

EARLY ZOEAL STAGES OF THE SEMITERRESTRIAL SHRIMP
MERGUIA RHIZOPHORAE (RATHBUN, 1900)
CULTURED UNDER LABORATORY CONDITIONS (DECAPODA
NATANTIA, HIPPOLYTIDAE) WITH A DISCUSSION OF
CHARACTERS IN THE LARVAL GENUS *ERETMOCARIS*

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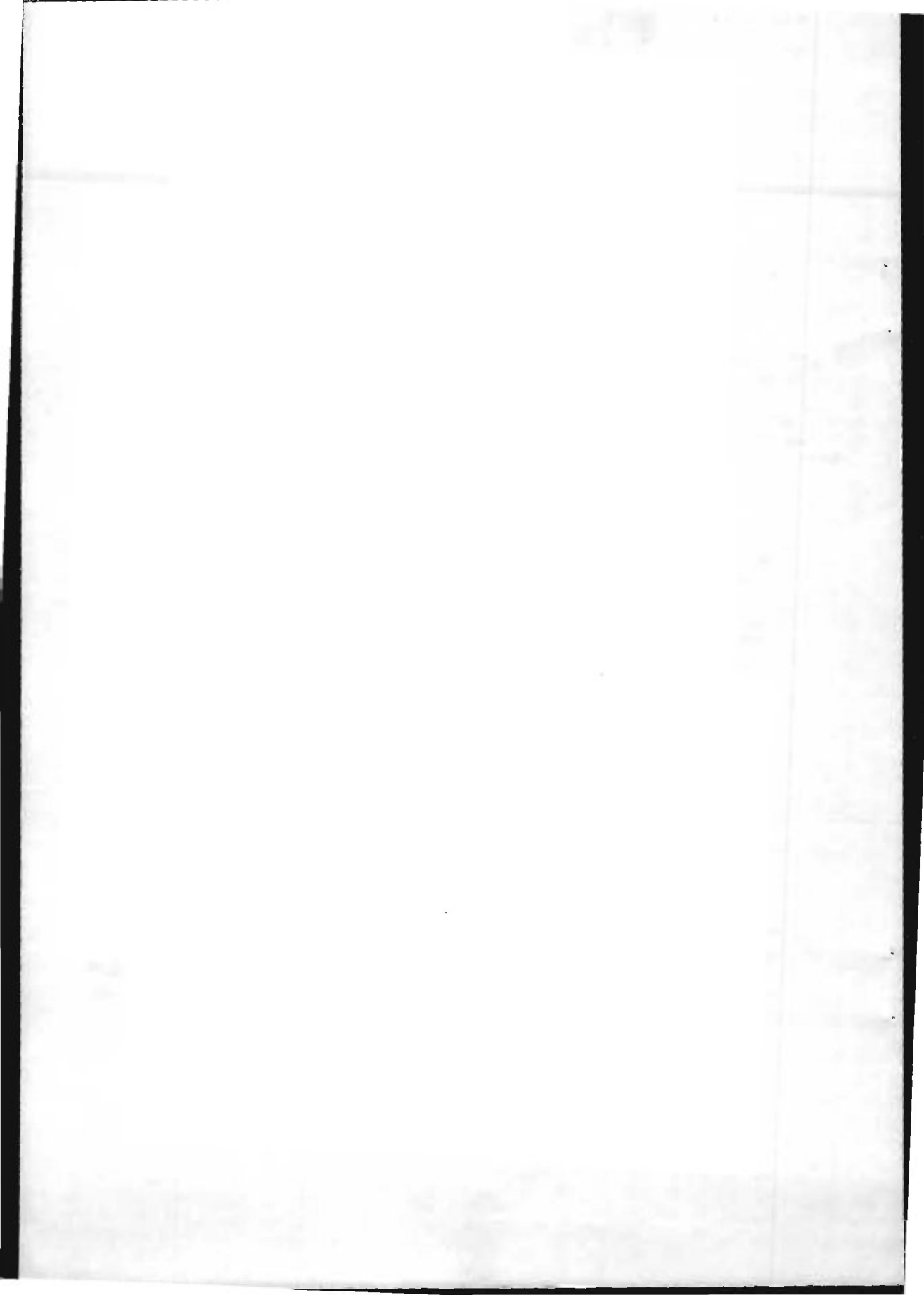
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Hippolytid shrimps of the genus *Merguia* are the only semiterrestrial shrimps known among decapod crustaceans (Bliss, 1968; Abele, 1970). Two species are described, *Merguia oligodon* (De Man) from the Mergui and Malay Archipelagoes, and *M. rhizophorae* (Rathbun, 1900) from the Caribbean coast of Panamá, Surinam, and Brazil (Holthuis, 1959). *Merguia rhizophorae* is nocturnal. Individuals in Panamá occur among piles of driftwood in supratidal areas of mangrove swamps, moving out from humid areas, where they spend the day, to driftwood and mangrove roots at night. The shrimp seemed to feed on algae and other material found on mangrove roots and damp driftwood in nature and in the laboratory. Stomach contents consisted of pieces of wood and algae, as well as unidentified material. The morphology of *Merguia rhizophorae* does not appear to be especially adapted for a terrestrial habitat but the shrimp may avoid problems associated with terrestriality through behavioral modifications (see Holthuis, 1959; Abele, 1970).

The eggs of *Merguia rhizophorae* are large (0.9 mm), suggesting an abbreviated larval development. Thus, when ovigerous females were collected in Panamá the opportunity arose: 1) to determine whether the species undergoes abbreviated development, 2) to compare larval morphology with that seen in other hippolytid and processid shrimps, and 3) as well as to describe for the first time larval stages within the genus *Merguia*.

In this paper we report on the early larval stages of *M. rhizophorae* cultured under laboratory conditions. We compare them to larvae of closely related hippolytid genera and discuss the relationships of *Merguia* with other caridean shrimp.



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MATERIALS AND METHODS

Ovigerous females of *Merguia rhizophorae* were collected at Galeta Island, Atlantic coast of Panamá, 18 October 1970, from driftwood in a swamp of red mangrove, *Rhizophora mangle* (L.). Females were maintained in the laboratory in individual 19 cm diameter glass bowls containing seawater of approximately 30-33‰. Upon hatching on 23 October, larvae were placed, one per compartment, in 18-compartmented plastic trays with seawater of salinity similar to that in which the adults were held, and maintained in controlled temperature units (CTU's) in two of three series: (A) starved, 26.0°C, 32.1‰; (B) fed ad libitum with *Artemia nauplii* at 26.2°C, 32.0‰; (C) fed ad libitum as before, at room temperature (24.8-28°C, average 25.8°C), 32.1‰. A diel light cycle of 12 hours on, 12 hours off, under fluorescent illumination prevailed for the duration of the experimental rearing. Water was changed and zoeae were fed daily. Culture methodology was otherwise similar to that of Gore (1968). Meristic data include the rostral carapace length (RCL) measured from the tip of the larval rostrum to the dorsomedian sinus on the zoeal carapace, and all measurements are the arithmetic average of the number of zoeae examined in each stage.

RESULTS OF THE REARING EXPERIMENT

Mortality was high, and the maximum number of instars recorded was seven, although, as will be discussed below, progressive development apparently did not proceed beyond morphological stage 4 or 5. All larvae hatched into a prezoal stage of undetermined duration, and some apparent first zoal stages still had incompletely extruded setae on the maxillipeds as late as day 3 in the culture series. These did not develop further. Duration and survival of all 3 series are summarized in table I. A synopsis of each series follows.

Series A: Starved. — Only two zoal stages were obtained, the first stage lasting 12 hours and the second lasting up to 10 days before dying. Zoeae in this series appeared noticeably smaller than their counterparts in the other series.

Series B: Diel cycle. — The first zoal stage lasted up to 15 hours and 13 of 18 larvae molted to stage II. Larvae continued in this stage for 5 to 6 days, at which time 70% of the zoeae molted to stage III. In stage III, two of the zoeae persisted for four days and another for five days. Six other individuals died within 12 hours after molting to stage III, before ecdysis to stage IV. The in-

TABLE I
Duration of larval stages of *Merguia rhizophorae* (Rathbun)

		Duration (days)			Total molting for next stage
		minimum	mean	mode	
Starved series					
32.1‰, 26.0°C					
Zoea	I	1	1	1	12
Zoea	II	3	7.6	9	0
Diel cycle					
32.0‰, 26.2°C					
Zoea	I	1	1	1	13
Zoea	II	5	5.3	5	9
Zoea	III	4	4.3	4	3
Zoea	IV*	10	-	-	1
Zoea	V*	3			0
Room temperature					
32.1‰, 25.8°C					
Zoea	I	1	1	1	13
Zoea	II	5	5.4	5	10
Zoea	III	4	-	-	2
Zoea	IV	1**			1
Zoea	V	"1"			0

* = A single individual molted to stage IV. It molted three more times 4, 3, and 5 days later, apparently reaching stage V only. ** = Molted after one day with no morphological change and died.

dividual in stage IV remained as such 10 days, before progressing to stage V. The surviving zoea lasted for three days, molting early on the fourth day (without further morphological development) to a sequential stage VI. From this stage a single individual molted five days later to a sequential stage VII. There was no apparent change in carapace morphology or setal formula. It survived two days before dying without further ecdysis.

