

THREE NEW SPECIES OF THE GENUS *MONOGNATHUS* AND THE LEPTOCEPHALI OF THE ORDER SACCOPHARYNGIFORMES

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ABSTRACT

Three new species of the genus *Monognathus*—*M. isaacsi*, *M. ahlstromi*, and *M. jesse*—are described from the Pacific Ocean, bringing the number of the species to six. *M. isaacsi* differs from the other species in having a relatively large head and dark brown pigmentation on the whole body. *M. ahlstromi* has a characteristic paddle-shaped caudal fin, and *M. jesse* has a lanceolate caudal fin. A key to the six species and their distribution in the Pacific and Atlantic are given. Leptocephali of *Monognathus* sp. are identified and described for the first time. The status and relationships of the Monognathidae are discussed.

Metamorphic forms of *Saccopharynx* and *Eurypharynx* are described. The identity of *Leptocephalus latissimus* to *Saccopharynx* and of *L. pseudolatissimus* to *Eurypharynx* is confirmed. An unknown leptocephalus closely resembling that of *Cyema* is described, and the possibility of a new genus in the Cyemidae is suggested. Relationships of the Cyemidae to the Nemichthyidae are refuted, and relationships of the Cyemidae to the Saccopharyngiformes are supported.

The deepsea gulpers of the order Saccopharyngiformes (Monognathidae, Saccopharyngidae, and Eurypharyngidae) are among the most curious and extremely modified bathypelagic fishes, and very little is known about them. Böhlke (1966) reviewed the literature on the attempts to relate them to diverse groups of fishes.

I describe three new species of *Monognathus* (*M. isaacsi*, *M. ahlstromi*, and *M. jesse*) and four metamorphic stages of *Monognathus* sp. A key to the six known species of the genus *Monognathus* is given. This is the first record of the family from the southern, central, and eastern Pacific. The three species of *Monognathus* described by Bertin (1934, 1938) from the Atlantic and Indo-Pacific regions are only juveniles. The lack of adult monognathids even led Böhlke (1966) to suspect that the then known monognathids might be postlarval saccopharyngids. The specimen named as *M. isaacsi* is in a more advanced stage than any of the other specimens of the six species. Many of its features clearly indicate that this family is distinct from the Saccopharyngidae. A leptocephalus stage in the life history of *Monognathus* is reported for the first time. Information on the ethmoid tooth, food, and distribution of *Monognathus* is given. The status and relationships of the family Monognathidae to the Saccopharyngiformes are discussed.

Two metamorphic forms, one belonging to *Saccopharynx* and the other to *Eurypharynx*, are described, and *Leptocephalus latissimus* Schmidt 1912 is assigned to *Saccopharynx* and *L. pseudolatissimus* Bertin 1934 to *Eurypharynx*.

An unknown leptocephalus closely resembling that of *Cyema* is described from the North Pacific, and the possibility of a new genus in the Cyemidae is suggested. The relationship of the Cyemidae to the Nemichthyidae is questioned, and its relationship to the Saccopharyngiformes is supported.

MATERIALS AND METHODS

The account is based on the study of one fully transformed juvenile, two early juveniles, and four metamorphic forms of the genus *Monognathus* collected from the central and eastern North Pacific during the Tethys (1960), CalCOFI (1962), and Scan (1969) expeditions. One specimen of *Leptocephalus latissimus* was obtained from the San Diego Trough (1950) and its metamorphic form off Baja California. A metamorphic form of *Eurypharynx pelecanoioides* was collected from the central North Pacific during the Styx expedition (1968). All the specimens were collected by the 10-foot Isaacs-Kidd midwater trawl (IKMT). Total length and body depth were measured with dial calipers, and measurements of head, snout, and eye were taken by ocular micrometer following the methods of Castle (1963). Some specimens

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were dissected. Drawings were made with the aid of a projector and camera lucida. All the holotypes are presently housed in the Marine Vertebrates Collection of the Scripps Institution of Oceanography.

Names: The new species of the genus *Monognathus* are named for John D. Isaacs of the Scripps Institution of Oceanography (SIO), La Jolla; Elbert H. Ahlstrom of the Southwest Fisheries Center, National Marine Fisheries Service, La Jolla; and Jesse N. Raju, wife of the author (noun in apposition).

KEY TO THE SPECIES OF THE GENUS *MONOGNATHUS*

- | | | |
|--|---|-----------------------|
| 1a. Pectoral fin present | 2 | |
| 1b. Pectoral fin absent | 3 | |
| 2a. Head large, about 13.3 in total length, caudal fin normal | | <i>M. isaacsi</i> |
| 2b. Head small, about 9 in total length, caudal fin lanceolate | | <i>M. jesse</i> |
| 3a. Caudal fin normal, vertebrae long | 4 | |
| 3b. Caudal fin either whiplike or paddle shaped, vertebrae short | 5 | |
| 4a. Vertebrae 94, teeth in mandible 8, adipose region of dorsal fin with 48-63 rays | | <i>M. jespersenii</i> |
| 4b. Vertebrae 88, teeth in mandible 12, adipose region of dorsal fin with 36-48 rays | | <i>M. bruuni</i> |
| 5a. Caudal fin whiplike, dorsal commences on myotome 3, two ethmoid teeth | | <i>M. taningi</i> |
| 5b. Caudal fin compressed, paddle shaped, dorsal commences on myotome 13, one median ethmoid tooth | | <i>M. ahlstromi</i> |

MONOGNATHUS ISAACSI SP. N.

Figures 1D, I; 2O

Holotype: SIO 69-353, western North Pacific, 32°02.3'N-32°07.9'N, 156°07.0'E-156°06.7'E, depth of capture 0-950 m, IKMT, 1(56 mm), 2 June 1969.

Description: Body elongate, compressed except at head. Trunk clearly marked from tail, 2.9 in total length. Maximum depth at middle of

body, 10.3 in total length. Head large, 7.6 in total length. Snout moderately long, 2.4 in head. Olfactory organ rudimentary, a short curved tube open at both ends. Eyes tubular, small, 18.7 in head. Upper jaw soft, maxilla not recognizable, no upper teeth. Skin inside of mouth dusted with melanophores. Median ethmoid tooth projects below level of lips, visible from side. Lower jaw slightly longer than upper jaw, with four small teeth. Mouth large, gape reaching far behind eye. Postorbital distance 1.7 in head. No branchiostegals recognizable. Gill opening small, ventrolateral. About 75 myotomes could be counted and another 25-30 are estimated for a total of about 100. Tail blunt at tip. Stomach bulging, extending beyond trunk as a sac. Dorsal fin high, originating behind gill openings, with 80 unsegmented rays. Predorsal distance 3.7 in total length. Anal fin high, originating behind vent, with 52 unsegmented rays. Preanal distance 1.5 in total length. Pectoral fins small, rays not distinct.

Pigmentation: Uniformly dark brown.

Remarks: This is the first known specimen of the Monognathidae with complete body pigmentation. The absence of an upper jaw and the presence of an ethmoid fang indicate that *M. isaacsi* is properly referable to the Monognathidae. Of all the members of the Saccopharyngiformes so far known, this species represents the most generalized form except for the reduced eye, presence of the enlarged ethmoid fang, and absence of the upper jaw. The shape of the body, the head with its long snout and large mouth, the nature of the median fins, and the presence of pectoral and absence of ventral fins are typical of eels. In *Eurypharynx* and *Saccopharynx* the mouth is enlarged and the suspensorium highly modified, and in *Saccopharynx* the tail is whip-like. The snout in these genera is reduced whereas it is long in *M. isaacsi*.

