LE DANOIS, Y.
1964. Étude anatomique et systématique des antennaires, de l'ordre des Pédiculates. Mém. Mus. Natl. Hist. Nat. Paris, Ser. A, Zool. 31:1-162.
1974. Étude ostéo-myologique et révision systématique de la famille des Lophiidae, (Pédiculates Haploptérygiens). Mém. Mus. Natl. Hist. Nat. Paris, Ser. A, Zool. 91, 127 p.
1979. Révision systématique de la famille des Chaunacidae (Pisces Pediculati). UO [Jpn. Soc. Ichthyol.] 30, 76 p.

MONOD, T.
1960. A propos du *pseudobrachium* des *Antennarius* (Pisces, Lophiiformes). Bull. Inst. Fondam. Afr. Noire 22(Ser. A):620-698.

NORMAN, J. R.
1966. A draft synopsis of the orders, families and genera of recent fishes and fish-like vertebrates. Trustees Br. Mus. (Nat. Hist.), Lond., 606 p.

NYBELIN, O.
1963. Zur morphologie und terminologie des Schwanzskelettes der Actinopterygier. Ark. Zool. 15(Ser. 2): 485-516.

PIETSCH, T. W.
1972. A review of the monotypic deep-sea anglerfish family Centrophrynidae: taxonomy, distribution and osteology. Copeia 1972:17-47.
1974. Osteology and relationships of ceratioid anglerfishes of the family Oneirodidae, with a review of the genus *Oneirodes* Lütken. Nat. Hist. Mus. Los Ang. Cty., Sci. Bull. 18:1-113.
1978. A new genus and species of ceratioid anglerfish from the North Pacific Ocean with a review of the allied genera *Ctenochirichthys*, *Chirophryne* and *Leptacanthichthys*. Nat. Hist. Mus. Los Ang. Cty., Contrib. Sci. 297, 25 p.
1979. Systematics and distribution of ceratioid anglerfishes of the family Caulophrynidae with the description of a new genus and species from the Banda Sea. Nat. Hist. Mus. Los Ang. Cty., Contrib. Sci. 310:1-25.
REGAN, C. T.
1903. A revision of the fishes of the family Lophiidae. Ann. Mag. Nat. Hist., Ser. 7, 11:277-285.
1912. The classification of the teleostean fishes of the order Pediculati. Ann. Mag. Nat. Hist., Ser. 8, 9:277-289.
RASQUIN, P.
1958. Ovarian morphology and early embryology of the pediculate fishes *Antennarius* and *Histrio*. Bull. Am. Mus. Nat. Hist. 114:327-371.
ROSEN, D. E., AND C. PATTERSON.
1969. The structure and relationships of the Paracanthopterygian fishes. Bull. Am. Mus. Nat. Hist. 141: 357-474.
SCHULTZ, L. P.
1957. The frogfishes of the family Antennariidae. Proc. U.S. Natl. Mus. 107:47-105.
TAYLOR, W. R.
1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus. 122(3596), 17 p.
WHITLEY, G. P.
1934. Abstract of proceedings. Proc. Linn. Soc. N.S.W. 59:xxix-xxxix.
1935. Studies in ichthyology. No. 9. Rec. Aust. Mus. 19:215-250.
WINTERBOTTOM, R.
1974. A descriptive synonymy of the striated muscles of the teleostei. Proc. Acad. Nat. Sci. Phila. 125:225-317.
ZIGNO, A. DE.
1887. Nuove aggiunte alla ittiofauna dell'epoca Eocena. Mem. R. Istit. Veneto 23:31 (not seen).

APPENDIX

The osteological evidence presented in this paper is based on the following list of specimens in addition to the lophiiform material listed in previous studies of the osteology and interrelationships of ceratioid anglerfishes (Pietsch 1972: 44, 1974:109, 1979).

Batrachoididae

Batrachoides pacifici (Günther): MCZ 41805, 153 mm.
Daector dowi (Jordan and Gilbert): LACM 31310-19, 1 (of 3), 97 mm.
Porichthys analis Hubbs and Schultz: LACM 22345, 1 (of 2), 125 mm.
Porichthys notatus Girard: LACM 22083, 1, 114.5 mm.
Porichthys porosissimus (Cuvier and Valenciennes): LACM 30727-11, 1 (of 4), 96 mm.

Lophiidae

Lophius americanus Valenciennes: MCZ 51259, 1, 121 mm.
Lophiodes caulinaris (Garman): MCZ 51260, 1, 33.5 mm.
Lophiodes monodi (Le Danois): MCZ 40928, 1, 92 mm.

Antennariidae

Antennarius avalonis Jordan and Starks: UW 20766, 1, 67 mm.
Antennarius maculatus (Desjardins): UW 20767, 1, 64 mm.
Antennarius sanguineus Gill: LACM 8125, 1 (of 2), 76 mm.
Antennarius striatus (Shaw and Nodder): UW 20768, 2, 65 and 67 mm.
Antennatus bigibbus (Latreille): LACM 32611-1, 1 (of 5), 63 mm.
Echinophryne crassispina McCulloch and Waite: NMV A537, 51 mm.
Histiophryne bougainvilli (Valenciennes): NMV A535, 64 mm.
Histrio histrio (Linnaeus): LACM 8975-1, 1 (of 6), 91 mm.
Histrio histrio (Linnaeus): MCZ 51261, 1, 68 mm.
Rhycherus filamentosus (Castelnau): NMV A536, 56 mm.
Tathicarpus butleri Ogilby: AMS IB.3043, 63 mm.
Trichophryne furcipilis (Cuvier): AMS IA.6631, 50 mm.

Tetrabrachiidae

Tetrabrachium ocellatum Günther: AMS IB.7177, 7188, 2, 56 and 61 mm.

Lophichthyidae

Lophichthys boschmai Boeseman: UW 20773, 2, 44 and 47 mm.

Brachionichthyidae

Brachionichthys hirsutus (Lacepede): AMS IA. 6064, 1, 69 mm.
Brachionichthys hirsutus (Lacepede): UW 20769, 1, 42 mm.
Histionotophorus bassani (Zigno): MCZ 5176A + 5176B, 35 mm; MCZ 5177A + 5177B, 37 mm; MCZ 5178, 33 mm.

Chaunacidae

Chaunax pictus Lowe: UW 20770, 1, 90 mm.

Ogcocephalidae

Dibranchus atlanticus Peters: MCZ 51257, 1, 105 mm.
Zalieutes elater (Jordan and Gilbert): LACM 8824-13, 1 (of 3), 98 mm.