Series C: Room temperature. — The first zoeal stage lasted up to 12 hours, with 77% of the larvae molting to stage II. Zoeae in this stage lasted five to seven days before ecdysis to stage III. Stage III zoeae persisted from four to 15 days with 10% of the larvae surviving to the next stage. Larvae in stage IV persisted for one day before a single individual molted to stage V. This individual remained as such for nine days before dying.

High mortality and the apparent lack of further morphological development beyond stage IV (or perhaps V) may be a result of several factors. Although caridean larvae have been successfully cultured in the laboratory on a variety of diets, including the time-honored *Artemia* (see e.g. Shield, 1978), insufficient amounts of this food source or the *Artemia* itself might lack a necessary nutritional factor essential for continued development in this species. That is, molting may continue but ontogenetic growth may not. This appeared to be

the case in the later zoeal stages (IV, V, VI, and VII), which showed little or no morphological difference. This condition has been observed in several other caridean shrimp (see Knowlton, 1974, for a summary) and one hypothesis is that laboratory conditions in which *Artemia* are used are not sufficient for some species to complete their development. This may be the case for *M. rhizophorae* especially since the adults appear to be herbivorous or omnivorous. We did not consider temperature or salinity to be factors affecting development (at least in the first three to four zoeal stages) because morphogenesis and molting continued without mortality greater than might be expected relative to these parameters. Unfortunately, at the time of culture, no other physical conditions except salinity and temperature were monitored, so that effects of physical and biological factors such as pH, diurnal periodicity, dissolved ammonia, or even bacterial or fungal growth, remain undetermined (see Dalley, 1980). However, we consider bacterial and fungal contaminants unlikely because none of the dead larvae showed noticeable evidence of bacterial or fungal infection when examined under the microscope. In addition to these factors, handling during water changes may have damaged the larvae.

Zoeae of *Merguia rhizophorae* are not large compared to some larvae in other hippolytid genera (Dobkin, 1968; Shield, 1978) but the small size of the rearing compartments (containing approximately 50 ml) could conceivably have affected larval size and survival if build-up of detrimental excretory products occurred.

First Zoea

Measurements. — 0.52 mm; 4 zoeae examined.

Carapace (fig. 1A). — Smooth, rounded, elongate, a small median spinule directly behind eyes on dorsal midline, a prominent oblique pterygostomian spine, ventrolateral margins unarmed, posterolateral margin convex rising to meet posterior median sinus. Eyes large, prominent, ovoid, occupying anterior third of carapace, fused.

Antennule (fig. 1B). — Elongate, uniramous, two-segmented, slightly flabellate rod; distal article $0.2 \times$ length of entire appendage, 4 terminal aesthetascs, plus 1 finely plumose seta subterminally; a small triangular tooth plus a fine hair at junction of proximal and distal articles.

Antenna (fig. 1C). — Biramous, endopod (flagellum) a spine-like process $1.5 \times$ length of scaphocerite, drawn into fine point, otherwise unarmed; scaphocerite about $0.6 \times$ length of endopod, armed distally around tip with about 12 plumose setae; distal portion indistinctly and incompletely segmented.

Mandible (fig. 1D). — Bluntly asymmetrical with reduced molar and incisor processes, former with about 8 spine-like teeth, latter with 3 large, more or less fused blunt teeth, adjacent to which a single large spine (proto-lacinia mobilis).

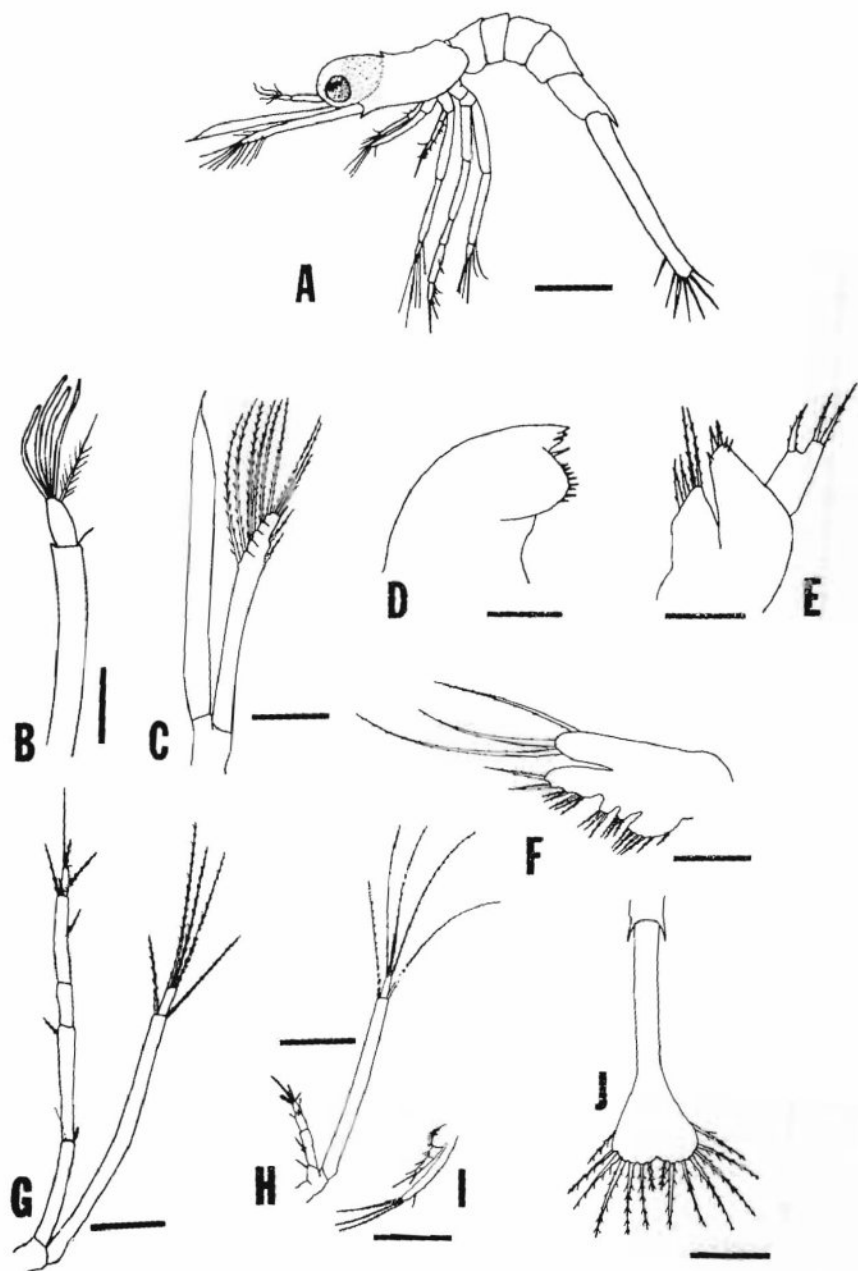


Fig. 1. *Merguia rhizophorae* (Rathbun), first zoea. A, lateral view; B, antennule; C, antenna; D, mandibles; E, maxillule; F, maxilla; G, maxilliped 1; H, maxilliped 2; I, maxilliped 3; J, telson. Scale bars are 0.52, 0.08, 0.16, 0.04 (D, E, F), 0.19, 0.22, and 0.55 mm, respectively.

Maxillule (fig. 1E). — Endopod unsegmented, 3 large spines (2 terminal, 1 subterminal); coxal endite with 4 elongate setae, basal endite with 2 stout terminal spines and 3 smaller subterminal tooth-like spinules.

Maxilla (fig. 1F). — Endopod indistinctly trilobed, setal formula progressing distally 3, 2, 2; basal endite bilobed, proximal and distal lobes with 3, 3 setae, respectively; coxal endite fused, unilobate, 5 terminal, 2 marginal setae; scaphognathite without apical lobe, 3 long, plumose, marginal setae, distally.