The meristic and morphometric characters of the three species described by Bertin (1938) and the three new species described in this account are given in Table 1. The relative lengths of the head, cranium, snout, and predorsal distance are the highest in *M. isaacsi*. The head is depressed. The teeth in the lower jaw are different in shape and fewer in number than in other species. The median ethmoid tooth is long and projects into

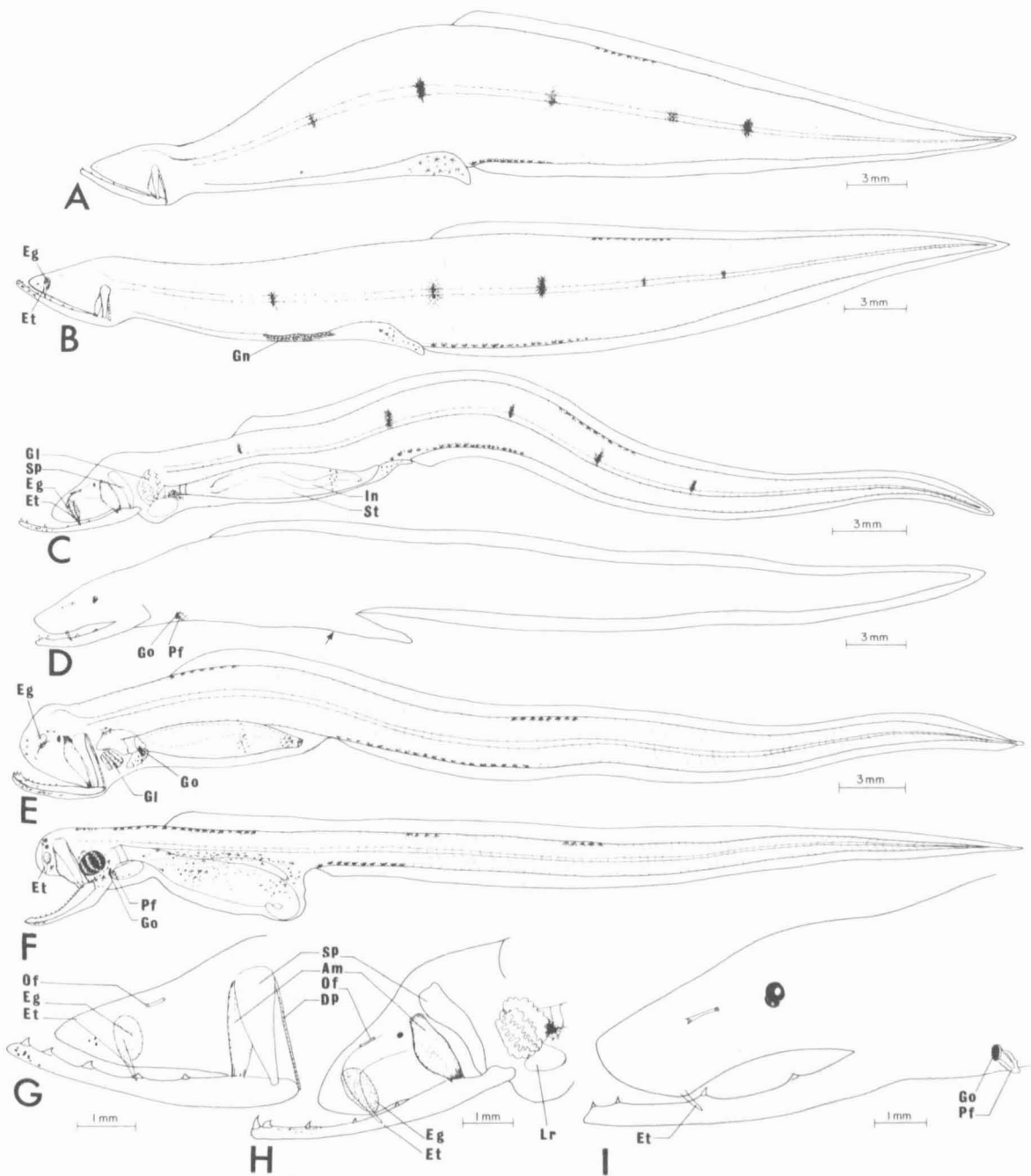


FIGURE 1.—A-C, metamorphic stages of *Monognathus* sp.: A, 42 mm TL; B, 48 mm TL and G, its head; C, 42.2 mm TL and H, its head. D, *M. isaacsi* and I, its head; E, *M. ahlstromi*; F, *M. jesse*. Am, adductor mandibulae; Dp, depressor; Et, ethmoid tooth; Eg, ethmoid gland; Ey, eye; Gl, gills; Go, gill opening; Gn, gonad; In, intestine; Lr, liver; Of, olfactory organ; Pf, pectoral fin; Sp, suspensorium; St, stomach.

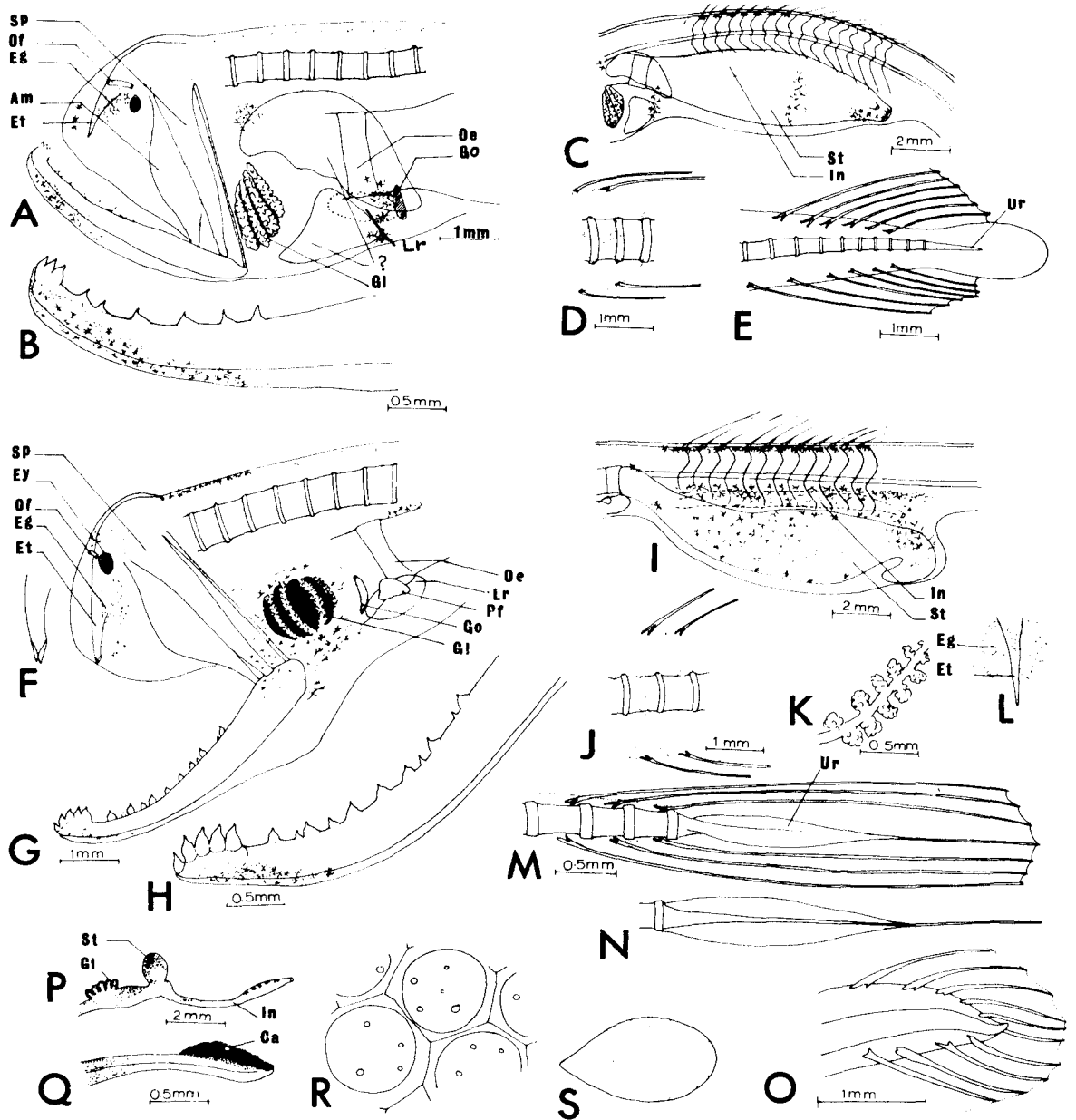


FIGURE 2.—A-E, *Monognathus ahlstromi*: A, head; B, lower jaw; C, midbody; D, vertebrae and myotomes; E, tail. F-N, *M. jesse*: F, ethmoid tooth; G, head; H, lower jaw; I, midbody; J, vertebrae of myotomes; K, gill arch; L, ethmoid gland and tooth; M, tail; N, dorsal view of urostyle. O, caudal fin of *M. isaacsi*. P, gut and Q, tail of metamorphic *Eurypharynx*. R, portion of the ovary of and S, ovary of adult *Eurypharynx*. Am, adductor mandibulae; Ca, caudal organ; Dp, depressor; Et, ethmoid tooth; Eg, ethmoid gland; Ey, eye; Gi, gills; Go, gill opening; In, intestine; Lr, liver; Oe, esophagus; Of, olfactory organ; Pf, pectoral fin; Sp, suspensorium; St, stomach; Ur, urostyle.

