B R E V I O R A

Museum of Comparative Zoology

US ISSN 0006–9698

CAMBRIDGE, MASS. 18 APRIL 1996 NUMBER 503

CYEMATID LARVAE OF THE *LEPTOCEPHALUS HOLTI* GROUP IN THE ATLANTIC AND PACIFIC OCEANS (PISCES: SACCOPHARYNGIFORMES)

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ABSTRACT. Cyematid larvae of the *Leptocephalus holti* group consist of three distinct species or species groups, each found in the Atlantic and Pacific oceans. Species 1 has four gut loops and lacks pigment along the lateral midline. Species 2 also has four gut loops, but it has lateral pigment. Species 3 has three gut loops and lacks lateral pigment. The name *Leptocephalus holti* is used as a convenient group name to refer to a complex of related species, none of which has been conclusively identified with an adult. Larvae of the *Leptocephalus holti* group may belong to *Neocyema* Castle, but this identification cannot yet be confirmed.

INTRODUCTION

The family Cyematidae is among the strangest and most highly modified of the deep-sea eels. Only the gulpers (Saccopharyngidae, Eurypharyngidae, and Monognathidae) exceed it in the degree of skeletal reduction. For nearly a century, the family was known from a single species, *Cyema atrum* Günther, 1878, found in all oceans at depths of 1,500–3,000 m (Bertin, 1937:25). Castle (1977) described a second genus and species, *Neocyema erythrosoma,* from two specimens collected in the South Atlantic Ocean. Evidence of a second cyematid species, however, had existed long before Castle's discovery in the form of an unidentified leptocephalus. The leptocephalus of *Cyema atrum* was first collected by the *Michael Sars* North Atlantic Expedition in 1910 and illustrated (but not named) by Murray and Hjort (1912, fig. 79). It was identified as *Cyema atrum* by Lea (1913:19), largely on the

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basis of the unusually low number of myomeres, and confirmed by Roule and Bertin (1929:108) through the discovery of metamorphic specimens. Even before this, however, Schmidt (1909: 6) described *Leptocephalus holti* from material collected by the Danish vessel *Thor* in the northeastern Atlantic. He made no attempt to identify it beyond speculating that it and some other leptocephali might represent "southern warm-water forms which have been taken at their northern limits in the 'Thor's' investigation." Larvae of the *L. holti* type were not reported again until Raju (1974:559) found a similar specimen in the South Pacific. Raju pointed out its resemblances to the larva of *Cyema atrum* and felt "compelled to relate it to an unknown species of the Cyemidae [sic]." Tabeta (1988:29) described two *L. holti*–like forms as "Cyematidae sp. 1" and "Cyematidae sp. 2"; species 1 differed from species 2 and from Schmidt's and Raju's specimens in lacking the conspicuous midlateral pigment spots. Fortuño and Olivar (1986; also Olivar and Fortuño, 1991) reported a specimen collected in the South Atlantic off Namibia. They noted that their specimen lacked lateral pigment and speculated that this character might appear later in development. Smith (1989b:945) reported three additional specimens from the Sargasso Sea and the equatorial Atlantic and agreed with Raju that they probably belonged to the Cyematidae. Smith's specimens also lacked midlateral pigment spots, and they had slightly fewer myomeres than Schmidt's holotype of *L. holti.* Based on the limited material available, he was unable to assess the significance of these differences.

In this paper, we report on 47 additional specimens from both the Atlantic and Pacific oceans. These have revealed previously unsuspected diversity in several characters and allow us to give a more complete account of these distinctive larvae than has heretofore been possible.