Maxilliped 1 (fig. 1G). — Endopod 2-segmented, $0.6 \times$ length of exopod, proximal segment with 2 lateral setae, distal segment with 3 setae plus elongate seta at tip adjacent to shorter hair; exopod unsegmented, 3 apical, 1 noticeably shorter subterminal seta; protopodal article with 8 short setae laterally, several of which more stout than others.

Maxilliped 2 (fig. 1H). — Endopod incompletely 5-segmented, $0.4 \times$ length of exopod, setal formula progressing distally 1, 1 + 1 hair, 1 hair, 1 + 1 hair, 4 + 1 elongate apical spine; exopod $2.5 \times$ length of endopod, 2-segmented, distal article noticeably shorter than proximal, bearing 3 long terminal setae; proximal article with 2 elongate setae at junction with distal segment, otherwise unarmed; protopodal segment naked.

Maxilliped 3 (fig. 1I). — Endopod $1.3 \times$ length of exopod, 5-segmented, setal formula progressing distally 2, 1, 0, 4, 1 + 1 elongate spinous process apically; subapical seta finely spinulate with thin hair adjacent; exopod 2-segmented, proximal longest, about $0.9 \times$ distal article, 2 setae at junction with latter; distal article with 3 terminal setae; protopodal segment naked.

Abdomen (fig. 1A). — Five somites, first 3 unarmed, fourth and fifth each with paired long thin posterodorsal spines; no pleopods.

Telson (fig. 1J). — Widely spatulate, length approximately $2.7 \times$ width; segment 3.75 longer than fifth abdominal somite, unarmed laterally; distal marginal spine and setal formula $7 + 7$, appearing as $1-7 + 1-7$ setae (see Gore, 1979, for details).

Second Zoea

Measurements. — 0.74 mm; 4 specimens examined.

Carapace (fig. 2A). — Similar to previous stage, but more elongate; a prominent sharp thin rostral spine, a smaller supraocular spine on anterodorsal margin, plus distinct pterygostomial spine; a median carina which may be developed distally into small tooth-like apex on dorsal midline behind rostral spine; carapace otherwise smooth; eyes stalked on greatly elongate peduncles, $1.6 \times$ length of carapace, terminating in distinctly ovoid ocellus twice as long as wide.

Antennule (fig. 2B). — As in previous stage but longer, distal article now about $0.15 \times$ total appendage length; 4 aesthetascs plus elongate plumose setae terminally; small triangular tooth of first stage now reduced to an acute spinule.

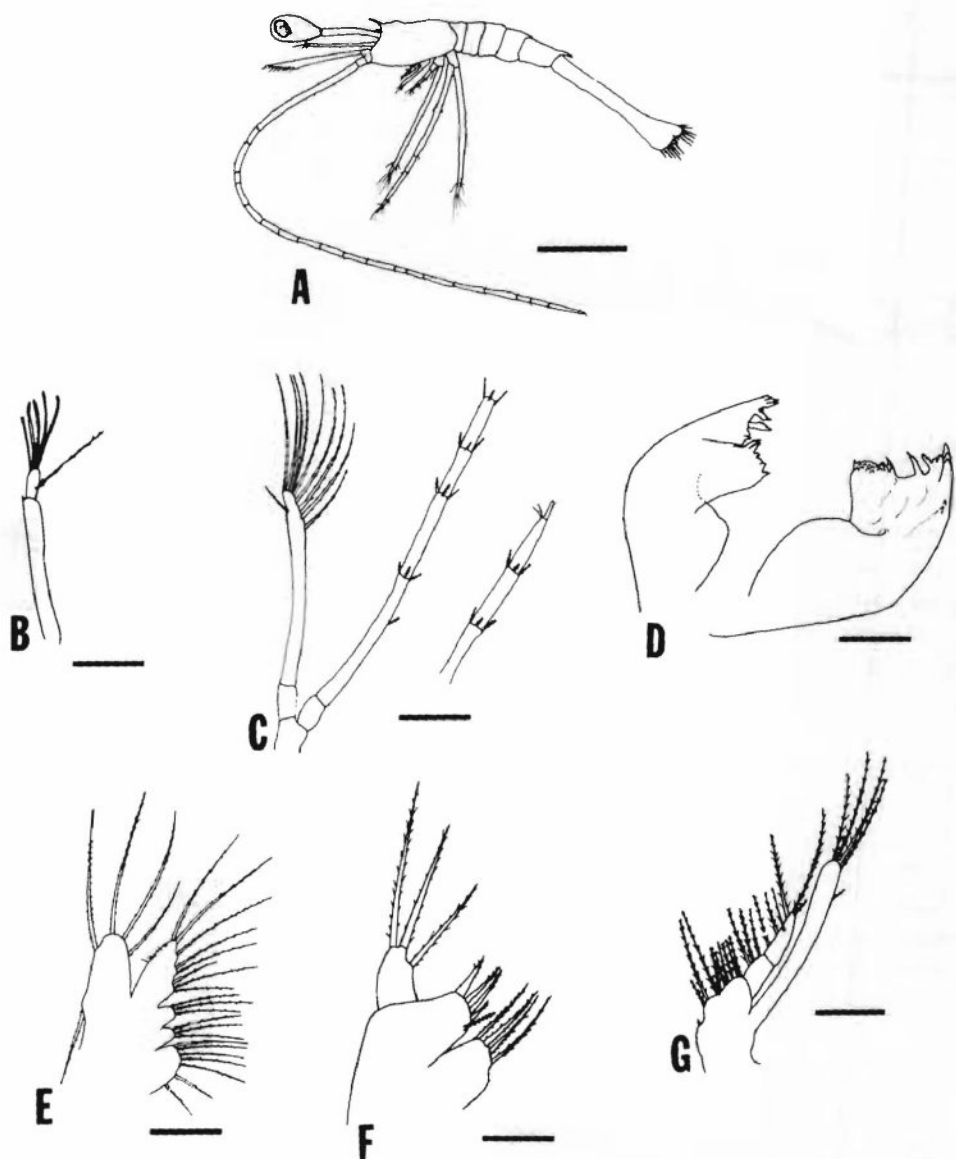


Fig. 2. *Merguia rhizophorae* (Rathbun), second zoea. A, lateral view; B, antennule; C, antenna; D, mandibles; E, maxillule; F, maxilla; G, maxilliped 1. Scale bars are 0.74, 0.24, 0.25, and 0.05 mm (D-G), respectively.

Antenna (fig. 2C). — Now with distinct flagella and elongate scaphocerite blade, latter about $12 \times$ longer than wide, armed distally with about 10 elongate setae; former with about 20 segments, each armed distally with 3 distinct spines, tip with 2 hairs at junction of penultimate and ultimate segments, plus another subapically.

Mandible (fig. 2D). — Asymmetrical as before, now heavily spinose and dentate; molar process with about 6 large sharp teeth plus numerous smaller, blunt dentition internal to these; incisor process with several sharp lateral teeth plus 2 distinctly spinous jagged cusp-like processes, larger of which is lacinia mobilis, developed from single large fixed spine in first stage.

Maxillule (fig. 2E). — Endopod spines now formed into 3 elongate stout setae; coxal endite setae longer, more spine-like, basal endite with 4 large spines plus 1 thinner smaller spine-like seta.

Maxilla (fig. 2F). — Endopod remains unsegmented, setal formula progressing distally 3, 2, 1, plus 2 apically, a group of fine hairs laterally as illustrated; basal endite and coxal unchanged from stage I, occasionally minus 1 seta; scaphognathite still without apical lobe, but with an elongate apical seta, 4 distal marginal setae as illustrated.

Maxilliped 1 (fig. 2G). — Endopod remains 2-segmented, about $0.6 \times$ length of exopod, setal formula progressing distally 3, 3+3 apically; exopod as in stage I, now with 4 terminal and 1 lateral seta; coxal and basal articles fused, now with 10 setae plus distinct small sharp tooth proximally.

Maxilliped 2 (fig. 3A). — Endopod now 4-segmented, setae progressing distally 1, 1, 2, 4; protopod with 2 setae; exopod $3.4 \times$ length of endopod, 2-segmented, distal article noticeably shorter, 5 long terminal setae, proximal article elongate with 2 lateral plus 1 seta just proximal to junction of distal article, as shown.

Maxilliped 3 (Fig. 3B). — Endopod still about $1.3 \times$ length of exopod, setal formula changed, progressing distally now 2+1, 1, 2, 3, 1+ an elongate sharp spine and a minute hair; exopod 2-segmented, proportions similar to first stage, setal formula 3, 4.

