LARVAL DEVELOPMENT OF THE CUBAN STONE CRAB, *MENIPPE NODIFRONS* (BRACHYURA, XANTHIDAE), UNDER LABORATORY CONDITIONS WITH NOTES ON THE STATUS OF THE FAMILY MENIPPIDAE[1]

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ABSTRACT

The complete larval development of the Cuban stone crab, *Menippe nodifrons*, is described and illustrated. Larvae reared in the laboratory passed through a prezoeal, five and uncommonly six zoeal, and one megalopal stage. At 30° C the megalopal stage was attained in 16-17 days, at 20° C, 28-37 days. The six zoeal stages of *M. nodifrons* are compared with those of its sympatric congener *M. mercenaria* and with the first zoeal stage of the Indo-Pacific species *M. rumphii*. Larvae of the genus *Menippe* may be distinguished from other xanthid larvae by a combination of morphological features, including antennal development (exopodite at least three-fourths the length of protopodite), lack of setae on the basal segment of the second maxillipedal endopodite, and number of larval stages (*Menippe*, 5 or 6; most other xanthids, 4). Using Lebour's criteria (emphasizing antennal development and number of zoeal stages) to determine the primitive or advanced status of decapod larvae, the genus *Menippe* is more closely related to the phylogentically primitive family Cancridae than to most of the Xanthidae. The possible reestablishment of the family Menippidae is discussed in view of new larval evidence.

The Cuban stone crab, *Menippe nodifrons* Stimpson 1859, is a medium-sized xanthid crab closely allied to the common commercial stone crab, *Menippe mercenaria* (Say 1818). The type-locality of *M. nodifrons* is the Indian River region located on the central eastern Florida coast between lat. 27° and 29° N. The western Atlantic range of the species extends from the Indian River, Fla., to the state of Santa Catherina, Brazil. Although Rathbun (1930) listed Cameron, La., as a collection site, subsequent sampling in this and other areas of the northwestern Gulf of Mexico had failed to produce any more specimens (Felder[3]). In the eastern Atlantic, specimens attributed to *M. nodifrons* have been recorded from Senegal to Angola, West Africa (Monod 1956).

Studies on *M. nodifrons* have been primarily taxonomic. Since Rathbun's monograph on the American cancroid crabs (1930), the major studies dealing with this species include faunal investigations of West Africa (Capart 1951; Monod 1956), a survey of stomatopod and decapod crustaceans of Portuguese Guiana (Vilela 1951), and an ecological investigation of the species on Floridan sabellariid worm reefs (Gore et al. 1978).

Although there are five (possibly seven) species in the genus *Menippe*, four occurring in the New World, *M. mercenaria* is the only species whose complete larval development has been described (Hyman 1925; Porter 1960). The first zoeal stage of a species identified as *M. rumphii* (Fabricius 1798) was described by Prasad and Tampi (1957) from an ovigerous female collected from the Indian Ocean (Mandapam Camp, South India). However, the taxonomy of *M. rumphii* is confused and the species is distinguished from *M. nodifrons* primarily by the presence of stridulating ridges on the palm (Stimpson 1871; Milne-Edwards 1873). Whether Rathbun (1930) and Monod (1956) were correct in synonymizing *M. rumphii* with *M. nodifrons*, remains to be seen; the former is also considered to be a Caribbean-Western Atlantic species (Dana 1852; Milne-Edwards 1873). If *M. rumphii* is indeed synonymous with *M. nodifrons* and not a separate species, Prasad and Tampi's Mandapam Camp record would be a remarkable range extension for *M. nodifrons*. Further investigation on larval morphology and development may answer this question.

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[2]Smithsonian Institution, Fort Pierce Bureau, Fort Pierce, FL 33450.

[3]Felder, D. 1973. An annotated key to the crabs and lobsters (Decapoda, Reptantia) from coastal waters of the northwestern Gulf of Mexico. LSU-SG-73-02, 103 p. Louisiana State University, Baton Rouge, LA 70803.

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To provide evidence for this problem, the complete larval development of *M. nodifrons*, reared under laboratory conditions, is described and illustrated here. Larvae of *M. nodifrons* are compared insofar as possible with descriptions of *M. mercenaria* and *M. rumphii*, and features used in separating the various larvae are noted.

MATERIALS AND METHODS

A 66.0 mm CW (carapace width) female with bright orange eggs was collected from a sabellariid worm, *Phragmatopoma lapidosa*, reef at Seminole Shores, Martin County, Fla. (Gore et al. 1978) on 15 June 1977. Ovigerous females were found from May through August. The berried crab was retained in a nonflowing marine aquarium at the Smithsonian Institution, Fort Pierce Bureau, and fed mullet, *Mugil* sp., strips daily. The egg mass progressively darkened from bright orange to dark brown until hatching on 26 June 1977. The larvae were cultured in the laboratory using methods developed by Costlow and Bookhout (1960, 1962), Gore (1968), and Provenzano (1967). Six 24-compartmented trays were used, and each compartment contained three zoeae. Equal numbers of zoeae were reared in oceanic water (35‰) at 20° C (±0.5°) in constant light; at room temperature (range = 21°-26.5° C; $\bar{x}$ = 24.5° C) in diurnal light; and at 30° C (±0.5°) in a constant temperature unit (CTU) in 12 h of light, 12 h of darkness. Seawater in the trays was changed and zoeae were fed freshly hatched *Artemia salina* nauplii daily. The number of zoeae was reduced to one per compartment on completion of the molt to the second zoeal stage.

Throughout the course of larval development all molts, dead zoeae, and some living representatives were preserved in 70% ethanol. Usually 10 specimens at each stage of development were dissected and examined for morphological characters using procedures described in studies by Gore (e.g., 1968). In the description that follows the first four zoeal stages of *M. nodifrons* are denoted as zoeae one (Z I) to zoeae four (Z IV). However, the fifth zoeal stage is discussed as either the penultimate fifth stage (Z Vp) which molts to a sixth stage before molting to megalopa, or the ultimate fifth stage (Z Vu) which molts directly to megalopa. Both fifth stages possess pleopods, appendages that typically develop in the stage preceding megalopa. Because there are few morphological differences between the penultimate and ultimate fifth stages, as noted in the larval descriptions, they are each considered one stage, and not substages. The sixth stage is referred to as an intercalated stage because it is inserted between the seemingly regular molt from fifth stage (i.e., Z Vu) to megalopa.

The measurement for each zoeal stage is the arithmetic mean of all specimens examined. Carapace length was measured from the base of the rostrum to the posterior edge of the carapace along the midline. Carapace width, in the megalopal stage, was measured across the widest part of the carapace. Direction of setation formulae in the descriptions progress proximal to distal.

A complete series of larvae, and/or their molts, were deposited in the National Museum of Natural History, Washington, D.C.; the Allan Hancock Foundation, University of Southern California, Los Angeles; the British Museum (Natural History), London; the Rijksmuseum van Natuurlijke Historie, Leiden; the Geneva Museum of Natural History, Geneva; and the Museum National d'Histoire Naturelle, Paris.

DESCRIPTION OF THE LARVAE

First Zoeae

Carapace length: 0.55 mm.
Number of specimens examined: 10.