MATERIAL AND METHODS

Most of our material (30 specimens) was collected during five cruises in the subtropical convergence zone of the Sargasso Sea between 1981 and 1989 (Kleckner *et al.,* 1983; Kleckner and McCleave, 1988; Miller, 1993). These cruises were designed to study the spawning and larval distribution of the eel *Anguilla rostrata.* The other new Atlantic specimen was collected near

Bermuda. Including the five previously recorded specimens (Schmidt, 1909; Fortuño and Olivar, 1986; Smith, 1989b), the total number of specimens known from the Atlantic is now 36. Of the 16 new Pacific specimens, 4 were found in collections at the Natural History Museum of Los Angeles County, 9 at Scripps Institution of Oceanography, and 3 at the National Marine Fisheries Service Honolulu laboratory. With the nine previously recorded specimens (Raju, 1974; Tabeta, 1988), 25 specimens are now know from the Pacific. Specimens examined are deposited in the Academy of Natural Sciences of Philadelphia (ANSP); Museum of Comparative Zoology, Harvard University (MCZ); Natural History Museum of Los Angeles County (LACM); National Museum of Natural History, Washington, D.C. (USNM); and Scripps Institution of Oceanography, La Jolla, California (SIO).

Counts and measurements follow the methods of Smith (1989a: 665). Near the tip of the tail, myomeres become difficult to count, and in most cases only approximate counts were possible. The small size of most of our specimens made it difficult to obtain precise numerical values for any of the characters. The position of the last vertical blood vessel (LVBV) could not be seen clearly at the point where it entered the dorsal aorta in any of the specimens. We estimate this point to be on the average some six to eight myomeres anterior to a vertical line through the anus. Numbers in parentheses following meristic values represent the number of specimens on which the count is based.

We use the term "*Leptocephalus holti*" in the sense of Orton (1964a;199, 1964b:438) as a convenient group name to refer to what is apparently a complex of closely related species. In referring to the three distinct types (whether each represents a single species or a complex within the larger *holti* complex), we follow Tabeta (1988) in calling them species 1, species 2, and (newly described here) species 3.

GENERAL DESCRIPTION OF *LEPTOCEPHALUS HOLTI* (AFTER SMITH, 1989b:946)

Body moderately deep, depth about one-sixth to one-third standard length (SL); body deepens gradually behind head. Gut with a distinct swelling at hepatogastric region and two or three loops or arches behind this; a compact liver lobe near 17th myomere,