Abdomen (fig. 2A). — Unchanged in form and armature from stage I, no pleopods or primordia observable.

Telson (fig. 3C). — As in stage I, length now $3.1 \times$ width, total segment about $4 \times$ longer than fifth somite; marginal process formula remains 7+7 (1-7).

Third Zoea

A complete specimen of this stage was unavailable for examination. The following description is based on preliminary notes and illustrations made of a single zoea which has since been destroyed.

Carapace. — Similar to previous stages, with rostral, supraocular and pterygostomial spines present.

Antennule. — Unchanged in form from previous stage, but now 3-segmented, with 3 or 4 aesthetascs on terminal article.

Antenna. — Flagella approximately $1.5 \times$ total length of zoea, with short spines as previously, 3 long plumose setae at tip; scaphocerite with about 10 marginal setae, now with distinct distolateral spine.

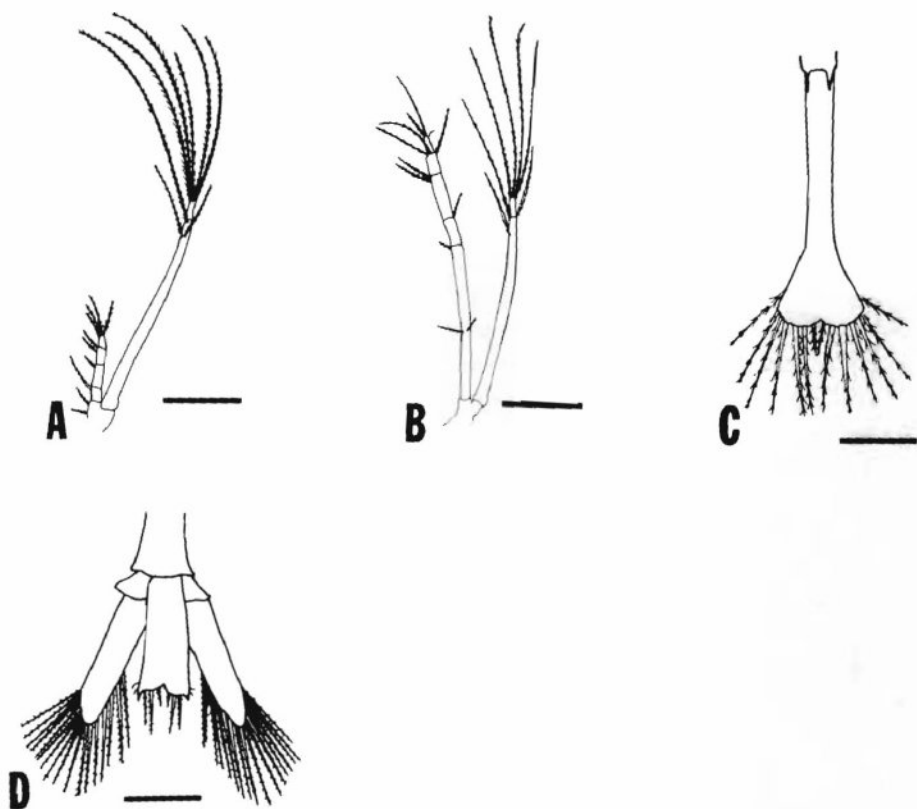


Fig. 3. *Merguia rhizophorae* (Rathbun). A-C, second zoea; D, third zoea. A, maxilliped 2; B, maxilliped 3; C, telson; D, telson of third zoea. Scale bars are 0.25 (A, B), 0.29, and 0.05 mm, respectively.

The mandibles, maxillulae and maxillae are unavailable for description.

Maxilliped 1. — Endopodite now 3-segmented; exopod approximately same ratio in length to endopod, with at least 3 setae on terminal article.

Maxilliped 2. — Endopodite 3-segmented (variable), with at least 4 setae on terminal articles; exopod ratio to endopod about the same as in previous stage, now with a total of 9 setae on distal articles.

Maxilliped 3. — Similar to previous stage, endopod with 6, exopod with at least 8 setae on respective terminal segments.

Pereopods. — Buds of first and second pereopods appear, that of the former having about 3 segments, that of the latter undifferentiated.

Abdomen. — Six somites, plus telsonal segment; armature as before.

Telson (fig. 3D). — Uropods present, each exopod with about 18 plumose setae; telson now rectangular, median notch present but reduced, posterior process formula $i + ii + III$ (movable) + 4-6, the outer lateral setae (i.e. 1, 2) now reduced to hairs ($i + ii$).

Fourth Zoea

Measurements. — 1.08 mm; 1 specimen examined.

Carapace (fig. 4A). — Noticeably larger, previously noted rostral, supraocular and pterygostomial distinct; dorsomedian carina present, with a bluntly rounded tooth anteriorly, lateral and posterior margins unarmed, latter noticeably convex, rising to wide median sinus.

Antennule (fig. 4B). — 3-segmented, proximal segment with 1 seta distally; length about 2 × length of distal 2 segments; latter subequal to each other, 2 aesthetascs, 1 hair at apex.

Antenna (fig. 4C). — Peduncular article developed, short; scaphocerite extremely long, about 12 × longer than wide, with 14 marginal setae and now with prominent distolateral spine, latter not overreaching tip of blade; carapocerite article developed, 2-segmented, subequal; flagellum as in previous stages.

Mandible (fig. 4D). — Similar to previous stages although enlarged; incisor process now more complex, with several jagged and rounded teeth, noticeable lacinia mobilis; molar process with several other cusp-like teeth and numerous smaller, rounded, blunt tubercle-like teeth.

Maxillule (fig. 4E). — Endopod setation now "stepped", 2 terminal, 1 subterminal on small lobe; basal endite with 3 strong spines, 3 setae, coxal endite with 5 strong setae plus a hair.

Maxilla (fig. 4F). — Endopod unsegmented; setal formula unchanged from stage II; basal and coxal armature as in stage II; scaphognathite still lacking apical lobe, with 7 marginal setae plus single elongate apical seta as illustrated.

Maxilliped 1 (fig. 4G). — Endopod indistinctly 3-segmented, slightly more than half length of exopod, 6 paired setae laterally, 3 terminally; exopod now 5-segmented, a single seta on penultimate, 4 elongate plumose setae on ultimate article; protopodal setation uncertain owing to breakage, at least 11 present.

Maxilliped 2 (fig. 5A). — Exopod 3-segmented, proximal article naked, middle with 3, distal with 7 setae as illustrated; exopod 5-segmented, about 3.8 × length of endopod, setation appearing as 1, 0, 4, 0, 4; protopodal articles fused, with at least 1 seta.

Maxilliped 3 (fig. 5B). — Endopod and exopod both 5-segmented; former now 1.25 × longer than latter, setation 2, 1, 2, 3, 3 (latter consisting of elongate spiny seta, 1 plumose, sometimes with plus 1 hair); setation on exopod 0, 2, 1, 1, 4.

Pereopod 1 (fig. 5C). — Endopod 5-segmented, protopodal article fused, naked; slightly longer (1.07 ×) than 2-segmented exopod; setation on former as 0, 1, 0, 3, 3 (as elongate strong spine, 1 seta, 1 hair); exopodal setation 1, 5 progressing distally.

Pereopod 2. — Undifferentiated bud.