TABLE 1.—Morphometric and meristic characters of the species of the genus *Monognathus*.

Item	<i>taningi</i>	<i>bruuni</i>	<i>jesperseni</i>	<i>ahlstromi</i>	<i>jesse</i>	<i>isaacsi</i>
Total length (mm)	56	80	109	48.5	63	56
Percentage of total length:						
Depth	3.9	5.9	4.6	9	8	9.6
Predorsal distance	7.7	35 ¹	13.8	13.2	11.9	19.5
Preanal distance	25	38.7	35.8	27.6	25.4	34.0
Head	8	10	9.1	10.7	9	13.3
Cranium	5	3.9	3.2	4.3	4.9	7.9
Percentage of head length:						
Snout	—	—	—	19	21.4	41.3
Eye	—	—	—	5.5	8.9	5.2
Suspensorium	70	56.2	65	63	57	—
Mandible	122	75	85	83	89	84
Number of vertebrae or myotomes	95(23)	88(26)	94(25)	113(31)	104(26)	115(24)
Dorsal fin rays	120	74	97	90	80	80
Anal fin rays	60	42	97	60	54	52
Teeth in mandible	8	12	8	9	16	4
Predorsal myotomes	3	12	11	13	11	—
Preanal myotomes	24	30	29	32	27	—

¹The predorsal distance given by Bertin is obviously wrong as the dorsal originates on myotome 12.

the mouth, but it does not do so in other species. There is a small pectoral fin. The vertebrae are weakly ossified, not distinct in radiographs, but about 75 myotomes could be counted, and about 30-35 more are estimated on the basis of the size of the myotomes. Differences of this magnitude could well indicate generic separation, but I hesitate to introduce new genera in this poorly known group.

MONOGNATHUS AHLSTROMI SP. N.

Figures 1E; 2A-E

Holotype: SIO 63-405, eastern North Pacific, 34°57.0'N, 129°19.0'W, 0-2,000 m, IKMT, 1(48.5 mm), 29 Mar. 1962.

Description: Body compressed except at head, very delicate, covered with loose semitransparent skin. Preanal region 3.6 in total length, very deep due to voluminous stomach. Tail (postanal region) very narrow, 1.3 in total length, tapering gradually to a point. Maximum depth before anus, 11.0 in total length (may vary according to quantity of contents of stomach). Head deep, large, 9.0 in total length; cranium very small and weak. Snout small, 5.4 in head, membranous. Olfactory organ reduced, a small curved tube open at both ends. Eye rudimentary, oval, vertical length 18.0 in head, lens round, extremely small. Gape of mouth reaching far beyond eye. Region of upper jaw membranous, devoid of teeth, no maxilla

distinguishable. Ethmoid tooth short, hollow, tip sharp and bifid, and does not project into mouth as in *M. isaacsi*; it appears as though it is lodged in a sheath and comes out of the sheath through an opening on the membranous palate only when pressed. Ethmoid glands paired, oval (0.8 mm × 0.4 mm) on either side of tooth. Lower jaw long, 9.7 in total length, tip armed with three sharp closely packed teeth followed by series of six pointed, equally spaced, triangular teeth. Opercular bones and branchiostegals absent. Gills four, covered by delicate transparent membrane. Gill filaments short, foliaceous. Gill openings ventrolateral, moderate in size. Pectoral fin absent. Myotomes 28 + 85 = 113, W-shaped. Esophagus short, followed by thickened girdle-like region. Stomach large, bulging with opening just posterior to anus. This opening of the stomach appears to be a structural feature and not a wound associated with capture. Intestine a narrow straight tube on right side of body, opening to exterior on right side. Liver small and lobular. Dorsal fin originating on myotome 14, moderately high, 90 unsegmented rays. Caudal fin represented by an enlarged, paddlelike structure without fin rays. Vertebral centra short.

Pigmentation: No trace of any larval mid-lateral pigmentation. A few dendritic melanophores on snout and lower jaw. Dendritic melanophores around esophageal and liver region inside body and on body wall in stomach and anal

regions. Dendritic, deep pigmentation at base of dorsal fin on myotomes 14-20 and 50-57, and on anal fin on myotomes 32-51.

Remarks: This species differs from all the three species of *Monognathus* described by Bertin (1938) and from *M. jesse* described in this account in having a high myotome count of 113. The structure of the caudal fin also is different. In *M. bruuni* and *M. jespersenii* the urostyle is produced into a needlelike structure forming a false caudal fin along with the dorsal and anal fin rays. In *M. tanningi* the urostyle is produced into a very long, whiplike structure. The urostyle in this species is spinelike, surrounded by a large paddle-shaped, compressed structure. The ethmoid tooth is small and does not project into the mouth. If Bertin's (1938) observations are correct, this species differs from the above three species also in having four gills as only one gill was figured in his drawings. There is a series of three closely packed teeth at the tip of the lower jaw, and such a series is not seen in the forms described by Bertin.

MONOGNATHUS JESSE SP. N.

Figures 1F; 2F-N

Holotype: SIO 60-245, central North Pacific, 12°07.1'N-12°23.8'N, 148°35.1'W-148°18.0'W, 0-2,100 m, IKMT, 1(63 mm), 9-10 July 1960.

Description: Body compressed except at head. Preanal region deep due to voluminous stomach, preanal region 3.9 in total length. Postanal region 3.6 in total length, tapering to point. Body covered with loose semitransparent skin. Maximum depth at middle of preanal region, 12.6 in total length. Head deep, large, 8.7 in total length. Snout blunt, membranous, small, 4.7 in head. Olfactory organ a slightly curved short tube, open at both ends. Eye rudimentary, 11.2 in head, oval, lens extremely small. Gape of mouth reaching beyond eye. Upper jaw degenerate, membranous, unsuitable to serve as jaw, no maxilla recognizable, no teeth. Median ethmoid tooth large, pointed, tip calcified and bifid, surrounded and hidden by soft tissue. Ethmoid glands paired oval bodies, one on either side of tooth. Lower jaw long, slightly

curved, tip armed by 5 closely packed large teeth followed by 11 teeth of characteristic shape. No opercular bones or branchiostegals recognizable. Gills four, small, but proportionally larger than those of *M. ahlstromi*. First gill slit smallest, second and third largest, last gill slit slightly larger than first. Gill filaments short and foliaceous, alternately on either side. First three gills holobranchs, fourth a hemibranch. All gills covered by membranous operculum. Gill opening vertical, moderate in size, in front of pectoral fin. Myotomes W-shaped, 26 + 78 = 104. Vertebrae heavy, shorter in length in trunk region, slender and elongate in tail region. Esophagus short with opaque girdlelike region. Stomach voluminous, recurved at end. Intestine a straight tube, shorter than stomach, situated on right side of stomach. Liver lobular. Pancreas and heart lost due to damage. Dorsal fin originates on myotome 11, relatively high, with 80 unsegmented rays. Anal fin originates on myotome 30, with 54 unsegmented rays. Urostyle depressed, lanceolate, with middorsal ridge. Pectoral fin small, triangular, rays indistinct.