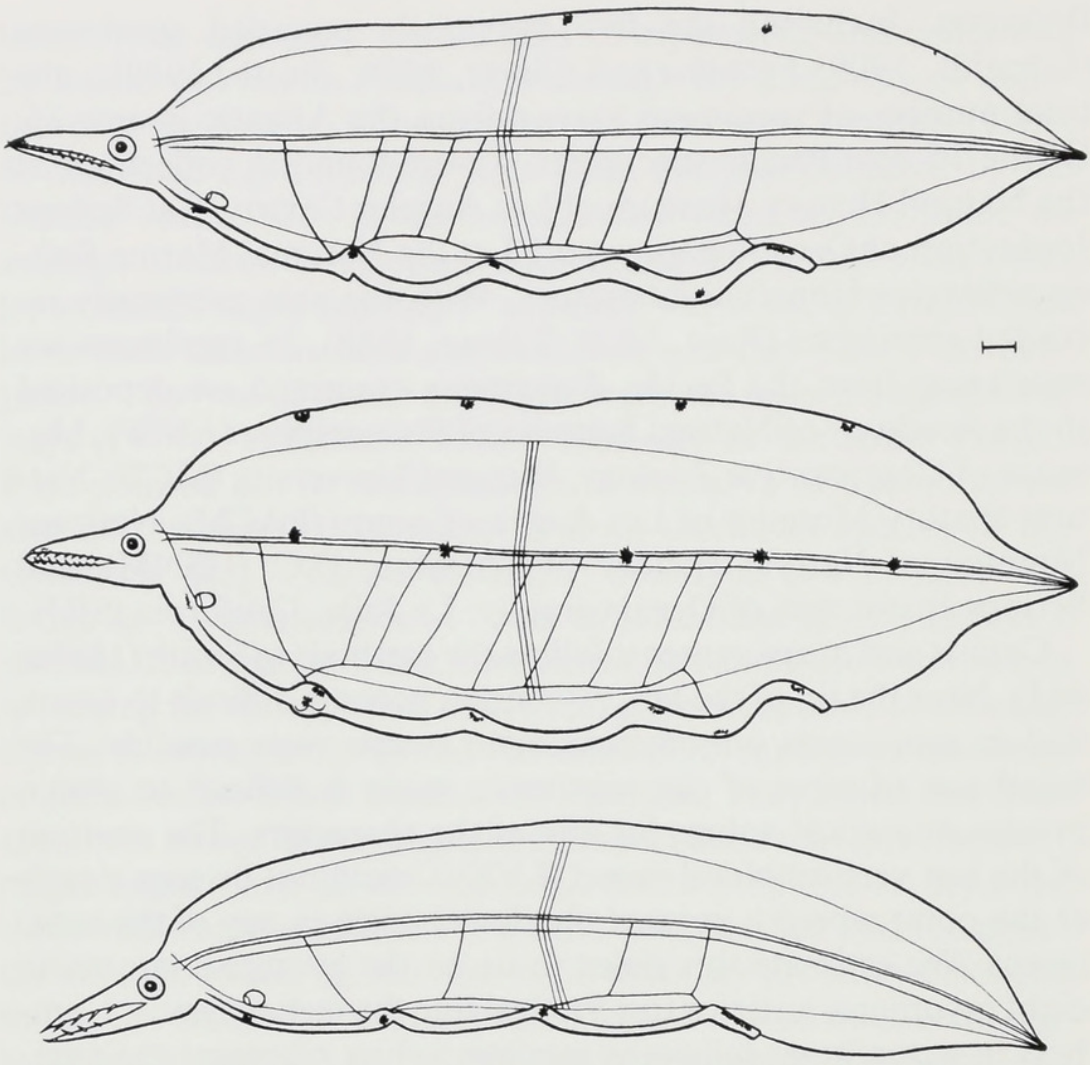

Figure 1. The *Leptocephalus holti* group. Top, species 1, MCZ 101007, 30 mm SL; Middle, species 2, MCZ 101003, 26 mm SL; Bottom, species 3, MCZ 101023, 25 mm SL. Drawn by L. Meszoly.

contributing to swelling of gut; pancreas compact, located just posterior to liver and gall bladder; dorsal aorta sending several conspicuous vertical blood vessels that enter a parallel ventral vessel that lies distinctly above the gut. Dorsal fin begins approximately 20 myomeres anterior to anus. Head and snout long; eye located posteriorly, close to anteriormost myomeres; snout long and pointed, profile relatively flat; nasal capsule small. Several expanded melanophores sometimes present on lateral midline. Moderately large melanophores on gut. One to four melanophores sometimes present near dorsal margin of body, in clear area above myomeres. Pigment usually present at anterior tip of