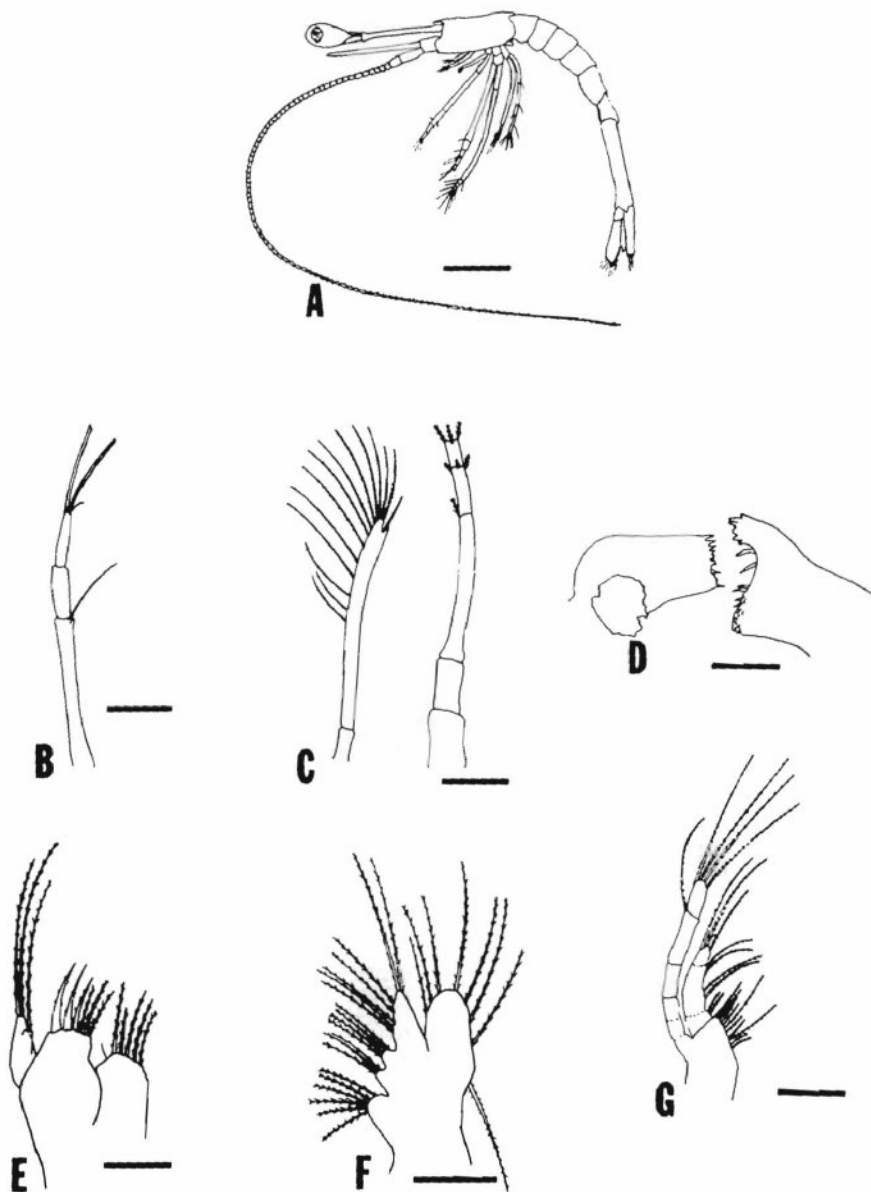


Fig. 4. *Merguia thizophorae* (Rathbun), fourth zoea. A, lateral view; B, antennule; C, antenna; D, mandibles; E, maxillule; F, maxilla; G, maxilliped 1. Scale bars are 1.05, 0.19, 0.26, 0.05 (D, E, F), and 0.09 mm, respectively.

Abdomen (fig. 4A). — Six somites plus telsonal segment; paired posterodorsal spines on fifth relatively strong, not nearly as long and acuminate as previous stages; those on fourth somite reduced to small teeth; no pleopod primordia evident.

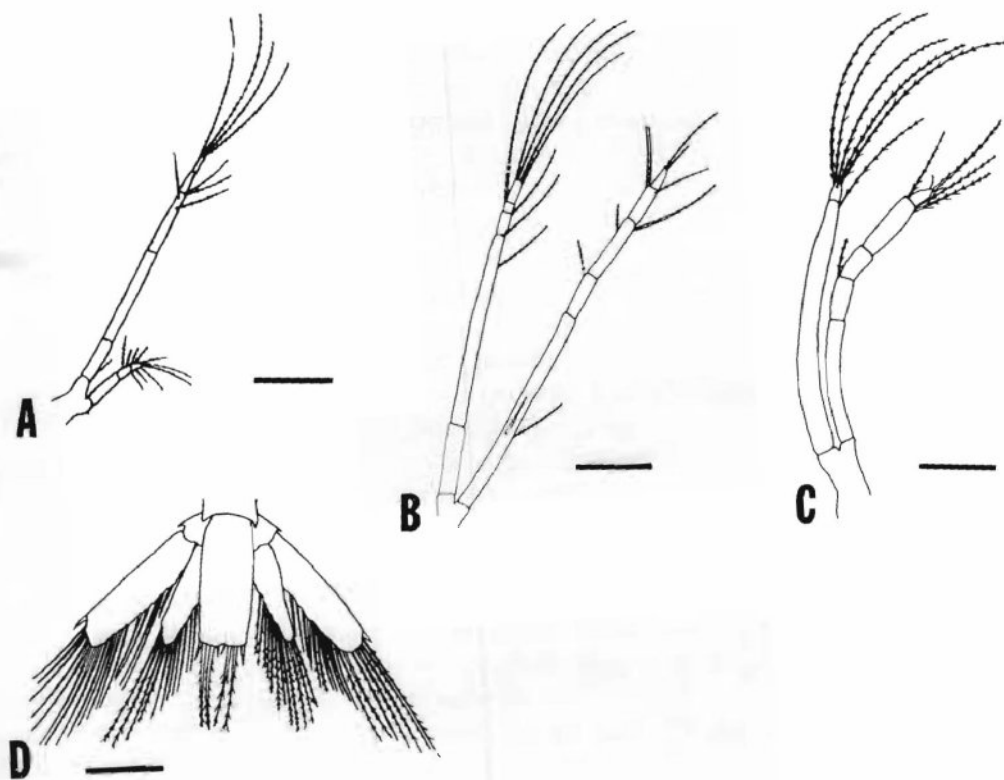


Fig. 5. *Merguia rhizophorae* (Rathbun), fourth zoea. A, maxilliped 2; B, maxilliped 3; C, pereopod 1; D, telson. Scale bars are 0.35, 0.40, 0.30, and 0.35 mm, respectively.

Telson (fig. 5D). — Uropods now consisting of exopodal and endopodal rami, former with up to 18 marginal setae (variable) plus distinct distolateral spine, latter with 9 to 12 marginal setae; telson proper distinctly rectangular, elongate, about $2 \times$ longer than wide, posterior margin formula (i + ii) + III (movable), 4-6.

Note. — Because of the incomplete observational data on stage III the appearance of features described as new for the fourth stage might have been present in stage III. The chief distinction between the latter and stage IV can best be seen in the presence of a well developed pereopod 1, and the addition of uropodal endopods in stage IV.

Fifth Zoea

Measurements. — 1.22 mm; 1 specimen examined undergoing premolt setal withdrawal.

Carapace. — Little changed from previous stage, larger, slightly more inflated. In the single specimen we examined the rostral supraocular and pterygostomial spines were not distinguishable owing to the poor state of preservation. The dorsomedian carina was present but it was not possible to determine its armature, if any.

Antennule (fig. 6A). — 3-segmented, relative length of articles progressing distally 1:0.3:0.7, terminal article with 3 long unequal aesthetascs.

Antenna (fig. 6B). — Carpocerite well-developed, inflated, somewhat truncate; flagellum as in earlier stages, maintaining 2 or 3 spines at distal articulation of each segment; scaphocerite extremely long, about 15 × longer than wide, distally with about 14 long setae; a prominent curved distolateral spine distinctly overreaching terminal margin of article.

Mandible (fig. 6C). — Heavily dentate and spinose processes; incisor process with 3-4 enlarged, thickened, rather smooth teeth, followed by about 6 jagged serrate recurved teeth; molar process with several smaller, bluntly pointed teeth plus 3 or 4 acute teeth; no evidence of palp bud.

Maxillule (fig. 6D). — Endopodal setae unchanged; spination on basal and coxal endites similar to previous stage but stouter.

Maxilla (fig. 6E). — General morphology of endopod, bilobed basal and unilobate coxal endite as in previous stage; setation undergoing withdrawal, indiscernible on basal endite, 7 strong setae on coxal endite; scaphognathite with 6 distal setae plus 2 setae on the distinctly developed, rounded, apical lobe.

Maxilliped 1 (fig. 6F). — Endopodite distinctly 3-segmented, about 0.4 × length of exopod, setation 4, 1, 3; exopod 3-segmented, setal formula 0, 1, 4 apically; protopodal segments fused, about 11 setae laterally, as illustrated.

Maxilliped 2 (fig. 6G). — Endopod 3-segmented, setation 1, 2, 3; exopod 5-segmented, about 4 × length of endopod, setal formula distally 0, 1, 1, 2, 4; protopodal segments fused, naked.

Maxilliped 3 (fig. 6H). — Endopod and exopod remain 5-segmented, former at least 1.3 × longer than latter, setal formula 2+1, 1, 2, 3, 3 (as elongate spine, 1 seta, 1 hair as shown) endopodal setation 0, 2, 1, 2, 4; protopodal segment fused, naked.