Pigmentation: Brown chromatophores on snout, tip of lower jaw, at angle of mouth. Dendritic brown chromatophores on head, predorsal region, gill membrane, lateral side of body as far back as anal region. Three deeply seated melanophore patches (seen only if cleared in glycerine) at base of dorsal fin inside myotomes, one long patch on myotomes 5-22, second on myotomes 40-43, and third on myotomes 58-62. Anal fin has similar large patch on myotomes 30-39.

Remarks: This species differs basically from the three species described by Bertin (1938) and from *M. ahlstromi* in the presence of a small pectoral fin, structure of the urostyle, myotome number, dentition of the lower jaw, relatively longer tail, and fin ray counts. Bertin (1938) gave no account of the pigmentation of his specimens, hence it is not possible to compare pigmentation. The pigmentation in this specimen differs from that of *M. ahlstromi* in the following respects. There is additional pigmentation on the head, angle of the lower jaw, and gill membrane, more profuse pigmentation on the lateral side of the body and predorsal region, and three patches at the base of the dorsal fin.

METAMORPHIC FORMS OF *MONOGNATHUS* SP.

Figure 1A, B, C, G, H

SIO 60-241, central North Pacific, 7°25.5'N-7°55.0'N, 144°29.0'W-144°35.0'W, depth of capture 0-2,100 m, IKMT, 1(42.2 mm), 7 July 1960. SIO 60-276, central North Pacific, 24°28.9'N-24°36.9'N, 147°55.5'W-147°27.0'W, 0-3,000 m, IKMT, 1(48 mm), 7-8 Aug. 1960. SIO 60-275, central North Pacific, 23°23.4'N-23°40.0'N, 151°04.0'W-150°38.8'W, 0-3,000 m, IKMT, 1(58 mm), 6 Aug. 1960. SIO 60-283, eastern North Pacific, 28°13.0'N-28°19.1'N, 135°21.8'W-134°54.1'W, 0-3,000 m, IKMT, 1(50 mm), 12 Aug. 1960.

Description (Figure 1B, G): Total length 48 mm, body elongate, compressed, and transparent. Depth 12.0 in total length, maximum depth at middle of body. Head long. Cranium weak, triangular, 10.7 in total length. Snout slightly blunt. Olfactory organ rudimentary, a small curved tube open at both ends. Eyes lost due to damage. Upper jaw membranous, without teeth. Ethmoid tooth long, projecting into mouth. Ethmoid gland paired, well developed. Lower jaw 8.6 in total length. Suspensorium 24.0 in total length. Adductor mandibulae well developed. Gills, liver, and part of gut damaged and lost. Posterior region of gut projects out of body outline. Opisthonephros a coiled tube extending behind vent (not shown in figure). Ovaries tubular, elongate, with few ova (250-300). Dorsal originates on myotome 32 and anal on myotome 30. Myotomes W-shaped, 30 + 83 = 113. Midlateral brown, chromatophore patches conspicuous, one on left and four on right side. Brown chromatophores on tip of upper and lower jaws, at base of dorsal fin rays on myotomes 50-60, and anal fin rays on myotomes 31-49. Juvenile pigmentation appears on body as minute, uniformly scattered brown chromatophores (not shown in figure).

Changes during metamorphosis: Most of the morphological changes undergone are similar to those observed in the metamorphosis of the eels. In the smallest specimen (42 mm, Figure 1A) the body is deeper, and the lower jaw and suspensorium are relatively shorter. A median ethmoid tooth is not yet formed. In later stages

(48 mm, 50 mm, 42.2 mm; A, B, C of Figure 1, respectively) there is a slight decrease in the length and depth of the body, and increase in the length of the head, snout, lower jaw, and suspensorium. A median ethmoid tooth is formed with its associated gland. Larval midlateral pigmentation begins to fade with the gradual development of juvenile pigmentation. The dorsal and anal fins move slightly forward. Two specimens have developed a pair of tubular ovaries containing about 250-300 spherical ova 0.06 mm in diameter (not shown in figure). An interesting aspect of the metamorphosis of monognathids is the degenerative changes that take place in the head, olfactory organ, and eye. The bones of the head become very weak and membranous. The eye and the olfactory organs are reduced to minute structures. A median ethmoid tooth with a pair of glands develops. The wide W-shaped myotomes become narrower with the decrease in the depth of the body, and in the larval condition they may approach a V-shape as in *Cyema* and *L. latissimus* and *L. pseudolatissimus*.

Remarks: The four metamorphic stages described above are assigned to *Monognathus* sp. on the basis of the characteristic median ethmoid tooth and the absence of an upper jaw. These stages share some features with *M. isaacsi* such as general shape of the body, large head, projecting ethmoid tooth, myotome number, and structure of the tail. But *M. isaacsi* has a pectoral fin which is not seen in the metamorphic forms. Assignment to the species is not possible at this time.

The leptocephali of monognathids are not identified as yet. But the features of metamorphic forms (Table 2) indicate that they are small (40-60 mm), elongate larvae with a series of five splanchnic, unequally placed, midlateral melanophores with pigmentation on the gut, and with about 100-120 wide V-shaped myotomes.

GENERAL REMARKS

Upper jaw: The name Monognathidae was given to these fishes by Bertin (1937a), who assumed that only one jaw (lower jaw) was present. But Tchernavin (1947b) pointed out that there is no evidence that a palatopterygoid cartilage is absent in the Monognathidae. As all

TABLE 2.—Number and position of midlateral melanophores in five metamorphic monognathids and Pacific leptocephalus.

Metamorphic monognathids and Pacific leptocephalus	Total number myotomes	Left side melanophores	Right side melanophores	Total number melanophores (pre + postanal)	Distribution of chromatophores on myotomes R = Right, L = Left
42-mm specimen	31 + 80 = 111	2	3	2 + 3 = 5	(15-16)R, (29-30)L, (44-45)R, (59-60)R, (67-68)L
48-mm specimen	30 + 83 = 113	1	4	1 + 4 = 5	(15-16)R, (32-33)R, (45-46)L, (57-58)R, (67-68)R
58-mm specimen	30 + 75 = 115	2	3	1 + 4 = 5	(12-13)L, (31-32)R, (46-48)R, (56-58)R, (70-71)L
50-mm specimen	31 + 82 = 113	3	2	2 + 3 = 5	(15-16)L, (28-29)L, (44-45)R, (55-56)R, (67-68)L
42.2-mm specimen	24 + 81 = 105	4	1	2 + 3 = 5	(9-10)R, (27-28)L, (43-44)L, (55-56)L, (67-68)L
Pacific leptocephalus	56 + 46 = 102	4	1	4 + 1 = 5	(13-14)L, (25-26)L, (40-41)L, (50-51)L, (59-60)R

other known leptocephali possess a maxilla with larval teeth until metamorphosis, monognathid leptocephali also possibly have a maxilla bearing larval teeth. Leptocephali of eels characteristically lose their larval teeth during metamorphosis, and the adult teeth develop after metamorphosis. Hence it is possible that monognathid leptocephali might have possessed the maxilla with its larval teeth which might have been lost during metamorphosis. Due to the extreme degenerative changes and deossification of the skull the maxilla might have lost its identity and the adult set of teeth failed to develop.

Median ethmoid tooth: The median ethmoid tooth is a structure unique to the Monognathidae, and its function is not known. It develops during metamorphosis and persists in the adult. It is larger in *M. isaacsi* than in other species. It is hollow and slightly curved with a minute opening at its sharp tip. There is a pair of glandular masses, one on each side of the tooth. The ethmoid tooth with its gland closely resembles the fangs of a poisonous snake and probably serves a similar function.

Gills: Only one gill arch is present in the monognathids according to Bertin (1937a). But a close examination of *M. ahlstromi* and *M. jesse* showed four distinct gill arches bearing short foliaceous gill filaments arranged alternately as in *Eurypharynx*. The gills and gill openings are very small as are those of *Eurypharynx* and *Saccopharynx*.