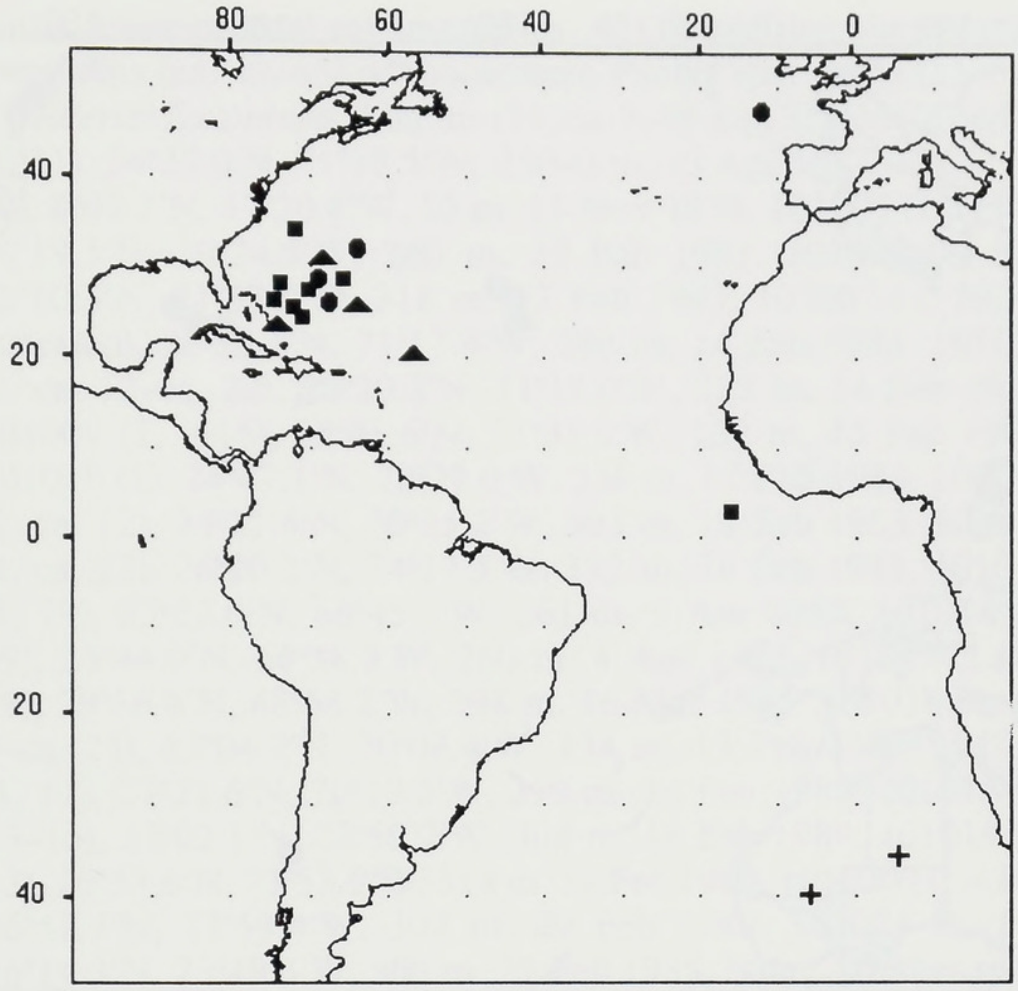

Figure 2. Distribution of *Leptocephalus holti* and *Neocyema erythrosoma* in the Atlantic. Square = species 1; circle = species 2; triangle = species 3; cross = *Neocyema erythrosoma.*

snout and lower jaw. Maximum size unknown, though probably not large. Largest specimen known 43 mm SL; all specimens premetamorphic.

Species 1
Figures 1 (top), 2, 3

Diagnosis. Four gut loops, including hepatogastric swelling. No pigment on side of body along lateral midline. One to three melanophores near dorsal margin of body above myomeres. Paired melanophores laterally on gut adjacent to pectoral fin and posteriorly between third and fourth gut loops; a single or complex melanophore dorsal to each gut loop. Pigment at tip of snout and