Carapace (Figure 1A, B). Cephalothorax smooth, globose, with dorsal, rostral, and 2 lateral spines. Posteriorly curving dorsal spine usually 0.1× longer, but in some specimens equal to or shorter than straight rostral spine. Length of dorsal spine about 2.75× that of short, ventrally curving lateral spines. A minute seta found posterior to and at base of dorsal spine throughout all zoeal stages. A dorsal tubercle present in all stages midway between bases of dorsal and rostral spines. Eyes unstalked.

Abdomen (Figure 1A, B). Five somites and telson; second through fifth with 2 small setae on posterodorsal margin (remaining throughout all zoeal stages); second with small pair of lateral spines or knobs curving anteriorly; third with pair curving posteriorly (both pair present in all stages); fifth with pair of large ventrally curved spines at dorsolateral angle, present in all zoeal stages.

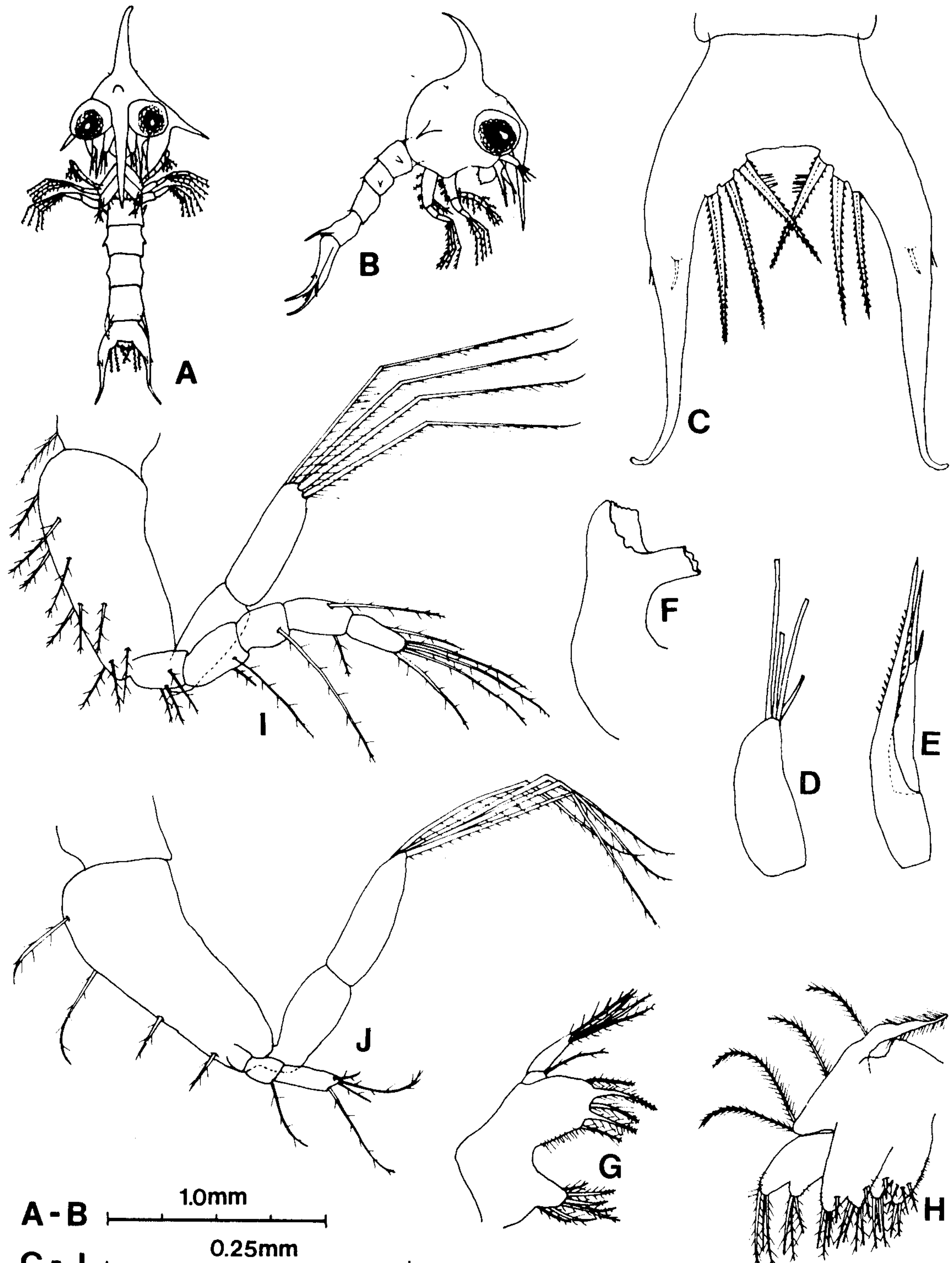

FIGURE 1.—First zoeal stage of *Menippe nodifrons*. (A) Ventral view; (B) lateral view; (C) telson; (D) antennule; (E) antenna; (F) left mandible (in ventral view as illustrated here and throughout all zoeal stages); (G) maxillule; (H) maxilla; (I) maxilliped 1; (J) maxilliped 2.

Telson (Figure 1C). One dorsal and two smaller lateral spines present on median portion of each upcurved furca. Three spines, each with three rows of spinules, on inner margin of each furca (present in all zoeal stages); setae replace spinules at midpoint of innermost spines, number variable but setae present in all zoeal stages.

Antennule (Figure 1D). Conical rod with 4 unequal aesthetascs terminally.

Antenna (Figure 1E). Protopodite a slender process bearing two rows of small teeth from about midlength to one-fifth from the distal tip. Exopodite tapered, approximately 0.75× length of protopodal process, with a slender spine (present in all zoeal stages) near distal end extending almost as far as tip of protopodal process; slender spine about 0.4× length of exopodite.

Mandible (Figure 1F). Assymetrically dentate, scoop-shaped process. Incisor process elongate with indistinct dentation. Molar process irregularly serrate on outer margin; left molar process with 2 or 3 small prominences along inner margin and at junction with incisor process; right side either smooth or with a prominence.

Maxillule (Figure 1G). Endopodite with two segments, proximal short with 1 long feathery seta laterally, distal with 4 long setae: 2 terminal, 2 subterminal. Coxal endite with 7 plumodentate setae (armed with hair proximally, spinules distally). Basal endite with 5 plumodentate setae, 2 of which are stouter; lower margin of endite with rows of fine hairs.

Maxilla (Figure 1H). Endopodite bilobed, each with 3 setae. Coxal and basal endites with 5 and 4 setae respectively, placed as shown. Anterior and posterior margins of endopodite, as well as basal and coxal endites, pubescent. Scaphognathite with 4 plumose setae on outer margin; distal portion tapering to a thin plumose process.

Maxilliped 1 (Figure 1I). Coxopodite with 1 seta; basipodite with 10 ventral setae progressing distally 2,2,3,3. Endopodite five-segmented, ventral setae 3,2,1,2,4+I (Roman numeral denotes dorsal setae). Exopodite two-segmented; 4 natatory setae terminally.

Maxilliped 2 (Figure 1J). Coxopodite naked; basipodite with 4 ventral setae. Endopodite three-segmented, ventral setae progressing distally 0,1,4 (3 terminal plus 1 subterminal). Exopodite two-segmented, 4 natatory setae terminally.