Pectoral fin: The pectoral fin is absent in the three species described by Bertin (1937a) and in *M. ahlstromi*. There is a small fleshy pectoral fin in *M. isaacsi* and *M. jesse*.

Caudal organ: A caudal organ, whose function is much disputed, is present at the tip of the tail in *Eurypharynx* and *Saccopharynx*. Although a typical caudal organ is not present in any of the known species of the monognathids, the caudal fin is modified either into a filamentous structure as in *M. taningi*, or into a flattened structure as in *M. ahlstromi* and *M. jesse*, or is relatively unmodified as in *M. isaacsi*.

Food: Fish eggs with a sculptured egg membrane, fish larvae, and copepods were found in the mouth and pharynx of the metamorphic forms, but they might have been taken accidentally while in the net.

Distribution (Figure 3): This family has previously been known only from the Atlantic off the coast of North Africa and from the western Pacific (Bertin, 1938). This study shows that it is widely distributed in the whole tropical and subtropical belt of the Pacific, and it is likely that the family may also be found in the tropical Indian Ocean.

RELATIONSHIPS

Bertin (1937a, 1938) erected the family Monognathidae based on his study of four juveniles.

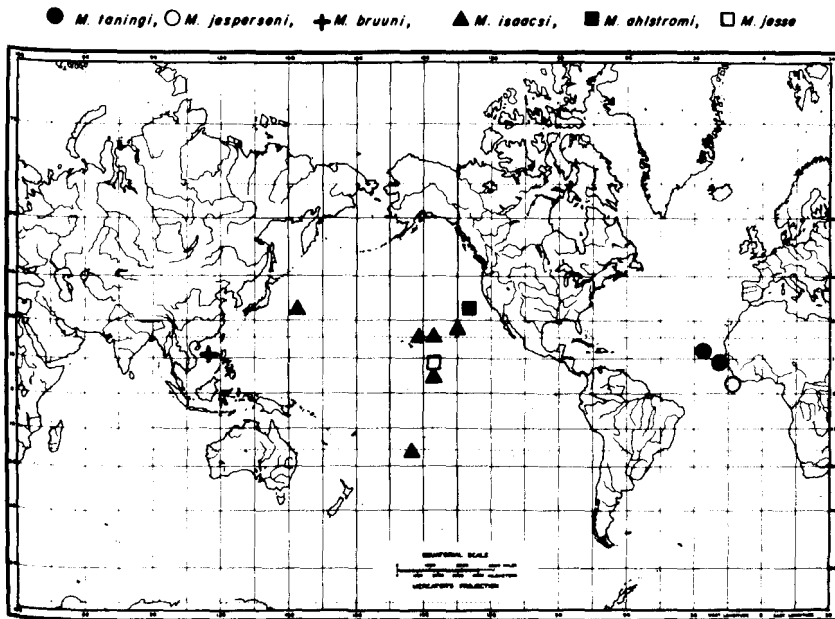


FIGURE 3.—Distribution of the six species of the genus *Monognathus*.

One of the four specimens had been earlier described by Roule (1934) as a semilarva of the *Lyomeri*. According to Bertin the family Monognathidae consists of a single genus, *Monognathus*, with three species, none of which was designated as the genotype. Myers (1940) recognized two genera, *Monognathus* (genotype *M. taningi* Bertin) and *Phasmatostoma* (new genus; genotype *M. jespersenii* Bertin), on the basis of the number of ethmoid teeth, position of the dorsal fin origin, and nature of the vertebrae and caudal fin. Böhlke (1966) accepted *Phasmatostoma* as a separate genus of the Monognathidae. As already pointed out, *M. isaacsi* may well represent a third genus of the family Monognathidae as the differences between *M. isaacsi* and *M. taningi* are even more pronounced than those between *M. taningi* and *M. jespersenii* or *M. bruuni*, which are separated as *Phasmatostoma*. *M. ahlstromi* and *M. jesse* may also turn out to be new genera as the caudal fin, which is a conservative structure in fishes, varies greatly in the two fishes. However, I would restrain myself to introduce new genera till a detailed study of many adult and larval specimens is undertaken, as the studies on these fishes are based only on very few specimens (1-2 in number), and even these are only juvenile and metamorphic forms.

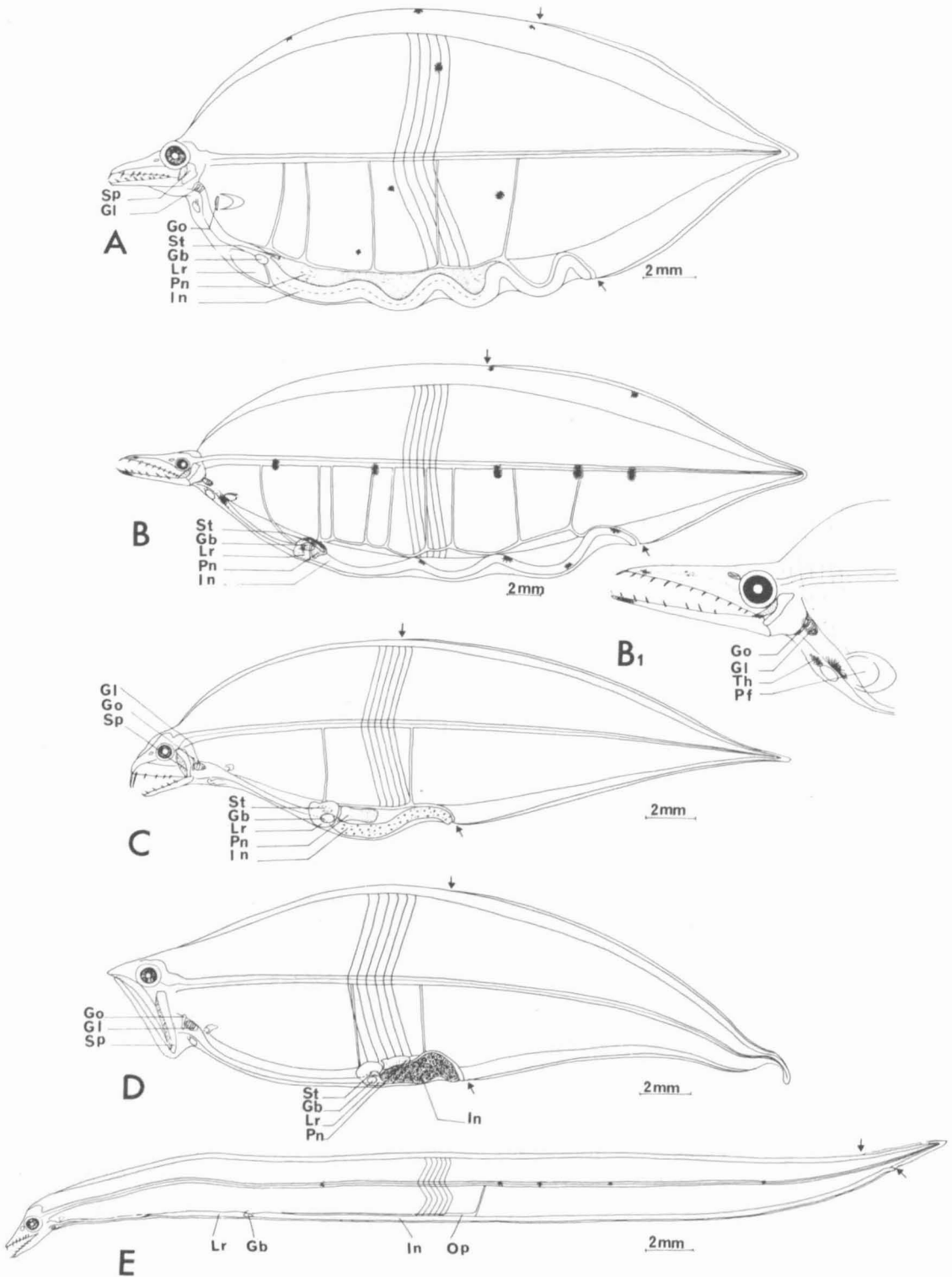
Tchernavin (1947a) stated that there is no evidence that the Monognathidae are related to the Saccopharyngiformes. His arguments were based

on some of the observations of Bertin such as the absence of pectoral fin, presence of only one gill arch, and other osteological characters. Greenwood et al. (1966) and Böhlke (1966) considered monognathids to be related to the Saccopharyngiformes. The general features of *M. isaacsi*—such as the elongated suspensorium, presence of small gill openings and four small gill arches, alternating arrangement of gill filaments on the arch as in *Eurypharynx*, voluminous stomach, occurrence of leptocephalus stage in the life history, the presence of the pectoral fin, and the modified caudal fin—indicate that the Monognathidae are related to the Saccopharyngiformes, more closely to the Saccopharyngidae than to the Eurypharyngidae.