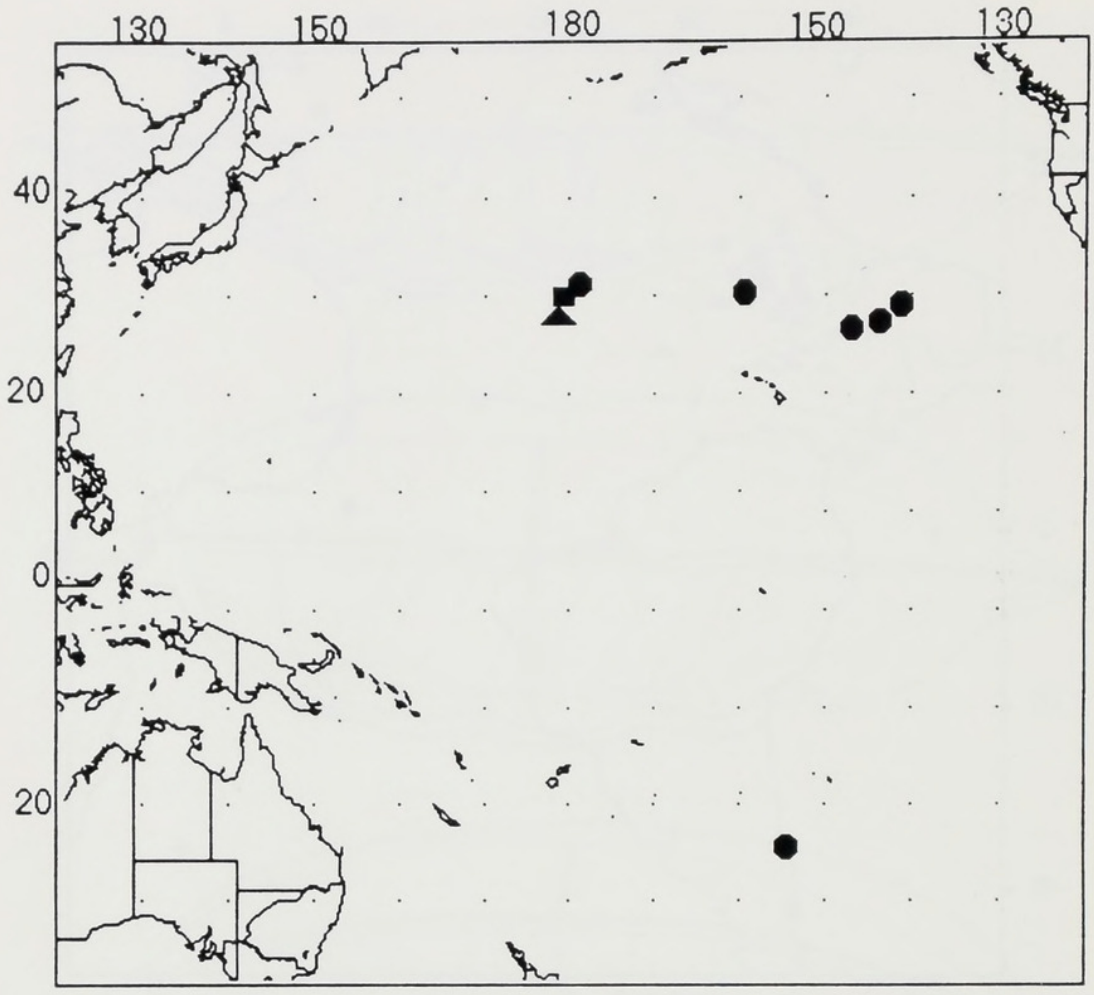

Figure 3. Distribution of *Leptocephalus holti* in the Pacific. *Square* = species 1; circle = species 2; triangle = species 3.

lower jaw. Myomeres: total ca. 99–117 (15 specimens), preanal 45–65 (20).

Size. Ca. 10–39 mm SL, all premetamorphic.

Variation. All but two of the Atlantic specimens came from the Sargasso Sea, the others from off the west coast of Africa (Fig. 2). The latter had approximately 99–105 total myomeres compared to ca. 108–117 for the western Atlantic specimens. There seem to be no other differences between the eastern Atlantic and western Atlantic specimens. Tabeta (1988:29) gave a range of 97–100 total, 51–62 preanal, and 46–49 LVBV myomeres for his seven western Pacific specimens, 16–31 mm in length. The single central Pacific specimen examined, USNM 324871, had signifi-

cantly fewer preanal myomeres (ca. 45) than either the Atlantic specimens (ca. 49–65) or the western Pacific specimens (51–62).

Material Examined. Atlantic (25, ca. 9–39 mm SL): MCZ 64484 (1, 31), 34°27.0′N, 71°18.5′W, 250–0 m, 13 Apr 1977. 65647 (1, 20), 4°05.2′N, 17°20.8′W, 75 m, 15 Nov 1978. 101005 (1, <10), 24°19.5′N, 70°24.5′W, 280 m, 27 Feb 1981. 101006 (1, 34), 25°10.3′N, 71°33.0′W, 318 m, 13 Feb 1983. 101007 (1, 30, illustrated), 26°25.1′N, 71°17.4′W, 280 m, 14 Feb 1983. 101008 (2, ca. 12–ca. 22), 26°20.3′N, 71°18.0′W, 232 m, 14 Feb 1983. 101009 (1, <15), 25°41.6′N, 71°31.0′W, 132 m, 15 Feb 1983. 101010 (1), 24°47.1′N, 70°27.0′W, 356 m, 17 Feb 1983. 101011 (1, ca. 12), 24°11.4′N, 70°25.2′W, 303 m, 18 Feb 1983. 101012 (1, ca. 22), 26°20.2′N, 74°12.5′W, 112 m, 26 Feb 1983. 101013 (1, 19), 27°52.0′N, 66°45.7′W, 261 m, 3 Apr 1983. 101014 (1, 39), 26°44.9′N, 66°38.8′W, 260 m, 4 Apr 1983. 101015 (1, ca. 11), 29°56.4′N, 68°58.2′W, 298 m, 16 Mar 1985. 101016 (2, ca. 9–ca. 25), 27°04.7′N, 70°03.4′W, 134 m, 13 Feb 1989. 101017 (1, 11), 27°21.6′N, 70°12.3′W, 299 m, 14 Feb 1989. 101018 (5, 13–15), 27°02.1′N, 73°59.7′W, 304 m, 16 Feb 1989. 101019 (1, 13), 26°33.6′N, 73°53.9′W, 318 m, 19 Feb 1989. 101020 (1, <10), 26°42.7′N, 73°59.4′W, 302 m, 20 Feb 1989. 101021 (1, 19), 26°14.3′N, 73°49.3′W, 300 m, 21 Feb 1989. Note: Another specimen, MCZ 101026 (<15 mm), probably belongs here, but it is badly damaged and we cannot determine the number of gut loops. Pacific (1, 9 mm SL): USNM 324871 (1, 9), 29°48′00″N, 179°03′54″E, 50–100 m, 9 Feb 1985.