Color. Zoeae transparent, appearing gold with emerald green eyes under reflected light. Chromatophore position follows Aikawa (1929). Single brown chromatophores placed as follows: precardiac, occasionally one at posterior tip of dorsal spine, postcardiac, carapacial (posterolateral margin of cephalothorax), labral, mandibular, and maxillipedal (distally on the basipodites of the first and second maxillipeds). Two brown chromatophores placed ventrally on all abdominal somites and telson. Singular orange chromatophores placed as follows: precardiac, postcardiac, and carapacial (posterolateral margin of cephalothorax).

Second Zoeae

Carapace length: 0.68 mm.
Number of specimens examined: 10.

Carapace (Figure 2A, B). Cephalothorax as in stage I, but with additional setae placed as follows: 1 on lateral, 2 on posterolateral margin, a pair of minute setae posterolateral to dorsal tubercle, 2 minute interocular setae. Dorsal and rostral spines increased in length, now 2× longer than lateral spines. Eyes stalked.

Abdomen (Figure 2A, B). First somite with 1 or 2 dorsal setae; second unchanged; third and fourth with an additional pair of small spines at posteroventral angle; fifth often with small blunt tooth at posteroventral angle.

Telson (Figure 2C). Dorsal and lateral spines on medial portion of elongate furcae now minute. A pair of small setae along posterior telsonal margin. Six spines between furcae as previously described and illustrated.

Antennule (Figure 2D). Similar in form to first stage; basal region swollen; aesthetascs increased to 5 or 6, unequal in length.

Antenna (Figure 2E). Similar in form to first stage; protopodal basal region produced as a small hump (= endopodite primordium); exopodite spine

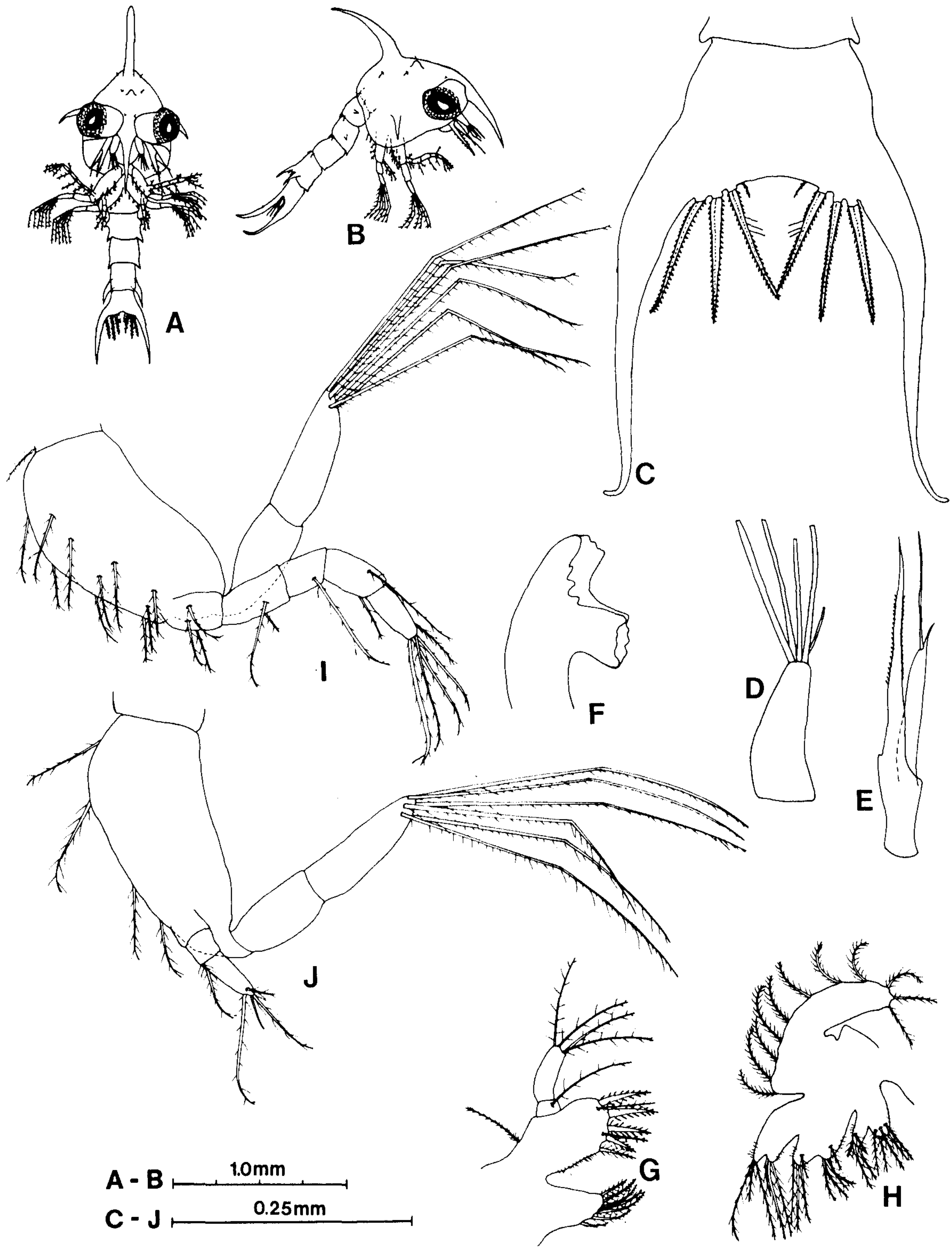

FIGURE 2.—Second zoeal stage of *Menippe nodifrons*. (A) Ventral view; (B) lateral view; (C) telson; (D) antennule; (E) antenna; (F) mandible; (G) maxillule; (H) maxilla; (I) maxilliped 1; (J) maxilliped 2.

equal to or surpassing protopodal process, about 0.5× length of exopodite.

Mandible (Figure 2F). Incisor process stouter, dentation irregular. Left molar process with 3 irregular teeth along inner margin to junction with incisor process, right molar process with 1 tooth.

Maxillule (Figure 2G). Setae on endopodite and coxal endites unchanged; basal endite now with 5 spines and 2 setae, plus 1 long feathery seta laterally.

Maxilla (Figure 2H). Setae on endopodite; coxal and basal endites unchanged. Scaphognathite with 11 plumose setae, no elongate distal process.

Maxilliped 1 (Figure 2I). Coxo-, basi-, and endopodites unchanged. Exopodite with 6 natatory setae.

Maxilliped 2 (Figure 2J). Coxo-, basi-, and endopodites unchanged. Exopodite with 6 natatory setae.

Color. Darker orange-brown, though chromatophore number and position unchanged from first stage; eyes with an orange-rose hue.

Third Zoeae

Carapace length: 0.80 mm.
Number of specimens examined: 10.

Carapace (Figure 3A, B). Cephalothorax inflated, posterolateral border with 8 (7-9) setae. Three pair of minute setae along dorsal midline as in stage II. Dorsal and rostral spines increased in length, usually 3.5× longer than lateral spines. Buds of third maxillipeds and thoracic appendages barely visible through carapace.

Abdomen (Figure 3A, B). Now with 6 somites, sixth with 2 dorsal setae posteriorly but no spines. Posterolateral spines of third, fourth, and dorsolateral spines of fifth somites elongate. Three dorsal setae on first somite.

Telson (Figure 3C). Dorsal and lateral spines on median portion of furcae miniscule. Spination and setation of posterior margin as before, occasionally an additional median seta. Furcae >0.75× length of telson.