Pereopod 1 (fig. 6I). — Endopod 5-segmented, about 1.25 × longer than exopod, setal formula progressing distally 1, 1, 1, 1+4, 2 (an elongate dentate spine and a small adjacent hair); exopod 4-segmented, setal formula 0, 1, 2, 5; protopodal segments fused, naked. Note: Because of premolt condition, articulation indistinct, and exopod may be 5-segmented.

Pereopod 2 (fig. 6J). — Much smaller than first; two rami about equal in length; endopod appears 4-segmented, exopod 3-segmented, neither with noticeable setae, although they may have been present and lost during preservation.

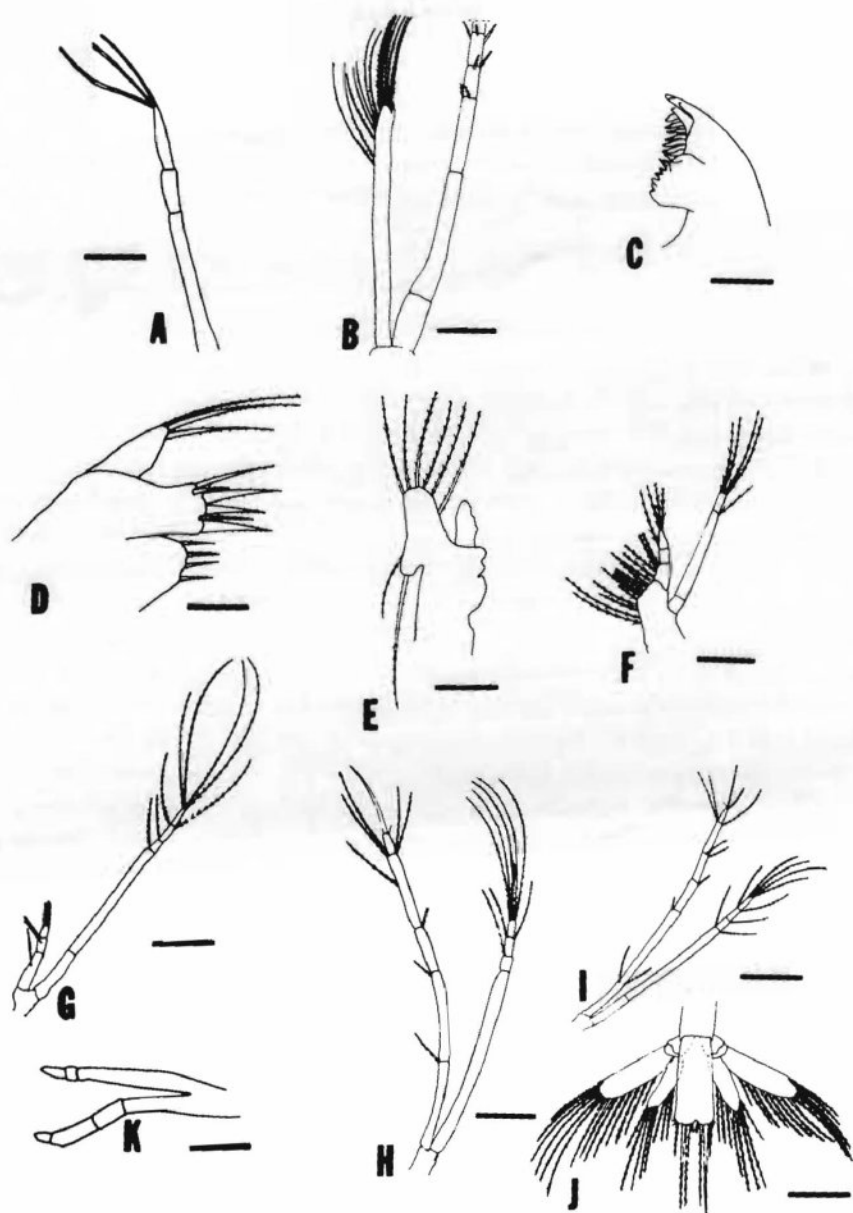


Fig. 6. *Merguia rhizophorae* (Rathbun), fifth zoea. A, antennule; B, antenna; C, mandible; D, maxillule; E, maxilla; F, maxilliped 1; G, maxilliped 2; H, maxilliped 3; I, pereopod 1; J, pereopod 2; K, telson. Scale bars are 0.20, 0.30, 0.06 (C, D), 0.10, 0.16, 0.35, 0.39 (H, I), 0.12, and 0.42 mm, respectively.

Abdomen. — Poorly preserved, 6 somites, plus telsonal segment; sixth $1.6 \times$ longer than telson, posterodorsal spines on fourth and fifth somites not seen; no pleopod primordia.

Telson (fig. 6K). — As in previous stage, length $2.4 \times$ longer than wide; uropodal endopods with about 12, exopods with about 18 setae, plus prominent fixed distolateral spine; posterior margin formula I (movable) + 2-4, indicating loss of lateral hairs i + ii. If development continues as in other caridean shrimp larvae, the movable spine will become fixed in the next or subsequent stage. The elongate setae are armed with fine spinules.

DISCUSSION

Caridean shrimp genera exhibit a bewildering array of larval forms, and those of the Hippolytidae are especially diverse. Neither Dakin & Colefax (1940) nor Gurney (1942) was able to provide any definition of hippolytid larvae because of this diversity, and the picture is little changed today. However, because of the mobile and greatly elongated eyestalks they possess, second and later stages of at least some caridean zoeae are assignable to the family Hippolytidae. As seen in this study, larvae of *Merguia* are one example, joining the composite larval genus *Eretmocarid* (Gurney & Lebour, 1941; Gopalakrishnan & Laurs, 1971), known to contain larvae of other hippolytid genera including *Lysmata* (Gurney, 1937, 1942). This larval genus also includes allegedly pandalid or nematocarinid larvae (Gurney, 1924, 1942). These larval forms possess greatly lengthened eyestalks beyond the first zoeal stage. As is typical for most caridean larvae, the eyes are sessile in the first zoeal stage.

The eyes of *Merguia* in the first zoeal stage may encompass nearly the entire front half of the larval cephalothorax. In the second stage, along with long and mobile eyestalks, larvae of *Merguia* possess a simple telson, and have only five abdominal somites. Thus, they follow a general trend seen in many other second stage decapod larvae. Third stage larvae of *Merguia* add a sixth abdominal somite before the telsonal segment, as well as uniramous uropods, again sharing this feature with other larval decapods. Fourth stage larvae of *Merguia* are similar to those in the preceding stage, but the telson now exhibits both endopodal and exopodal rami on the uropods, and the posterior telsonal margin has a formula different from stage III. In the fifth stage (and later?) there appears to be little to differentiate larvae of *Merguia* using the evidence at our disposal, and the only salient difference seems to be the greatly increased length of the endopod of the first maxilliped. Throughout the first five stages the setal count on the maxilliped exopods progresses from four, seven, nine, eleven, and perhaps thirteen, but certainly additional larvae will need to be obtained before the fifth stage enumeration can be accepted. Larvae of *Merguia* are also distinctive in possessing (as far as can be determined) a greatly lengthened antennal flagellum from the second stage onward, a feature not seen often in other *Eretmocarid*-type larvae. Otherwise, the zoeae of *Merguia* show little notable variation in ontogenetic characters from those associated with other caridean zoeae.

Larval characters of *Merguia* are compared with those seen in other larvae possessing elongated eyestalks in second and later stages in Table II. Knowledge of all these larvae is so scanty and speculative that such comparisons must be considered provisional. However, in zoeae of *Merguia* certain features characterize the early larval stages, and these are summarized (following Gurney's 1937 format) below:

1) Rostrum short, not reaching beyond end of antennular or antennal peduncle; without dorsal or ventral teeth in all stages.

2) Carapace with supraorbital and pterygostomial spines, but without antennal spine; a postrostral middorsal tooth in stage I, becoming a tubercle in stage II and later.

3) Abdominal somites 2 and 3 without, somites 4 and 5 with, paired spines on the posterodorsal margin; all pleura rounded.

4) Eyes large; fused in stage I, occupying entire frontal region; carried on long eyestalks (about $0.8 \times$ rostral carapace length), but not excessively long.

5) Endopod of antenna in stage I a slender rod, drawn into a spine, without single long seta; in stage II an elongate peduncle with multiarticulate flagellum.

6) Antennular aesthetascs normal, not membranous.

7) No pereopodal development seen in stages I-IV.

8) At least seven, and probably nine, larval stages are postulated, based on the morphological development of larvae in this report.