Species 2

Figures 1 (middle), 2, 3

Diagnosis. Atlantic specimens (including data from holotype, Schmidt, 1909): Four gut loops. Five expanded melanophores along lateral midline at myomeres 14–16 (4 specimens), 29–31 (4), 44–48 (4), 57–65 (4), 71–78 (4), centered below surface and often extending onto body wall on one side or other; two to four melanophores near dorsal margin of body, in clear area above myomeres. Myomeres: total ca. 108–ca. 130 (4), preanal 65–75 (4).

Pacific specimens: Four gut loops. Four or five expanded lateral melanophores, at myomeres 12–19 (14), 25–38 (14), 42–53 (14),

53–68 (13), 61–75 (7); one or two dorsal melanophores; other pigment as in Atlantic specimens. Myomeres: total ca. 100–110 (9), preanal 57–70 (11).

Size. Atlantic specimens 23–35 mm SL, Pacific specimens ca. 19–43 mm; all premetamorphic. The specimen reported by Raju (1974) was given as 40 mm; we remeasured it as 37 mm.

Variation. Three of the four Atlantic specimens came from the Sargasso Sea, the other (the holotype of *Leptocephalus holti*) from the northeastern Atlantic south of Ireland (Fig. 2). Despite its geographic separation from the others, the holotype shows no obvious differences from the three western Atlantic specimens. The holotype and MCZ 101003 have fewer total myomeres (ca. 108–112) than MCZ 101002 and 101004 (ca. 120–130 and ca. 128). The former pair also has fewer preanal myomeres (65–67 vs. 74–75). In one specimen (MCZ 101003), the last vertical blood vessel enters the kidney slightly more anteriorly than in the others, i.e., in the trough between the third and fourth gut loops instead of near the top of the fourth loop. Another specimen (MCZ 101002) has extra ventral melanophores, between the first–second and second–third gut loops. With the limited material available and the difficulty of obtaining precise myomere counts, we are unable to assess the significance of these differences.

Thirteen of the 15 Pacific specimens came from an area north to northeast of the Hawaiian Islands, one came from Southeast Hancock Seamount in the central North Pacific, and one from the South Pacific, southwest of the Austral Islands (Fig. 3). The South Pacific specimen is at the low end of the range of a few meristic characters (preanal myomeres, position of some lateral melanophores), but the only character that is clearly outside the range of the other specimens is the position of the fifth lateral melanophore (61–62 vs. 64–75). Seven specimens have four lateral melanophores, seven others have five, and one has three. Tabeta's (1988) specimen has five lateral melanophores, and its total and preanal myomere counts (99 and 59, respectively) fall within the range of our specimens. The Pacific specimens appear to have fewer total myomeres (99–110) and preanal myomeres (57–70) than the Atlantic specimens (ca. 108–130 and 65–75, respectively). The position of the first four lateral melanophores coincides in the Atlantic and Pacific specimens. Only the fifth

appears to differ, at myomere 61–75 in the Pacific vs. 71–78 in the Atlantic specimens. All four Atlantic specimens have five lateral melanophores, whereas more than half of the Pacific specimens examined by us have only three or four.