Antennule (Figure 3D). Similar in form to second stage; terminal aesthetascs usually 4 (3-5): 3 long, 1 short.

Antenna (Figure 3E). Endopodal bud enlarged. Exopodal spine extended slightly beyond slender protopodal process, and equal in length to exopodite.

Mandible (Figure 3F). Incisor process similar in form to second stage, 3 or 4 irregular teeth on left side, 2 on right.

Maxillule (Figure 3G). Basal endite with 1 additional seta, now 5 spines, 3 setae, plus lateral seta as before. Setae of endopodite and coxal endites unchanged.

Maxilla (Figure 3H). Endopodal setation as in stage II: basal endite lobes 5,5; coxal endite lobes usually 5,4 (6,4). Scaphognathite with 19 or 20 marginal plumose setae.

Maxilliped 1 (Figure 3I). Similar in form to second stage; coxo- and basipodal setae unchanged; exopodite with 8 natatory setae; endopodite usually with an additional lateral seta on the distal segment (formula now 3,2,1,2,5+I; rarely 3,2,1,2,4+I).

Maxilliped 2 (Figure 3J). Similar in morphology to second stage; exopodite with 8 natatory setae.

Color. Two orange chromatophores ventrally on first through fifth abdominal somites; other chromatophores as before. Entire zoea dark orange-rose; rose coloration concentrated on posterior and posterolateral margins of cephalothorax. Lateral carapace and abdominal spines, now pale orange-rose. Dorsal carapace spine clear except for orange-rose hue at base and along posterior margin. Mandible and labrum dark brown. Eyes with rose coloration concentrated dorsally. Abdominal somites 1 through 5 darker orange-brown than in previous stage. Sixth somite pale orange-brown.

Fourth Zoeae

Carapace length: 1.0 mm.
Number of specimens examined: 10.

Carapace (Figure 4A, B). Cephalothorax

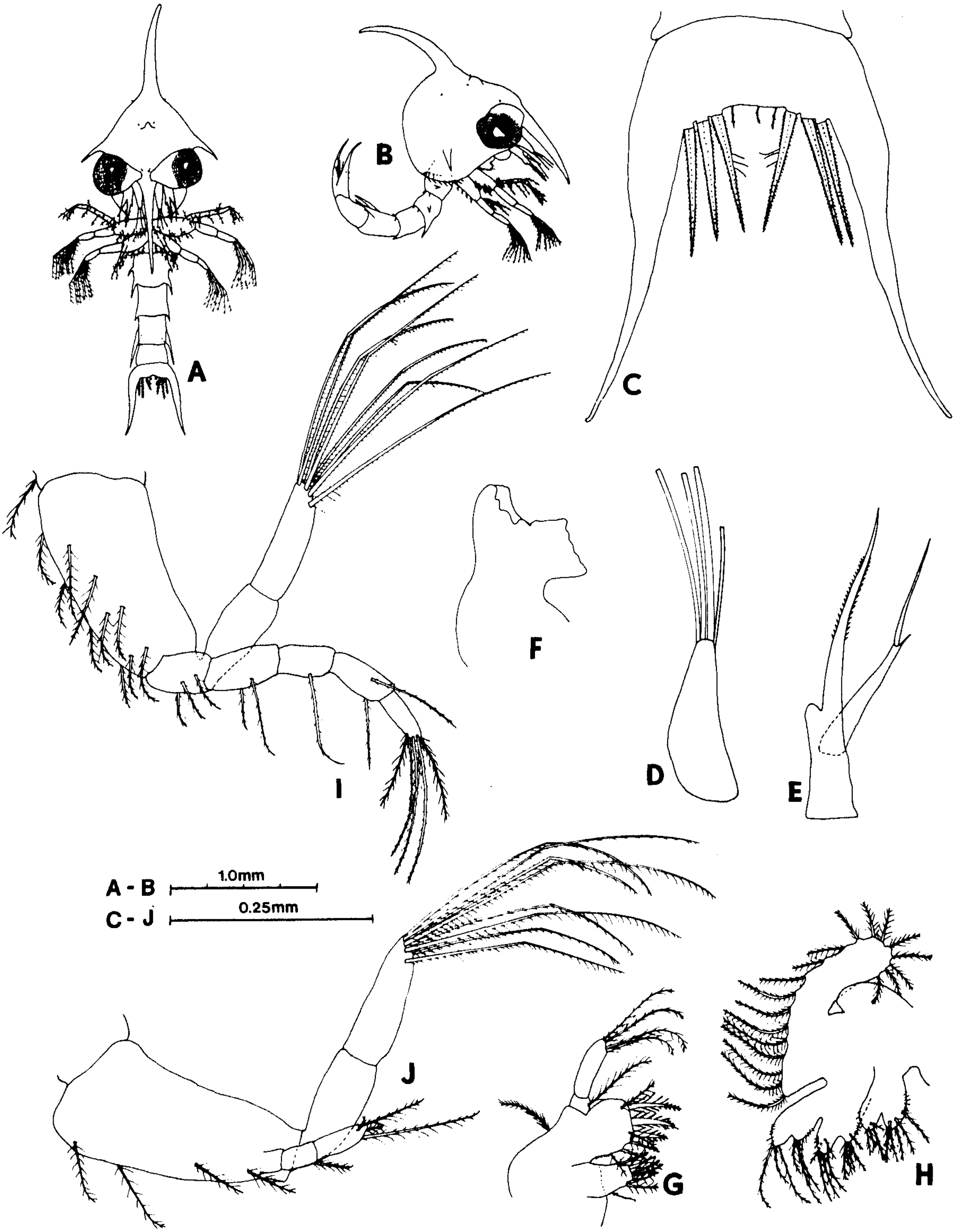

FIGURE 3.—Third zoeal stage of *Menippe nodifrons*. (A) Ventral view; (B) lateral view; (C) telson; (D) antennule; (E) antenna; (F) mandible; (G) maxillule; (H) maxilla; (I) maxilliped 1; (J) maxilliped 2.

globose, enlarged, posterolateral border with 11 or 12 setae; three pairs of minute interocular setae; other setae as in stage III. Bud of third maxilliped and thoracic appendages enlarged, more evident under carapace.

Abdomen (Figure 4A, B). Pleopod buds now present on second through sixth somites, but much reduced on sixth. First somite with 5-7 setae on dorsal posterior margin; sixth with a pair of small posterolateral spines or knobs. Posterolateral spines on third, fourth, and dorsolateral spines on fifth somites more elongate than in previous stage.

Telson (Figure 4C). Similar in form to third stage; 4 setae on posterior telsonal margin. Dorsal and lateral spines on median portion of furcae miniscule as in previous stage.

Antennule (Figure 4D). Similar in form to third stage aesthetascs increased to 7 or 8, arranged in three tiers progressing distally: 2 small, 1 small, 3 large plus 1 or 2 small.

Antenna (Figure 4E). Exopodal spine usually extending 0.1× beyond protopodal process and only 0.75× length of exopodite. Terminal tip of endopodal bud extending to base of lateral spinules of protopodal process and about 0.4× its length.

Mandible (Figure 4F). Left molar process unchanged, right molar process with 2 or 3 irregularly rounded prominences which join margin of incisor process.