LEPTOCEPHALUS LATISSIMUS SCHMIDT 1912

Figure 4C

Leptocephalus latus Schmidt 1909. SIO 66-353, San Diego Trough, 32°40'N, 117°35'W, 480-366 mwo, Tucker net, 1(30 mm), 23 Aug. 1950. LACM, 6525-16, Santa Catalina Basin, 33°18'27"N-33°24'40"N, 118°44'00"W-118°51'35"W, 0-213 mwo, IKMT, 1(39 mm), 22 Aug. 1963. LACM, 9830-10, No Name Basin, 32°01'30"N-32°04'00"N, 117°59'00"W-117°56'00"W, 600 mwo, IKMT, 1(40 mm), 28 July 1967.



Description: Specimen described (SIO 66-353): Body deep, compressed except at head, total length 30 mm. Maximum depth in middle of body, 3.8 in total length. Posterior end of body attenuate, caudal organ not yet developed. Head short, 7.5 in total length. Skull membranous and transparent. Snout short, 4.0 in head. Olfactory organ rudimentary. Eyes round, dark brown, 5.7 in head. Upper jaw soft, maxilla indistinct. Lower jaw partly damaged. Teeth six in upper jaw, five in lower jaw. Gill opening small, four gill arches. Pectoral fin small, thick. Esophagus a narrow tube, reaching middle of body. Stomach rudimentary. Intestine short, swollen, looped. Liver a small ventral lobe. Pancreas rectangular, dorsal to gut. Opisthonephros a short tube. Myotomes 45 + 125 = 170.

Pigmentation: Minute dark brown chromatophores on swollen part of intestine.

LEPTOCEPHALUS PSEUDOLATISSIMUS BERTIN 1934

Figure 4D

Leptocephalus gastrostomi bairdii Lea 1912.

Leptocephalus pseudolatissimus Bertin 1934.

Material examined: SIO 56-127, Marshall Islands vicinity, western Pacific, 1(32 mm).

Description: Body deep, compressed except at head, posterior end tapering. Maximum depth in the middle of body, 4.0 in total length. Head large, very deep, 7.6 in total length. Skull bones transparent and membranous. Teeth in both jaws lost due to damage. Gill opening small, gill arches five in number. Pectoral rudimentary. Esophagus a narrow tube. Stomach small. Liver a small ventral lobe. Pancreas rectangular. Opisthonephros a short tube. Myotomes 38 + 65 = 103.

Pigmentation: Dense brown pigmentation in the form of small patches on the swollen part of the intestine.

FIGURE 4.—A, leptocephalus of *Cyema atrum*; B, unknown Pacific leptocephalus; Bl, head of unknown Pacific leptocephalus; C, *Leptocephalus latissimus*; D, *Leptocephalus pseudolatissimus*; E, leptocephalus of *Nemichthys scolopaceus*. Gb, gall bladder; Gl, gills; Go, gill opening; In, intestine; Lr, liver; Op, opisthonephros; Pf, pectoral fin; Sp, suspensorium; St, stomach; Th, thyroid gland?; Pn, pancreas.

Remarks: *Leptocephalus latissimus* and *L. pseudolatissimus* resemble each other in many characters except for the differences in myotomal count, number of gill arches, length and number of intestinal loops, and pigmentation. *L. latissimus* has a higher myotomal count ranging from 170 to 250 and four gill arches whereas *L. pseudolatissimus* has 103-125 myotomes, five gill arches, a short intestinal loop, and more pigmentation on the loop.

Murray and Hjort (1912) discovered the leptocephalus stage in the life history of Saccopharyngiformes. The larva was later described by Lea (1913), who named it *Leptocephalus gastrostomi bairdii* (*Gastrostomus bairdii* = *Eurypharynx pelecanooides*) and suggested that *L. latissimus* Schmidt (1909, 1912) was a larva of another saccopharyngiform. Bertin (1938) described a series of four saccopharyngiforms and assigned both *L. latissimus* and *L. pseudolatissimus* to *Saccopharynx* on the basis of the nature of suspensorium and myotomal counts. The lowest myotomal count in his larvae was 115, and since the highest vertebral count of *Eurypharynx* known to him at that time was 110, he assigned the larvae to *Saccopharynx* as the number exceeded the highest vertebral count of *Eurypharynx*. It is now known that the vertebral count of *E. pelecanooides* ranges from 103 to 125 (Orton, 1963). Tchernavin (1947a) disputed Bertin's allocation of larvae of *Saccopharynx* on the basis of myotomal count and suggested that the low count forms might belong to *Eurypharynx* and the high count forms to *Saccopharynx*. Orton (1963) and Böhlke (1966) also suggested the identity of *L. pseudolatissimus* with *Eurypharynx* on the basis of vertebral counts (97-125).

METAMORPHIC FORM OF SACCOPHARYNX

(Not illustrated)

LACM 9579-36, 30°00'00"N-29°30'21"N, 118°40'59"W-118°29'18"W, 2,910 mwo, IKMT, 1(80 mm), 30 Aug. 1966.

Description: Body elongate, posterior region whiplike. Head large, depressed, 14.3 in total length. Snout small, 4.7 in head. Olfactory organ small, two nostrils placed closely one above the other in front of eye. Eye small, 7.0 in head.

Jaws unusually long, with minute recurved teeth on both jaws. Gills plumose. Esophagus short, thin, no girdlelike region. Stomach well developed, empty, white. Intestine long, thick walled, empty, posterior end with series of 12 melanophores on dorsal side till vent. Posterior end of intestine of metamorphic *Eurypharynx* also has similar series of five melanophores on dorsal side. Liver elongate, pale yellow. Gall bladder oval, thin, transparent. About 40 preanal and 110 postanal myotomes can be counted. Myotomes in whiplike portion of tail are not distinct. Tip of tail (caudal organ) enlarged into bulblike structure. Median fin delicate, low. Pectoral fins large, fleshy.

Pigmentation: Microscopic brown dotlike juvenile pigmentation scattered sparsely all over body, but dense on snout and jaws. Larval pigmentation before vent as a row of linear patches. Tip of tail unpigmented.

METAMORPHIC FORM OF *EURYPHARYNX PELECANOIDES*

Figure 2P, Q

SIO 68-451, central North Pacific, Hess Seamount, 17°59.0'N, 174°24.1'W, 0-1,250 m, IKMT, 1(39 mm), 31 Aug.-1 Sept. 1968.

Description: Body elongate, compressed except at head. Depth 8.0 in total length, maximum depth near middle of body, posterior half tapering gradually to whiplike tail with rudimentary caudal organ (Figure 2Q). Head small, broad, depressed, badly damaged. Snout very short, blunt. Eyes large, round, black. Olfactory organ rudimentary. Upper jaw cartilaginous, maxilla toothless, its boundary not clear. Lower jaw lost due to damage. Gills extremely small, five holobranchs, six gill slits, white in color, gills of both sides placed very close together, gill filaments very small, gill arches very soft, and do not appear to have any bony or cartilaginous elements. Esophagus short, slightly bulged, brown, followed by rudimentary stomach (Figure 2P). Stomach bulged, muscular, with brown pigment. Liver lost due to damage. Intestine short, continued as rectum with five black dendritic chromatophores on dorsal side. Opisthonephros lost due to damage.