Material Examined. Atlantic (3, 23–26 mm SL): MCZ 101003 (1, 26 illustrated), 28°31.4′N, 69′02.1′W, 475 m, 4 Mar 1981. 101002 (1, 23), 26°59.7′N, 68°52.0′W, 150 m, 23 Mar 1985. 101004 (1, 23), 31°27.0′N, 64°21.0′W, 9 Apr 1990. Pacific (15, 19–45 mm SL): LACM 36437-1 (1, 28), 26°32′N, 147°13′W, 0–160 m, 10 Apr 1966. 36438-2 (1, ca. 21), 26°32′N, 147°13′W, surface, 10 Apr 1966. 36447-4 (1, ca. 24), 27°55′N, 144°10′W, 11 Apr 1966. 36454-3 (1, 22), 28°48′N, 141°59′W, surface, 12 Apr 1966. SIO 70-118 (1, 37, specimen described by Raju, 1974), 24°30.5′S, 154°54′W, 0–175 m, 4 Oct 1969. 89–57 (2, 42–43), 31°N, 159°W, 200–0 m, 13–14 Apr 1989. 89-63 (4, 19–39), 31°N, 159°W, 200–0 m, 18 Apr 1989. 89-65 (2, 42–42), 31°N, 159°W, 400–0 m, 19 Apr 1989. 89-68 (1, 34), 31°N, 159°W, 0–900 m, 22 Apr 1989. USNM 324872 (1, 26), 29°49′46″N, 179°07′54″E, 0–100 m, 20 Apr 1987.

Species 3

Figures 1 (bottom), 2, 3

Diagnosis. Three gut loops, including hepatogastric swelling. Lateral and dorsal pigment absent; paired melanophores on lateral surface of gut adjacent to pectoral fin; a melanophore dorsally and one on each side of hepatogastric swelling; a complex melanophore dorsally on the two posterior gut loops, extending laterally on each side of gut; no melanophore between second and third gut loops; pigment present at tip of snout and lower jaw. Myomeres: total ca. 104–115 (4), preanal ca. 54–57 (6).

Size. Largest specimen ca. 25 mm; all specimens premetamorphic.

Variation. Five specimens came from the Sargasso Sea and one from the central North Pacific. Significant variation is not evident.

Material Examined. Atlantic (5, 16–ca. 25 mm SL): ANSP 153490 (1, 19), 21°03′N, 57°54′W, 0–150 m, 30 Mar 1979. MCZ 101022 (1, 23), 26°17.1′N, 66°44.6′W, 253 m, 8 Apr 1983. 101023 (1, 25, illustrated), 26°17.0′N, 66°45.0 W, 150 m, 9 Apr 1983. 101024 (1, 23), 28°31.4′N, 69°02.1′W, 302 m, 17 Mar 1985.

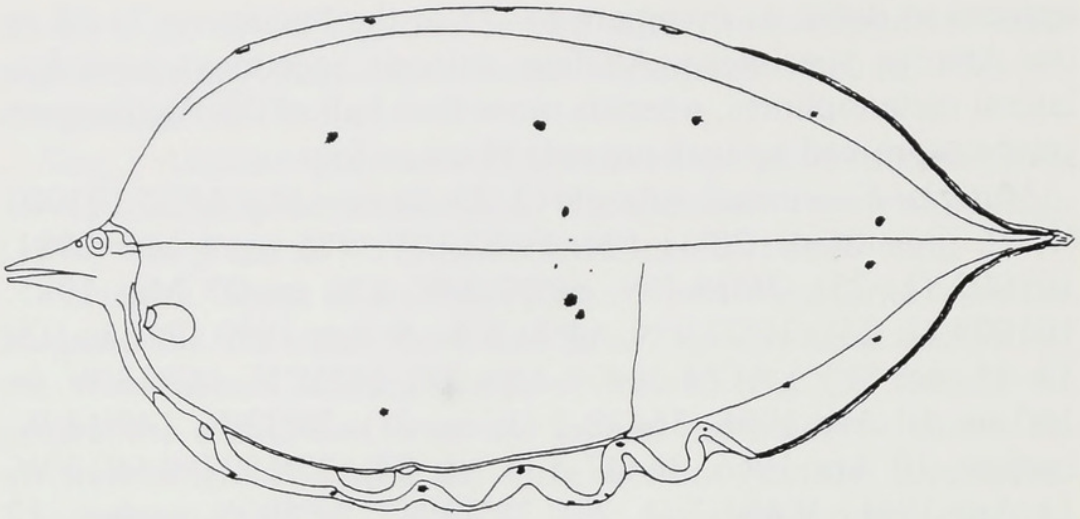

Figure 4. Leptocephalus of *Cyema atrum* (after Smith, 1989b).