Maxillule (Figure 4G). Endopodal setation unchanged; basal endite with 12 setae (6 or 7 strong, 5 or 6 thinner) plus a long plumose lateral seta as in previous stage; coxal endite with 8 setae (5 strong plus 3 thinner).

Maxilla (Figure 4H). Endopodite unchanged; setae on each basal endite usually 6,5 (5-7, 5-6); coxal endite setae 6,4 (uncommonly 7,4). Scaphognathite with 25-29 plumose setae.

Maxilliped 1 (Figure 4I). Coxopodite now with 2 setae; basi- and endopodite setae unchanged. Exopodite with 10 natatory setae.

Maxilliped 2 (Figure 4J). Coxo-, basi-, and endopodal setae unchanged. Exopodite with 10 natatory setae.

Maxilliped 3 (Figure 4K). Bilobed, rudimentary process, without setae, visible through carapace.

Color. Zoeae similar in color to third stage. Basipodite of first and second maxillipeds now orange-yellow. In lateral view, abdomen gold dorsally, brown medially, deep orange-rose ventrally. Ommatidia more evenly rose colored, cornea emerald green. Other chromatophore placement and color unchanged.

Fifth Zoeae (ultimate)

Carapace length: 1.55 mm.
Number of specimens examined: 11.
Remarks: Ultimate fifth stage zoeae molted directly to megalopae without an intercalated molt to sixth stage.

Carapace (Figure 5A, B). Distinctly increased in size from fourth stage. Carapace length, as in previous stages, about 1.2-1.3× longer than dorsal and rostral spines. Posterolateral margin with 15-20 setae. Other carapacial setae as described and illustrated for fourth stage. Third maxilliped and pereiopods increased in size, visibly extended from beneath carapace, segmentation evident.

Abdomen (Figure 5A, B). First somite usually with 10 (8-10) dorsal setae. Setae on second through fifth somites unchanged, each bearing 2 on posterodorsal margin. Small lateral spines on second and third, posteroventral spines on third and fourth, and dorsolateral spines on fifth somite elongate. Posteroventral prominence of sixth somite broad, unlike slender spines of preceding somites. Pleopods on second to fifth somites, each with well-developed exopodite and a rudimentary endopodite; sixth rudimentary.

Telson (Figure 5C). An additional fifth seta may occur on the posterior margin of the telson. When exopodite of the second maxilliped has 12 plus 1 setae, telson exhibits 2 small medial setae dorsally near telsonal posterior margin as shown; if there are only 12 natatory exopodal setae, telson is naked.

Antennule (Figure 5D). Endopodal bud now present below tiers of aesthetascs, latter progressing distally 7,7,1,5; basal region swollen but unsegmented, with 2 small basal setae.

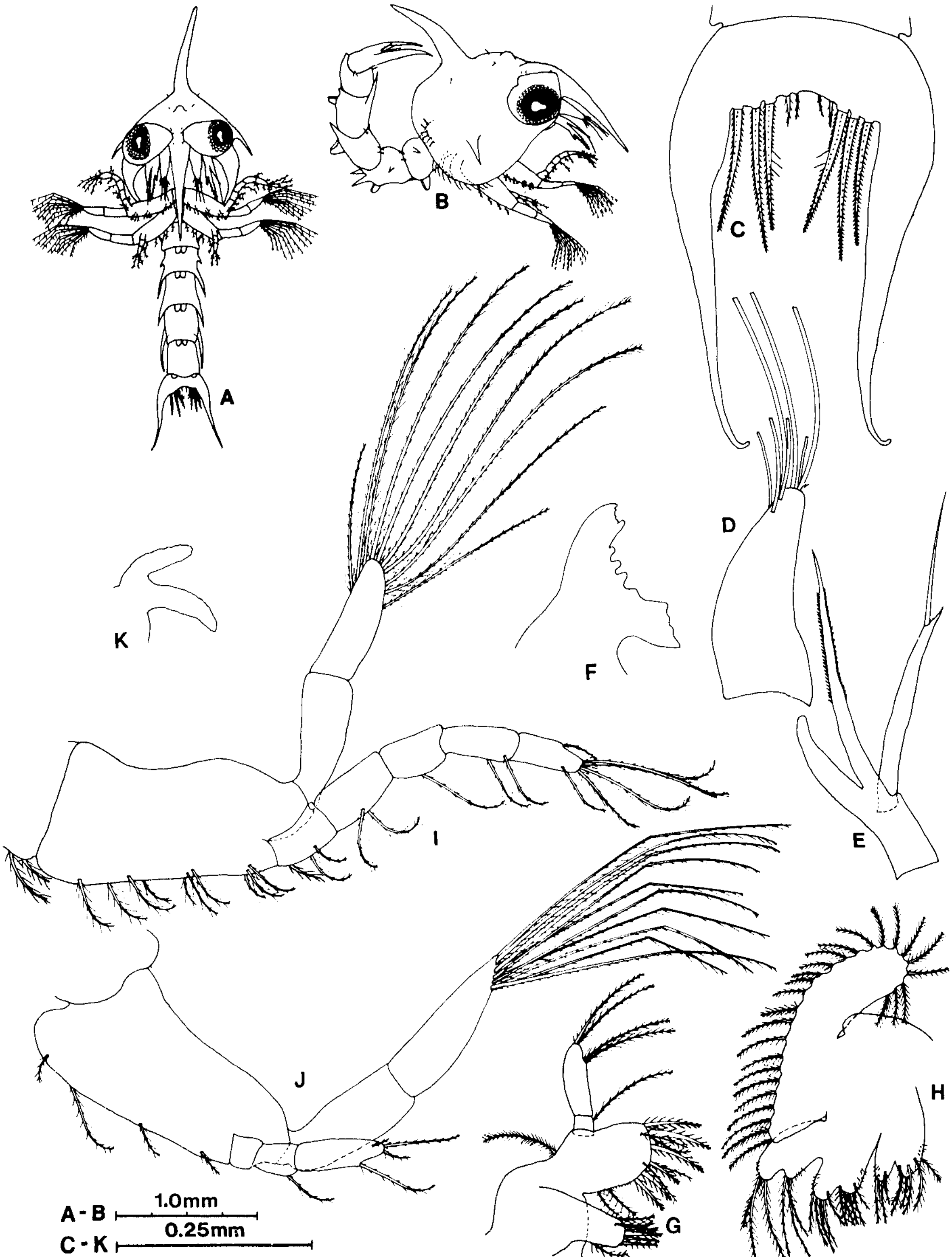

FIGURE 4.—Fourth zoeal stage of *Menippe nodifrons*. (A) Ventral view; (B) lateral view; (C) telson; (D) antennule; (E) antenna; (F) mandible; (G) maxillule; (H) maxilla; (I) maxilliped 1; (J) maxilliped 2; (K) maxilliped 3.

FIGURE 5.—Fifth (ultimate) zoeal stage of *Menippe nodifrons*. (A) Ventral view; (B) lateral view; (C) telson; (D) antennule; (E) antenna; (F) mandible; (G) maxillule; (H) maxilla.

Antenna (Figure 5E). Exopodal spine extending (as in stage IV) beyond distal tip of protopodal process and remaining 0.75× length of exopodite. Endopodal bud elongate, unsegmented, about 0.7× length of protopodal process.