Bourdillon-Casanova (1960) also provided a list of characters held in common between the genera *Lysmata* and *Caridion*. Among the more noteworthy differences between these two genera and *Merguia* are that the latter have: 1) a long rostrum; 2) carapace with antennal spine; 3) abdominal somite 5 with paired spines (at least in the early stages); 4) antennal endopod terminating in two setae; 5) a membranous antennular aesthetasc (apparently a subgroup feature in some hippolytids); and 6) pereopodal development in early larval stages. Larvae of *Caridion* and *Lysmata* share with *Merguia* greatly elongated eyestalks in the second and later stages, and perhaps the development through nine zoeal stages as well. Bourdillon-Casanova noted that variation in the number of larval stages within *Lysmata* (at least in Mediterranean species) could be a result of confusing the larvae of very closely related species (e.g. *Lysmata seticaudata* (Risso) and *L. nilita* Dohrn & Holthuis) that occur in the region, or be a consequence of skipped or intercalated stages, because some larval stages might be facultative and not indispensable. She provided examples of morphological variation noted by other authors, who may not have observed larvae of the same species, to support her contention.

ERETMOCARIS LARVAE AND THE GENUS MERGUIA

The larval genus *Eretmocaris* Bate, 1888, an intriguing group with substantial variation in appendage morphology and setation, was correctly considered by

Gurney (1937) to be a composite, representing larvae of several, perhaps not so closely related, genera. Gurney described 12 long-eyestalked forms, which he placed in this genus, and attempted to relate these types to some 11 "latreutid group" genera within the Hippolytidae. For example, *Eretmocarid* R.S. I. was assigned to *Hippolysmata*, and R.S. II, B.R. I, II, III, and A.I, II and III were considered "with some probability" to belong to the genus *Lysmata*. Four other Atlantic *Eretmocarid* (A.IV, V, VI, VII) were not identifiable with either *Lysmata* or *Hippolysmata* as defined by Gurney, and so remained to be categorized. Toward this end, Gurney dismissed from consideration the genera *Tozeuma* and *Latreutes*, neither of which have *Eretmocarid*-like larvae, and *Bythocaris* because it has no planktonic larval stages. *Gelastocaris* and *Lysmatella* (and erroneously *Merguia*) were eliminated on zoogeographical grounds, because they had no Atlantic representatives to which the A-series of larvae could be assigned. Left as possible candidates for *Eretmocarid* A.IV-VII were *Mimocaris*, *Trachycaris* and *Paralatreutes*.

Dakin & Colefax (1940) summarized the history of the known *Eretmocarid* larvae. However, several taxonomic changes have taken place since both Gurney's (1937) and Dakin & Colefax's considerations. In 1955, Holthuis synonymized *Eretmocarid* under the genus *Lysmata*, and placed *Lysmatella* as a subgenus of *Hippolysmata*. In 1972, Chace considered *Hippolysmata* a junior synonym of *Lysmata*, thereby uniting three previous genera under the latter taxon. In so doing, he alleviated several problems created by the diversity of form seen in larvae assigned to *Eretmocarid*. For example, the insubstantial differences between *Eretmocarid* larvae assigned to *Lysmata* (e.g. Gurney's R.S.II) and *Hippolysmata* (Gurney's R.S.I) could not be accommodated within the single genus *Lysmata*. However, those differences between Gurney's R.S.I or II and the *Eretmocarid*-like *Merguia* are of more consequence. A comparison of the synopsis provided by Gurney (1937) for *Lysmata* larvae with that presented in this report for *Merguia* shows that the two taxa differ in many characters, although the larvae are, nevertheless, somewhat related. In fact, of the 12 forms discussed by Gurney in his 1937 report, only the zoea named R.S.I "*Hippolysmata*?" [= *Lysmata*] shows a close relationship to *Merguia* larvae. Gurney's species differ in lacking paired posterodorsal spines on abdominal somite 4, in having a longer rostral spine, 4 (instead of 1) pterygostomial spines, a flabellate or membranous aesthetasc on the antennule (as in *Caridion*), a different setal formula on the maxillule, maxilla and maxillipeds, and a telson process formula of 1-7 in stage I, 1-8 in stage II and i + 2-7 + viii in stage III. These differences are clearly on the order of generic distinctions.

None of the 12 forms considered by Gurney (table II) are assignable to *Merguia*. Larvae of *Merguia* are easily distinguished from all *Eretmocarid* in possessing a long, well-developed antennal flagellum from stage II onward. Only *Eretmocarid* A.VI and A.VII have similar, long, well-developed antennal flagella and these two forms are clearly advanced stages, possessing chelate

TABLE II
Comparison of selected characters in the larval genus *Eretmocarid* and derivative genera

<i>Eretmocarid</i>	Stages known	Rostrum	Carapace spines	Abdominal spination	Eye: Stalk ratio	Ant 1:2 ratio	Telson formula	Special characters
Gurney, 1937								
R.S.I. (<i>Lyssmata multiscissa?</i>)	1-3	Long, unarmed	Middorsal tubercle, pty., s.o.	Paired, somite 5	$E \approx 1/2 S$	$A1 \sim > A2$ $F > SK$	7+7 (I) 8+8 (II)	Antennule w. membranous acetabasc [Also <i>Caridion</i>]
R.S.II. (<i>Lyssmata</i>)	2 (4, 5, 8, 9?)	Short, unarmed	Middorsal? Pty.	None	$E \approx 1.2 S$	$A1 > A2$ F absent?	8+8	Pereopod 5 propodus paddlelike
B.R.I. (<i>Lyssmata</i> sp.?)	Zoea 4 or later	Short, 1 dorsal tooth	Middorsal, pty., ant., s.o. (\pm)	None	$E \approx S$	$A1 \approx A2$ $F. 2.5 \times SK$	7+7	Pereopod 1 chelate, pereopod 2 subchelate, pereopod 5 paddlelike, serrate distodorsally
B.R.II. (<i>Lyssmata</i> sp.?)	Zoea 4 or later	Long, slender, 3 teeth 1 tooth	Ant., pty.	None	$E < S$	$A1 < A2$ $F 2.0 \times SK$	5+5	Middorsal spine a pro-curved hook; pereopod 1 & 2 subchelate; pereopod 5 paddlelike, serrate distodorsally
B.R.III. (<i>Lyssmata</i> sp.?)	Late zoea	Very small, unarmed	Middorsal, pty.	None	$E 1/2 S$	No data	7+7	Antennular peduncle w. stylocerite rudiment; pereopod 5 "fully developed"
A.I. (<i>Exhipolysmata ensirostris?</i>)	Late zoea	Intermediate 3 teeth 0	Middorsal, ant., pty., s.o.	None	$E > S$	$A1 < A2$ $F = SK$	5+5	Eyestalk w. 1ge spine; pleopods present
A.II. (<i>Eretmocarid stylorostris?</i>)	Late Zoea	Short, 1 0	Middorsal tooth ant., pty.	None	$E < S$	$A1 = A2$ $F > SK$	5+5	Elongate pleopods present
A.III. (<i>Lyssmata?</i>)	Late zoea	Short, 1 tooth 0	Middorsal, ant., pty., s.o.	None	$E \approx S$	$A1 \sim = A2$ $F < SK$	7+7	Pereopod 5 paddlelike, distally serrate both dorsally and ventrally
	Late zoea	Short, 1 tooth 0	Middorsal, ant., pty., s.o.	None	$E \approx S$	$A1 \sim = A2$ $F < SK$	5+5	Older specimens w. rudimentary chelae pereopods 1, 2.