101025 (1, 16), 27°02.1′N, 73°59.7′W, 304 m, 16 Feb 1989. Pacific (1, 10 mm SL): USNM 324783 (1, 10), 29°47′36″N, 179°03′54″E, 50–100 m, 9 Feb 1985.

IDENTIFICATION AND RELATIONSHIPS

Leptocephalus holti and the larva of *Cyema atrum* (Fig. 4) share the following characters: a long, peg-like snout with a straight profile; a posteriorly placed eye; a gut with an anterior swelling at the hepatogastric region followed by two to four arches or loops; pigment dorsally on each gut loop; pigment near the dorsal margin of the body; an acute tail without distinct hypural elements; a large ventral blood vessel conspicuously separated from the gut tube; and V-shaped myomeres with a highly obtuse angle at the midlateral line. These characters distinguish *Cyema atrum* and *L. holti* from all other leptocephali and support the hypothesis that they belong to the same family. *Cyema atrum* (Fig. 4) has a deeper body than *L. holti* with a steeper anterior profile, it has an expanded mass of pancreatic tissue that fills much of the space between the dorsal margin of the intestine and the ventral margin of the myomeres, and its lateral pigment is scattered over the side of the body instead of being restricted to the midline.

If *L. holti* is accepted as a cyematid, which cyematid is it? Both Castle (1977:75) and Smith (1989b:947) have made the obvious suggestion that *L. holti* is the larva of *Neocyema,* but they con-

sidered such an identification inconclusive. Particularly troublesome was the absence of any trace of the conspicuous lateral melanophores in the specimens of *Neocyema,* despite the semi-leptocephaloid appearance of the latter. Bertin (1937:17) showed that the lateral pigment of the leptocephalus was retained in a 115-mm juvenile *Cyema atrum.* Both the holotype of *L. holti* and Raju's Pacific specimen had conspicuous lateral pigment. Castle in particular felt that the pigment character made an identification of *L. holti* with *Neocyema* unlikely. Smith agreed but pointed out that the age of the *Neocyema* specimens was unknown and that at least some specimens of *L. holti* lacked lateral pigment.

The present material further reduces the objections to identifying *L. holti* as the larva of *Neocyema.* It is now clear that the majority of Atlantic *L. holti* lack lateral pigment, so the main obstacle has been removed, at least in theory. The number of myomeres is in the same range (Castle [1977] reported that the one intact specimen of *Neocyema erythrosoma* had 108 total myomeres). Although the identification cannot be disproved, it cannot be confirmed, either, especially in the absence of metamorphic specimens. The only known specimens of *Neocyema* were taken far from the known range of *L. holti,* but lack of adequate collecting weakens this objection. After all, for more than 60 years *L. holti* was known from a single specimen.

Larval fishes can provide important and valuable information that is not available from the study of adults alone. Regardless of whether *L. holti* is the larva of *Neocyema* or another still unknown genus, these larvae enable us to say without question that such a genus exists, it contains at least three species, and it is found in all oceans.

ACKNOWLEDGMENTS

We thank Dr. J. D. McCleave for access to the specimens from the University of Maine's Sargasso Sea collections. The following provided the opportunity to examine specimens in their collections: R. J. Lavenberg (LACM), R. H. Rosenblatt (SIO), and B. C. Mundy (National Marine Fisheries Service, Honolulu). The collection and identification of the University of Maine specimens were made possible with financial support from the National

Science Foundation (OCE-7719440, OCE-8208394, and OCE-8811005). Publication costs were covered in part by a grant from the Wetmore-Colles Fund.

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