Mandible (Figure 5F). Palp bud now present on anterior surface. Left molar process with 4 or 5 rounded to angular prominences along margin of inner angle and junction with incisor process, right molar process with 2 or 3 prominences.

Maxillule (Figure 5G). Endopodite unchanged. Lateral margin of basal endite with 2 long feathery setae; usually 8 (8-10) spines and 8 (8-10) setae terminally; coxal endite with 6 strong plus 5 thinner setae distally and 1 long feathery seta basally.

Maxilla (Figure 5H). Endopodite unchanged; basal endites with 7,7 processes; coxal endite lobes with 8 or 9, and 4 or 5 processes, respectively. Scaphognathite with 36-45 plumose setae.

Maxilliped 1 (Figure 6A). Coxopodite with 5 (5 or 6) setae; basi- and endopodal setae unchanged. Exopodite with usually 11 distal plus 1 lateral natatory setae.

Maxilliped 2 (Figure 6B). Coxopodite with 1 seta; basi- and endopodal setae unchanged. Exopodite with 12 distal and commonly 1 smaller lateral setae.

Maxilliped 3 (Figure 6C). Exopodite two-segmented, distal segment with up to 6 terminal setae of variable length; endopodite indistinctly four- or five-segmented; unsegmented naked epipodite now present, commonly with 1 seta.

Color. Cephalothorax and abdominal coloration similar to fourth stage. Placement and color of chromatophores unchanged except for additional orange chromatophore at the posterior margin of the yellow telson. In lateral view, abdomen gold dorsally, brown medially, and orange ventrally; pleopods colorless carapace rose-gold dorsally, brown medially, rose posteroventrally, and brown anteroventrally. Ommatidia light rose throughout but concentrated dorsally; cornea reflecting emerald green to irridescent turquoise depending on the position of the larvae. Mandibles and labrum dark brown; antennules and antenna colorless. On the first day in stage V, chelae barely visible and colorless except for dark brown chromatophores on the interior margin of each manus. Chelae progressively turn deep orange-rose and continue to extend beneath the carapace by the fourth day.

Fifth Zoeae (penultimate)

Number of specimens examined: 10.

Remarks: Penultimate fifth stage zoeae molted to an atypical sixth stage before molting to megalopae. The morphological characters compared and discussed below are the ones that differ from the regular fifth stage and may be used as a guide to distinguish between the two fifth stages. The abdominal setation should be one of the first characters to check in distinguishing between the two fifth stages.

Carapace. Carapace similar to ultimate fifth stage zoeae. Setation on the posterolateral border of penultimate fifth stage zoeae 15 or 16 (15-20 in ultimate stage).

Abdomen. First abdominal somite usually with 8 (7-10) dorsal setae (10 in ultimate stage).

Antennule. Endopodal bud less developed, its distal tip not extending beyond the midpoint between the base of the first tier of aesthetascs and the base of the bud itself (ultimate stage bud extends about one-fourth past this midpoint). Aesthetascs arranged in tiers: progressing distally 3-7,7,1,5 (the ultimate stage proximal tier usually has 7 aesthetascs).

Antenna. Endopodal bud less elongate, often not reaching distal end of protopodal spinules, never surpassing them (as in ultimate stage).

Mandible. Palp bud smaller in penultimate stage, other prominences equal in both fifth stages.

Maxilliped 1. Coxopodite with 4 setae (5 in ultimate stage). Exopodite with either 11 or 11 plus 1 natatory setae (latter condition usual in ultimate stage).

Maxilliped 2. Exopodite exhibits either 12 or (as usual in ultimate stage) 12 plus 1 natatory setae.

FIGURE 6.—Fifth (ultimate) (A-C) and sixth (D-F) zoeal stages of *Menippe nodifrons*. (A) Maxilliped 1; (B) maxilliped 2; (C) maxilliped 3; (D) maxilliped 1; (E) maxilliped 2; (F) maxilliped 3.

Maxilliped 3. Epi- and endopodites usually naked.

Sixth Zoeae (intercalated)

Carapace length: 1.60 mm.
Number of specimens examined: 5.

Carapace. Cephalothorax little inflated from previous stage. Posterolateral border with 20-22 setae, other setation and armature unchanged.

Abdomen. Pleopods elongate, one specimen with setae partially extruded. First abdominal somite with 11-14 dorsal setae.

Telson. Similar in morphology to fifth stage.

Antennule (Figure 7A). Endopodal bud elongate with up to 3 setae on distal end. Exopodite showing evidence of five segments; aesthetasc number variable, arranged in tiers: (progressing distally) 0,6-11,9-10,7-9,2 subterminal plus 5 terminal (note: not all aesthetascs illustrated); unsegmented basal region swollen with 2 small setae placed as shown.

Antenna (Figure 7B). Endopodite surpassing protopodal spinous process, showing evidence of five segments; setation variable, 0 or 1 on proximal segment, 0-3 on remaining four. Distal tip of exopodal spine surpassing protopodal process but attaining length of endopodal distal tip. Exopodal spine now 0.5× length of exopodite; latter about equal in length to protopodal process.

Mandible (Figure 7C). Palp unsegmented, elongate, with up to 3 distal setae. Molar process similar in form to fifth stage, 4 or 5 rounded to angular prominences along margin of inner angle and junction with incisor process; right molar process with 2 or 3 prominences.

Maxillule (Figure 7D). Proto- and endopodal setation unchanged; basal endite with 11 spines plus 10-12 stout setae plus 2 laterally; coxal endite with 6 strong plus 7 thinner setae plus 1 basally.

Maxilla (Figure 7E). Endopodite unchanged; basal endite lobes with usually 8 (8 or 9), 10 (8-10) setae respectively; coxal endite setae usually 11,7. Scaphognathite with 43-50 plumose setae on outer margin plus 2 small setae on lower surface of the blade.

Maxilliped 1 (Figure 6D). Coxopodite with 6 setae; basipodal setal formula similar to fifth stage with 2-4 additional setae dispersed as illustrated; endopodal setae 3,2,1,2-3,5+I; exopodite with usually 11 (11 or 12) plus 1 lateral natatory setae.

Maxilliped 2 (Figure 6E). Coxo- and basipodal setation unchanged, 1 and 4 setae, respectively; endopodal setae 0,1,5; exopodite with 12 plus 2 natatory setae.

Maxilliped 3 (Figure 6F). Exopodite two-segmented with 8 setae on distal segment; unsegmented endopodite unchanged from previous stage; epipodite with up to 6 setae.

Color. Entire zoea much lighter orange-rose than in previous stage. Eyestalks each with one brown-orange chromatophore anteriorly. Rostrum pale rose. Proximal segment of exopodites of maxillipeds 1 and 2 now yellow. Brown-orange postcardiac chromatophores, present in first five zoeal stage, now absent.

Megalopae

Carapace length × width: 1.50 × 1.31 mm.
Number of specimens examined: 10.
Remarks: Megalopae (VI) molting from stage VI zoeae differed only slightly from those megalopae (V) molting from stage V zoeae. These differences are noted under the appropriate headings.

Carapace (Figure 8A). Cephalothorax subquadrate overall, sparsely covered with hairs as shown; posterior and posterolateral border with up to 60 setae. Frontal region rectangular, rostrum strongly deflexed, nearly vertical, bluntly rounded with distinct median cleft, slightly expanded laterally to meet bluntly angular interorbital prominence. Orbit excavated, nearly rectangular; eyes large, eyestalks with 5 anterior setae.