TABLE II (continued)
Comparison of selected characters in the larval genus *Eretmocarid* and derivative genera

<i>Eretmocarid</i>	Stages known	Rostrum	Carapace spines	Abdominal spination	Eye: Stalk ratio	Ant 1:2 ratio	Telson formula	Special characters
A.IV. (<i>Eretmocarid</i> X?)	Postlarva?	Intermediate 1 tooth	Ant., pty., s.o.	None	E>S	A1<A2 F>SK	5+5	Pereopod 4 small, ovoid irregularly setose; pereopod 5 large ovoid paddlelike, fringed w. short hairs
A.V. (<i>Eretmocarid</i> <i>corniger</i>)	Penultimate zoea?	Very long, slender, 6 teeth 0	Middorsal, ant., pty., s.o.	Large spine somite 3	E>S	A1<A2 F<SK	5+5	Supraorbital and antennal spines large, pterygostomial minute; pleopods present
A.VI. (<i>Eretmocarid</i> <i>dolichops</i>)	Late zoea	Short, unarmed	Middorsal tubercle, ant., pty.	Pleura of somite 3-5 "rather acute"	E>S	A1>A2 F 3.0 x SK	4+4	Eyestalk 2-segmented, constricted proximally; pereopods 1 & 2 chelate, pleopods present
A.VII.	Late zoea	Short, upturned, unarmed	Ant., pty., s.o.	Somites 1-4 w. dorsal spines	E<S	A1<A2 F>SK	3+3	Pereopods 1, 2 chelate; pereopod 5 not paddlelike
Lebour, 1941 <i>Eretmocarid</i> <i>dolichops</i>	Late zoea (advanced)	Short, unarmed	Middorsal & posterodorsal tubercles, ant., pty.* teeth	Pleura not acute*	E>S	A1>A2* F~3.0 x SK*	4+4 or 5+5	Pereopods 3-5 propodi inflated, not paddlelike; pleopods w. appendix interna; eyestalk 2-segmented
<i>Eretmocarid</i> X (<i>Plesionika</i> or <i>Nematocarcinus</i> ?)	5 late zoeal stages	Short, unarmed	Middorsal, ant., pty. teeth (3) later molt	Pleura rounded	E>S	A1<A2* F~3.0 x SK	4+4	Pereopods 3-5 propodi broad paddles, other segments setose; eyestalks 2-segmented
Kurian, 1956 <i>Lysmata</i> <i>seticaudata</i>	2, 4-9	Short to long, doubly curved in later stages; 1-2 teeth	"Marginal teeth" in stage 4	No data	"Great elongation"	No data	4+4 to 7+7	"Fifth pereopod long, propodus flattened" (paddlelike)

TABLE II (continued)
Comparison of selected characters in the larval genus *Eretmocarid* and derivative genera

<i>Eretmocarid</i>	Stages known	Rostrum	Carapace spines	Abdominal spination	Eye: Stalk ratio	Ant 1:2 ratio	Telson formula	Special characters
Bourdillon-Casanova, 1960								
<i>Caridion gordonii</i>	1, 2	Intermediate, unarmed	No data	No data	No data	No data	No data	Antennule w. membranous aesthetasc
<i>Caridion stevensi</i>	1, 4	No data	No data	No data	No data	No data	No data	Antennule w. membranous aesthetasc
<i>Lysmata seticaudata</i>	1-9	Intermediate, unarmed (1-3), 1-2 teeth 0 later stages	Middorsal, ant., pty. s.o.	Somite 5 w. paired lateral, 3 dorsal spines	No data	Variable	7+7 to 8+8	Pereopod 5 with natatory "palette"; antennule with membranous aesthetasc; pleopods in stage 4
Dakin & Colefax, 1940								
<i>Eretmocarid</i> , Sydney species No. 1 (<i>Eretmocarid remipes?</i>)	mysis	Short, 3 teeth - 0	Middorsal (gibbous), ant., pty., s.o.	None	E < S	A1 < A2* F > SK	No data	Pereopod 5 with elongate paddlelike propodus, distally serrate dorsally and ventrally
No. 2	4 stages obtained, 1 described (mysis)	Long, 2 small teeth 0	Middorsal (hooklike), ant., pty.	None	E > S	A1 = A2* F 1.3 x SK	6+6?	Pereopod 5 with short ventrally serrate paddlelike propodus; pereopods 1 & 2 not chelate
Bate, 1888								
<i>Eretmocarid remipes</i>	Probably zoea 4 or later	Long, armed 2 teeth 0 teeth	Middorsal, ant., pty., s.o.	None	E > S	A1 < A2 F > SK	No data	Subrostral lobe with small ocellus; pereopods 4, 5 with elongate paddlelike propodus, spined dorsally and ventrally; pleopods present
<i>Eretmocarid longicaulis</i>	Late zoea	Short, unarmed	Middorsal, pty.?	None	E < 0.2 x S	A1 = A2 F broken F > SK	No data	Eyestalk greatly exceeds eye length; pleopods present, pereopods missing
<i>Eretmocarid stylostris</i>	Early zoea (of <i>E. longicaulis</i>)	Short, unarmed, needlelike	Frontal, pty.?	None	E 1/2 S	A1 = A2 F broken	No data	No pleopods; pereopods not oarlike
<i>Eretmocarid corniger</i>	Early zoea	Present, broken	Middorsal, long s.o. long pty.	Recurved spine somite 3	E > S	A1 = A2 F < SK	No data	Pleopods present; pereopods not paddlelike; cephalothorax short

pereopods. *Merguia* is separated from *Eretmocaris dolichops* Ortmann in the segmentation of the eyestalks, which in *Merguia* occurs immediately behind the ocular segment. In *E. dolichops*, as well as *Eretmocaris* X (Gurney & Lebour, 1941), *Eretmocaris* A.IV and A.VII (Gurney, 1937), the segmentation occurs within the proximal half (or shorter) of the eyestalk itself. The general form and setation of the maxilliped propodi also separate *Merguia* from these forms, which have expanded or even paddle-shaped propodal articles, and are often heavily setose (see, e.g., Lebour's *Eretmocaris* X). In addition, the telsons in these *Eretmocaris* differ substantially from that seen in *Merguia*, in having either a greater number or a different arrangement of posterior marginal processes. These differences, as well as those occurring in the other listed species of *Eretmocaris*, are of such magnitude that we need not dwell on them further (see table II). It should be noted here, however, that the table provided by Gurney (1937: 374) does not agree in several respects with information given in the text of his report. Therefore, data here are taken entirely from Gurney's text and illustrations.

Finally, we suspect that when the larvae of *Merguia oligodon* become known they will exhibit characteristics similar to those delineated for *M. rhizophorae*. As to the composite larval genus *Eretmocaris*, we presently see no reason to discard it until the zoeal features within the genus *Lysmata* (and its subgenera) become clearly defined, and the larvae of other genera such as *Mimocaris*, *Paralatreutes* and *Trachycaris* are described.

RÉSUMÉ

Les larves de *Merguia rhizophorae* élevées en laboratoire présentent beaucoup des caractéristiques typiques des larves attribuables à la famille des Hippolytidae et au genre larvaire composite *Eretmocaris*. Les larves ont un flagelle antennaire fortement allongé, à partir du second stade, ce qui semble les distinguer des autres *Eretmocaris*. On ne peut comparer ces stades larvaires avec ceux des autres Carides que de façon approximative, par manque de connaissances sur la plupart des larves de la famille. Nous suggérons que le genre larvaire *Eretmocaris* soit conservé jusqu'à ce que les caractéristiques larvaires des espèces soient mieux connues.

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ELECTROPHORETIC INVESTIGATION OF POPULATIONS
OF THE CIRRIPEDE *BALANUS BALANOIDES* (L.) AROUND
THE NORTH ATLANTIC SEABOARD

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INTRODUCTION

Balanus balanoides (L., 1758) is an abundant, intertidal cirripepe found in circumboreal waters. In the Atlantic Ocean it is to be found as far south as Cape Hatteras on the eastern seaboard of North America, around Labrador, Greenland, Iceland, the White Sea and as far south as north-west Spain in Europe (Hutchins, 1947; Fischer-Piette & Prenant, 1956; Wells et al., 1960; Peterson, 1966). The possibility of the existence of subspecies or physiological variants in such widespread cirripepe species has been demonstrated by Southward (1964), using the relationship between cirral activity and temperature. Although it was not clear whether the observed relationship was under phenotypic or genotypic control, he was able to show slight but consistent differences in cirral activity between subspecies of *B. balanoides*.

Balanus balanoides shows small but significant differences in reproductive phenology and egg size between the east and west coasts of the Atlantic. Crisp (1959a) found a slower rate of embryonic development in British *B. balanoides* than that recorded by Barnes & Barnes (1959) for a North American population. North American *B. balanoides* from New England have a larger egg and breed about one month earlier than those from Britain (Barnes, 1958; Crisp, 1959b). These differences are retained for at least one year when specimens are transplanted from the North American continent to Europe and vice versa (Crisp, 1964, 1968). Barnes & Barnes (1976) increased the number of populations examined on both sides of the Atlantic seaboard and their results confirmed those of Crisp (1964) that racial differences exist in terms of the timing of fertilization and the rate of embryonic development. Crosses between North American and European specimens of *B. balanoides* produce viable offspring which have successfully metamorphosed and settled in the laboratory with egg and larval size determined by the female of the cross (Crisp & Flowerdew, unpublished observations). The maintenance of characteristic reproductive differences in transplanted animals led Crisp (1964) to propose that North