Myotomes about 105. Dorsal and anal fins damaged.

Pigmentation: Body covered uniformly with dark brown juvenile pigmentation. Tip of tail white except for black caudal organ.

Ovary of adult (Figure 2R,S): Examination of the ovary of one large specimen of *E. pelecanoioides* (600 mm, vertebrae 31 + 87 = 118) in the Scripps Institution of Oceanography (group 25, H.52.376) gives the following information. Ovary large, oval, paired, brown in isopropyl alcohol, two ovaries of same size, 62.2 mm in length, 29 mm in breadth, oval in shape, maximum thickness in center 10 mm, weight of two ovaries 18.4 g, about 33,000 ova in both ovaries, eggs arranged in single layer which is folded into laminae of double layers. Thus, each ovary is a long sheet of ova. Ova embedded in sheet of jellylike mass divided into hexagonal meshes, each mesh enclosing single ovum. Ova well developed, round, average diameter 0.9 mm, yellow, containing 4 or 5 yellow oil globules of varying sizes, diameter of largest oil globule 0.15 mm.

Remarks: The two metamorphic forms *L. latissimus* and *L. pseudolatissimus* were badly damaged and distorted, making it very difficult for illustration. But characters such as pigmentation and the caudal organ provided some information on their identity to the adults.

The metamorphic specimen of *L. pseudolatissimus* has juvenile pigmentation, and the caudal organ is well developed and is more advanced than the larvae described before. The myotomal count, the number of gill arches, the position and structure of the caudal organ, the juvenile pigmentation, and other characters clearly establish the identity of *L. pseudolatissimus* as the larva of the deepsea gulper *Eurypharynx pelecanoioides*.

The higher myotomal count of *L. latissimus* certainly indicates its identity with *Saccopharynx*, as suggested by Tchernavin (1947a). Orton (1963), in discussing the relationship of *L. latissimus*, pointed out its possible identity as the larva of *Saccopharynx* but also warned that the then unknown monognathid larva might be a possible candidate for *L. latissimus*. The characters of the metamorphic monognathid and saccopharyngid

larvae described in this account help to identify *L. latissimus* as the larva of *Saccopharynx*. Böhlke (1966) pointed out that the similarities between saccopharyngids and monognathids might warrant consideration of monognathids as postlarval saccopharyngids. The characters of the metamorphic *Saccopharynx* and *M. isaacsi* do not support his contention. The ethmoid tooth persists into the fully transformed stage in monognathids (*M. isaacsi*), but it is absent in the metamorphic *Saccopharynx*. A girdlelike region is present on the esophagus, and the liver is a short lobe in monognathids, whereas no girdlelike region is present; the liver is elongate, and the tail is extremely attenuate and whiplike in metamorphic *Saccopharynx*.

A new type of saccopharyngiform larva has been recently studied (Castle and Raju, unpublished data), and the details will be published elsewhere. This larva (myotomes $62 + 43 = 105$) resembles *L. latissimus* and *L. pseudolatissimus* in the shape of the body, myotomes, and other features, but differs from them in having a large eye, absence of long needlelike teeth in the upper jaw, and the structure of the intestine. At present, it is not possible to assign the larva to any of the known families of the Saccopharyngiformes.

UNKNOWN PACIFIC LEPTOCEPHALUS

Figure 4B

Holotype: SIO 70-118, 24°33'S, 154°55'W-154°56'W, IKMT, 1(40 mm), 4 Oct. 1969.

Description: Body elongate, compressed except at head, tapering toward both ends of body. Maximum depth in middle of body, 3.2 in total length. Head long, 3.6 in total length. Snout long, about 4.0 in head. Olfactory organ small, an elongate cup, nostrils not formed. Eye fairly large, 13.7 in head, round, black, surrounded by a transparent area. Upper jaw elongate, maxilla distinct, dentition 1 + 11. Lower jaw elongate, slightly projecting beyond upper jaw, dentition 1 + 7. Suspensorium long. Gill opening wide. Opercular elements present, cartilaginous. Gills very small, four. Branchiostegals absent. Myotomes wide, V-shaped, $56 + 46 = 102$, muscle fibers very broad. Dorsal fin origin on myotome 38, fin rays not formed, predorsal distance 2.0 in total length.

Anal fin rays not formed. Pectoral fin small, behind gills. Esophagus a straight tube. Stomach a rudimentary, fingerlike process at myotomes 17-19. Intestine long, muscular, thrown into three loops of increasing depth posteriorly opening to exterior at myotome 56. Liver small. Gall bladder and stomach enclosed by liver. Pancreas a small, thick lobe. Opisthonephros tubular, wavy, opening behind vent. First and last blood vessels to viscera at myotomes 8 and 48, respectively.

Pigmentation: A thick black patch at tip of lower jaw, a small black patch at tip of upper jaw on ventral side. Sparse black pigment along midline of snout and olfactory region, a series of midlateral patches, one each on myotomes 13, 25, 40, 50, 59, the last patch on right side and the rest on left, two stellate melanophores on dorsal finfold, and a series of five on heart, liver, and intestinal loops on ventral side.

Remarks: This is the first report of this type of larva from the Pacific. It appears that there is only one record of a similar larva, *L. holti*, from the North Atlantic off the coast of northern Spain (Schmidt, 1909). *L. holti* resembles this larva in most characters such as the shape of the body, head, and snout, in dentition, myotomes, gut, liver, and pigmentation. The preanal and total myotomal counts ($67 + 45 = 125 + ca$) of *L. holti* are higher than the myotomal counts of this larva, which undoubtedly belongs to a different but closely related species.

Schmidt did not allocate *L. holti* to its adult, but simply suggested that it may belong to some southern warm-water eel. Although it is difficult to establish the identity of the larva conclusively in the absence of successive metamorphic and juvenile stages, certain morphological and anatomical characters of the larva are closer to the larval features of *Cyema*, saccopharyngids, and monognathids, and a comparison of its characters is made with their larval features.

Comparison with Cyema: This larva has striking resemblances to that of *Cyema* in the following features: The shape and the size of the body are similar although less deep; the head is elongate; the teeth are similar in shape; the eye is larger and circular; the myotomes are V-shaped; the intestine is thrown into loops; the gill opening and gills are small. But the larva differs from

Cyema in the following respects: *Cyema* has five intestinal loops (four in early stages) which are more compact and deeper whereas this larva has only three shallow intestinal loops; the liver in *Cyema* is small, laminar, and situated at myotome 6 whereas in this larva the liver is a very thick lobe at myotome 17; the pancreas in *Cyema* is a large and thin film of tissue extending along all the intestinal loops except the last and does not form a bulge with the liver whereas it is a thick lobe forming a bulge with the liver in this larva; the position of the gills in *Cyema* is more anterior than in this larva; the body depth in this larva is less than that of *Cyema*; the pigmentation on the myotomes in *Cyema* is scattered all over the body whereas it is limited to a series of five midlateral melanophore patches in this larva. But the basic characteristics of the larva are so strikingly similar to those of the larva of *Cyema*, I am compelled to relate it to an unknown species of the family Cyemidae. If the larva is a cyemid larva, it will probably belong to a new genus other than *Cyema* as the differences between the larva of *Cyema atrum* and this larva appear to be at generic level.

Comparison with saccopharyngid and eurypharyngid larvae: In all three kinds of leptocephali the size and shape are approximately similar, the myotomes are V-shaped, the suspensorium is elongated, the gills are small and more posterior in position, the liver is a thick lobe, the pancreas is a thick lobe forming a bulge with the liver, the intestine is looped, and the opisthonephros and the last blood vessel are on the last intestinal loop. However, this larva differs from saccopharyngid and eurypharyngid larvae in the shape of the head and the nature of the teeth, in having more intestinal loops and a longer intestine, and in the presence of a midlateral series of pigmentation spots.