Abdomen (Figures 8A, 9A). Pleurae 1 through 5 with lobes at posteroventral angles, that of somite 6 subquadrate. First abdominal somite with up to 32 setae arranged in a transverse row, somites 2 through 6 sparsely covered with setae.

FIGURE 7.—Sixth (A-E) zoeal stage of *Menippe nodifrons:* (A) Antennule (not all aesthetascs illustrated); (B) antenna; (C) mandible; (D) maxillule; (E) maxilla. Megalopa (F-J): (F) Antennule (not all aesthetascs illustrated); (G) antenna; (H) mandible; (I) maxillule (J) maxilla.

FIGURE 8.—Megalopal stage of *Menippe nodifrons*. (A) Dorsal view; (B) maxilliped 1; (C) maxilliped 2; (D) maxilliped 3.

Telson (Figure 9A). Subquadrate, posterior angles rounded, 5 setae on posterior margin, other setation variable.

Antennule (Figure 7F) Biramous. Peduncle three-segmented; bulbous basal segment partially bilobed; middle segment subcylindrical, smaller than proximal segment, setae appearing distally as shown; distal segment ovoid, setation variable in all segments. Lower ramus one-segmented with 8 setae; upper ramus five-segmented, aesthetascs arranged in tiers: usually 0,12,10,8 (+ 2 setae), 5 subterminal plus 3 terminal (note: all aesthetascs not illustrated).

Antenna (Figure 7G). Peduncle with lateral lobe extending to about midpoint of the first basal segment. First basal segment the largest; setation of the 11 flagellar segments variable, usually 4,3,2,0,0,4,0,4,0,4,5.

Mandible (Figure 7H). With truncately spade-shaped cutting edge; palp two-segmented, setae 0, 10-13.

Maxillule (Figure 7I). Protopodite with 1 long feathery seta on the dorsal margin; endopodite two-segmented, longer and more swollen proximal segment with 1 lateral seta, distal segment with 4 setae; basal endite with 28-33 spines and setae; coxal endite with 15-19 setae.

Maxilla (Figure 7J). Endopodite now unsegmented with 4-6 setae; setation of basal endites variable: 10-13, 11-15, setae on coxal endites also variable: 9-15, 4-10. Scaphognathite of megalopae (V) usually with 66 plumose setae on the outer margin plus up to 12 small setae on blade, megalopae (VI) with 76 plus 18.

Maxilliped 1 (Figure 8B). Exopodite two-segmented, proximal segment usually with 5 (4-6) setae distally, distal segment usually with 6 (5-7) setae. Endopodite unsegmented, usually with 6 (6-9) setae. Basal endite setation variable, 30-34 on megalopae (V), 40-44 on megalopae (VI); coxal endite setae 12-18 on megalopae (V), 20-25 on megalopae (VI). Epipodite with naked processes (in appearance similar to antennular aesthetascs), 12-20 on megalopae, (V), 26 on megalopae (VI).

Maxilliped 2 (Figure 8C). Exopodite two-segmented, proximal segment with 2 small setae medially, distal segment with 8 terminal setae. Endopodite four-segmented, setation variable usually: 8-12, 0-5, 6-10, 9-12, placed generally as shown. Epipodite with up to 10 naked aesthetasclike setae.

Maxilliped 3 (Figure 8D). Exopodite two-segmented, 4 medial setae on proximal segment, 6-10 on distal segment. Endopodite five-segmented, third and fourth segments partially bilobed, setation on all segments variable, usually: 25, 14, 10, 11, 8. Epipodite usually with 18 naked aesthetasclike setae on distal two-thirds plus 8 normal setae on proximal one-third in megalopae (V); 28 plus 8 in megalopae (VI). Protopodal setation variable (example illustrated).

Pereiopods (Figure 9B, C, c, D, d). Chelipeds (B) elongate, equal; dactyl with 4 irregular teeth in gape, propodus with 3, the curved tips overlapping distally. Second to fourth pereiopods (e.g., C) similar; dactyls with 5 teeth ventrally. Fifth pereiopod dactyl (D, d) with 3 long pectinate setae distally (= brachyuran feelers) in megalopae (V), 4 on megalopae (VI).

Pleopods (Figure 9A, E, F). Pleopods of decreasing size on second to sixth abdominal somites; pleopods (uropods) of sixth somite without endopodite. Megalopae (V) with 20-21, 20-21, 20-21, 16-17, and 11 plumose setae on the exopodite respectively; megalopae (VI) with 22-23, 22-23, 21-22, 19-20, and 12 plumose setae. Endopodites of pleopods (= appendices internae) 1-4 and both (V) and (VI) megalopae with 3 hooked setae.

Color. Under incident light, the megalopae exhibit a rose-orange coloration especially pronounced around posterolateral borders of carapace. Eyes iridescent turquoise. Eyestalks with black chromatophores dorsally, rose colored posteriorly. Cephalothorax with iridescent turquoise chromatophores on epibranchial, posterolateral, and entire gastric region. Abdomen with 1 large black chromatophore on first somite, 2 each on second to sixth somites. Second to fifth pereiopods light rose, darker at joints. Chelipeds deep orange-rose with black chromatophores interspersed, teeth of hand colorless.