Comparison with metamorphic monognathids: This larva resembles the metamorphic forms in myotome shape, the elongate snout, the total number of myotomes and the midlateral melanophores (Table 2), the structure and position of the melanophores in relation to myotome number, and the pigmentation at the tip of the jaws. But this larva has a well-developed eye whereas the metamorphic forms have rudimentary eyes. But degeneration of the eye may take place during

metamorphosis as in *Cyema*, which has a degenerate eye in the adult and a very large eye in the larva. The gills, liver, and intestine are lost due to damage in the 42-mm and 48-mm metamorphic specimens, and a comparison of these structures cannot be made. A pectoral fin is absent in metamorphic forms whereas this larva has a pectoral fin. The position of the vent is more anterior in the metamorphic forms than in *Monognathus*, which may be attributed again to metamorphosis. The deep pigmentation at the base of the median fins, which increases progressively in later stages, is obviously juvenile pigmentation. Although the midlateral pigmentation, myotome number and shape, and other characters agree with those of metamorphic forms of *Monognathus*, the differences preclude a close relationship.

AFFINITIES OF SACCOPHARYNGOIDEI WITHIN THE ANGUILLIFORMES

The Saccopharyngiformes have not been successfully related to any family within the Anguilliformes. In the most recent classification of the teleostean fishes (Greenwood et al., 1966), the group is placed next to Aoteidae and Cyemidae as a suborder (Saccopharyngoidei) of the order Anguilliformes. The family Cyemidae has been traditionally regarded as related to nemichthyid eels because of the superficial resemblances of the beak. I suggest that the Cyemidae be considered as related to the Saccopharyngiformes and not to the Nemichthyidae for the following reasons.

The adults of *Cyema* differ from the nemichthyids in morphological and osteological characters. All the nemichthyid eels are extremely elongate, but *Cyema* is very short. The adult *Cyema* has a small degenerate eye and a large stomach (about one-fourth of the total length excluding the beak), as in the Saccopharyngiformes, whereas the nemichthyids have large eyes.

The differences in their larvae are even more basic. The larvae of *Nemichthys scolopaceus* Richardson, 1848 (Bertin, 1937b) and other nemichthyids (Beebe and Crane, 1936, 1937a, 1937b) are also elongate and become extremely attenuate during growth and metamorphosis, but the larva of *Cyema* has a short and deep body.

The myotomes of the nemichthyid larvae are W-shaped whereas those of *Cyema* are V-shaped. The intestine is looped in *Cyema* whereas it is straight in the nemichthyid larvae. On the other hand, the larva of *Cyema* closely resembles those of the Saccopharyngiformes in the size and shape of the body, myotome shape, looped intestine, position of the vent, and elongate suspensorium. Bertin (1937b) has pointed out some of the larval and osteological resemblances between the Cyemidae and the Saccopharyngiformes and attributed the similarities of the beak of the Cyemidae and Nemichthyidae to convergent evolution as the beak in *Nemichthys* is mainly formed by the elongation of the vomer, but in *Cyema* by the two maxillaries.

The four families—Cyemidae, Monognathidae, Saccopharyngidae, and Eurypharyngidae—share some basic characters such as short, deep bodied larvae with V-shaped myotomes, looped gut, elongated suspensorium, and a degenerate eye in the adult condition. The striking similarities of these larvae and their differences with the larva of *Nemichthys* are shown in Table 3 and Figure 4. The gross differences in the adults of the four families are probably due to the drastic changes undergone during metamorphosis and other causes. At present, I can only point out the similarities of the Cyemidae to the Saccopharyngiformes. Further studies may provide information to help include or exclude the Cyemidae in the Saccopharyngiformes.

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LITERATURE CITED

BEEBE, W., AND J. CRANE.
 1936. Deep-sea fishes of the Bermuda Oceanographic Expeditions. Family Serrivomeridae. Part I: Genus Serrivomer. *Zoologica* (N.Y.) 20:53-102.
 1937a. Deep-sea fishes of the Bermuda Oceanographic Expeditions. Family Serrivomeridae. Part II: Genus *Platuronides*. *Zoologica* (N.Y.) 22:331-348.
 1937b. Deep-sea fishes of the Bermuda Oceanographic Expeditions. Family Nemichthyidae. *Zoologica* (N.Y.) 22:349-383.
 BERTIN, L.
 1934. Les poissons apodes appartenant au sous-ordre des Lyomères. *Dana Rep. Carlsberg Found.* 3, 55 p.
 1937a. Un nouveau genre de poissons apodes caractérisé par l'absence de machoire supérieure. *Bull. Soc. Zool. Fr.* 61:533-540.
 1937b. Les poissons abyssaux du genre *Cyema* Günther (anatomie, embryologie, bionomie). *Dana Rep. Carlsberg Found.* 10, 30 p.
 1938. Formes nouvelles et formes larvaires de poissons apodes appartenant au sous-ordre des Lyomères. *Dana Rep. Carlsberg Found.* 15, 26 p.
 BÖHLKE, J. E.
 1966. *Order Lyomeri, Deep-sea gulpers.* In *Fishes of the western North Atlantic.* Part Five, p. 603-628. *Mem. Sears Found. Mar. Res.* 1.

TABLE 3.—Comparison of larval characters.

Characters	<i>Cyema atrum</i>	Pacific leptocephalus	<i>Leptocephalus latissimus</i>	<i>L. pseudo-latissimus</i>	<i>Nemichthys scolopaceus</i>
Size of body (mm)	Small (20-60)	Small (35-40)	Small (20-40)	Small (20-40)	Large (over 100)
Shape of body	Oval	Oval	Oval	Oval	Ribbonlike
Myotomes	V-shaped (obtuse angle)	V-shaped (obtuse angle)	V-shaped (obtuse angle)	V-shaped (obtuse angle)	W-shaped
Intestine	Looped	Looped	Looped	Looped	Straight
Position of vent	About three-fourths from head	About three-fourths from head	About one-half from head	About one-half from head	Subterminal
Liver	Short lobe	Short lobe	Short lobe	Short lobe	Elongate
Pancreas	Very large	Large lobe	Large lobe	Large lobe	Small and elongate
Suspensorium	Elongate	Elongate	Elongate	Elongate	Small

- CASTLE, P. H. J.
1963. Anguillid Leptocephali in the Southwest Pacific. Zool. Publ. Victoria Univ. Wellington 34:1-14.
- GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN, AND G. S. MYERS.
1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Am. Mus. Nat. Hist. 131:339-455.
- LEA, E.
1913. Muraenoid larvae. Rep. Sci. Results "Michael Sars" North Atl. Deep-sea Exped., 1910. Bergen Mus., Bergen, 1933 ed. 3(1):1-48.
- MURRAY, J., AND J. HJORT.
1912. The depths of the ocean. A general account of the modern science of oceanography based largely on the scientific researches of the Norwegian steamer Michael Sars in the North Atlantic. Macmillan and Co., Lond., 821 p.
- MYERS, G. S.
1940. A note on *Monognathus*. Copeia 1940:141.
- ORTON, G. L.
1963. Notes on larval anatomy of fishes of the order Lyomeri. Copeia 1963:6-15.
- ROULE, L.
1934. Les poissons et le monde vivant des eaus. Paris, 7:242-243.
- SCHMIDT, E. J.
1909. On the occurrence of leptocephali (larval muraenoids) in the Atlantic W. of Europe. Medd. Komm. Havunders., Ser. Fiskeri 3(6):1-19.
1912. Contributions to the biology of some North Atlantic species of eels. Vidensk. Medd. Dan. Naturhist. Foren. Kbh. 64:39-51.
- TCHERNAVIN, V. V.
1947a. Six specimens of Lyomeri in the British museum (with notes on the skeleton of Lyomeri). J. Linn. Soc. Lond. Zool. 41:287-350.
1947b. Further notes on the structure of the bony fishes of the order Lyomeri (*Eurypharynx*). J. Linn. Soc. Lond. Zool. 41:377-393.