DISCUSSION OF REARING RESULTS

Few brachyuran decapod larvae exhibit vari-

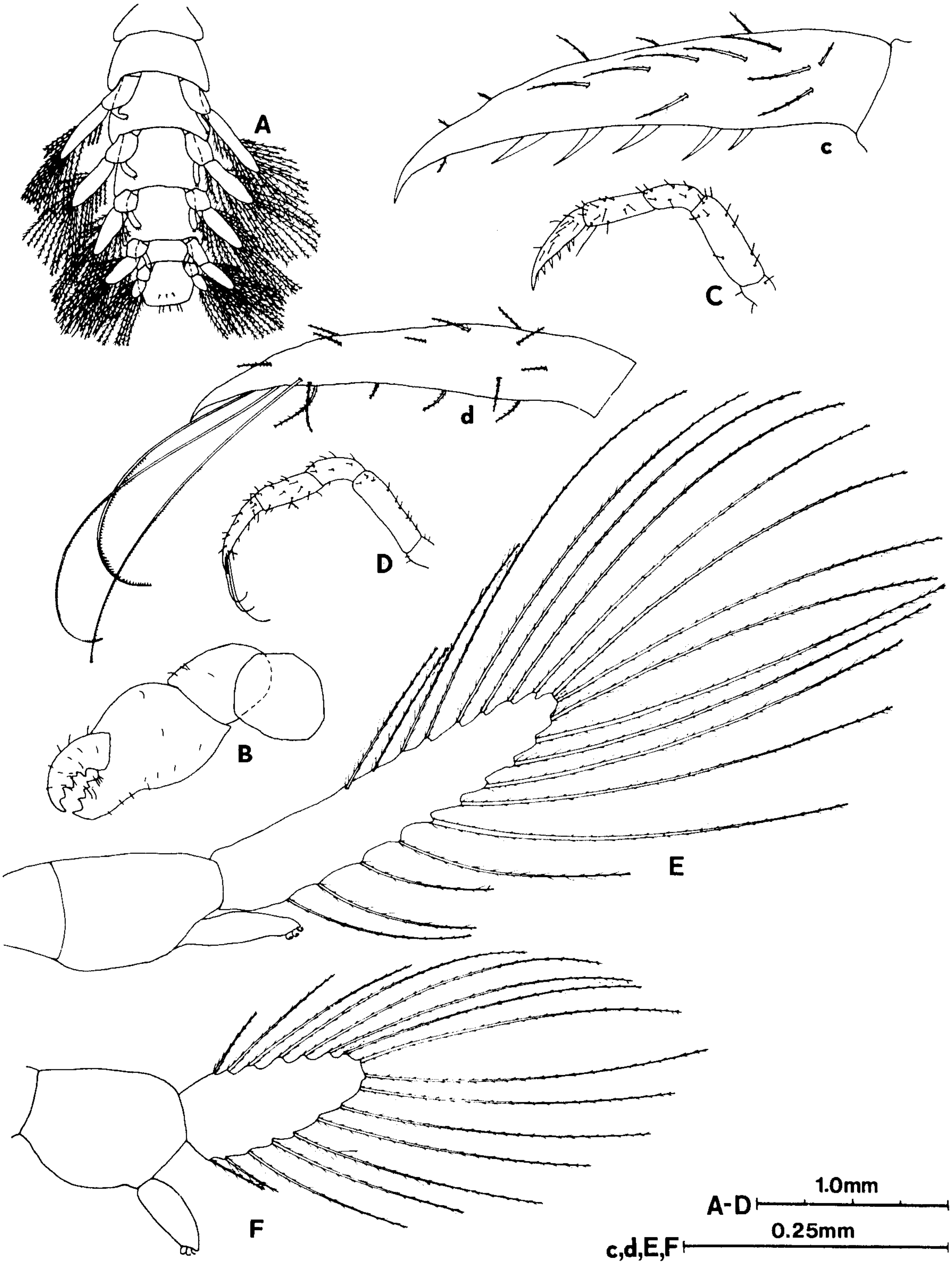

FIGURE 9.—Megalopal stage of *Menippe nodifrons*. (A) Abdomen; (B) cheliped; (C) third pereiopod; (c) third pereiopod dactyl; (D) fifth pereiopod; (d) fifth pereiopod dactyl; (E) first pleopod; (F) fourth pleopod.

ability in number of larval stages. *Callinectes sapidus*, *Dromidia antillensis*, *Rhithropanopeus harrisii*, *Menippe mercenaria*, and now *M. nodifrons* larvae have exhibited an extra instar at the end of larval development (Knowlton 1974). In summarizing earlier studies, Knowlton (1965, 1974) speculated that the amount of food, temperature, and photoperiod contribute to controlling the number of instars in decapod crustaceans. Knowlton (1974) reared *Palaemonetes vulgaris*, a caridean shrimp, under varying environmental conditions and concluded that "larvae maintained at increasingly higher temperature levels were inclined to pass through more instars." In contrast, Sandifer (1973) found that larvae of *P. vulgaris* "passed through fewer instars at the moderate temperature (25°C) than at higher or lower temperatures, ..."

Menippe nodifrons has five or (uncommonly) six zoeal stages, and one megalopal stage, as does its congener *M. mercenaria* (Porter 1960; Ong and Costlow 1970). As expected (Ong and Costlow 1970; Costlow and Bookhout 1971; Gore 1971; Christiansen and Costlow 1975) larval development of *M. nodifrons* was substantially slower at 20° C than at 30° C. The first five zoeal stages exhibited modal durations ranging from 5 to 8 days at 20° C, 4 to 5 days at room temperature ($\bar{x}$ = 24.5° C), and 2 to 4 days at 30° C (Table 1). A decrease in the number of zoeal stages was observed concomitant with this decrease in duration of each stage at the higher temperature, i.e., only five zoeal stages were attained at 30° C, while an atypical sixth stage was infrequently obtained at both room temperature and 20° C.

In summary, duration of larval development, duration in days of each stage, and number of zoeal stages of *M. nodifrons*, are all temperature-dependent (Figure 10). Although similar results were obtained by Ong and Costlow (1970) with regard to larval development of *M. mercenaria*, a difference in survival rate can be noted. At 30° C none of the *M. nodifrons* larvae survived to crab stage 1, while 30 (60%) *M. mercenaria* larvae (in 35‰) attained crab stage 1. At similar room temperatures (about 25° C), 1 *M. nodifrons* larva (2%) reached crab stage 1, while 37 (74%) *M. mercenaria* larvae attained crab stage 1. At 20° C, *M. nodifrons* exhibited the highest survival with 7 (15%) megalopae molting to crab stage 1, while survival of *M. mercenaria* sharply decreased to 0% with no first crab stages reached (Ong and Costlow 1970).

TABLE 1.—Duration of larval stages of *Menippe nodifrons* at three temperatures.

Temp (° C)	Stage	Duration (days) Min	Mean	Mode	Max	Total no. molting to next stage
20°	Zoeae I	5	5.8	6	7	48
	II	3	4.3	5	5	42
	III	4	5.1	5	7	39
	IV	5	6.0	6	7	38
	V(p)[1]	5	5.2	5	6	5
	V(u)[2]	6	7.6	8	9	24
	VI	8	8.7	9	9	3
	Megalopa (V)[3]	15	16.8	17.5	18	6
	(VI)[4]	16	16.0	16.0	16	1
24.5° (mean room temp)	Zoeae I	3	4.7	5	6	48
	II	3	3.9	4	6	44
	III	3	5.1	5	8	28
	IV	3	4.2	4	5	25
	V(p)[1]	3	4.4	5	5	7
	V(u)[2]	5	6.3	5	11	9
	VI	6	6.0	6	6	1
	Megalopa (VI)[4]	13	13.0	13	13	1
30°	Zoeae I	3	3.2	3	4	48
	II	2	2.5	2.5	3	48
	III	1	2.6	3	4	47
	IV	2	3.1	3	5	46
	V	3	4.0	4	5	35
	Megalopa	(1)			(9)	0

[1]Zoea V molting to Zoea VI (penultimate).
[2]Zoea V molting to Megalopa (ultimate).
[3]Megalopa molted from Zoea V.
[4]Megalopa molted from Zoea VI.
( ) = Died in stage.

Ong and Costlow (1970) suggested that 30° C is the optimum survival temperature for the larvae of *M. mercenaria* with optimum salinity ranging from 30 to 35‰. The megalopal stage was attained in 14 days, first crab on day 21, with total larval survival ranging from 60 to 72%. Conversely, my results indicate highest survival of *M. nodifrons* (15%) at 20° C. The megalopal stage was attained in 28-34 days and first crab on days 45-49 from fifth stage zoeae. Because of the additional sixth stage, the megalopal stage in that series was attained in 36-37 days and first crab on day 52.

DISCUSSION

Comparative Morphology of *Menippe* Larvae

The only other species of *Menippe* whose complete larval development has been described is *M. mercenaria*. Hyman (1925) described the prezoeal and first zoeal stages of that species, and Porter (1960) obtained a complete series of five (atypically six) zoeal stages. *Menippe nodifrons* also attains five and atypically six zoeal stages, depending on the rearing temperature.

There is but one easily observed and recurring feature which may be used to distinguish between all zoeal stages of *M. nodifrons* and *M. mercenaria*. The fourth abdominal somite of *M. mercenaria* has

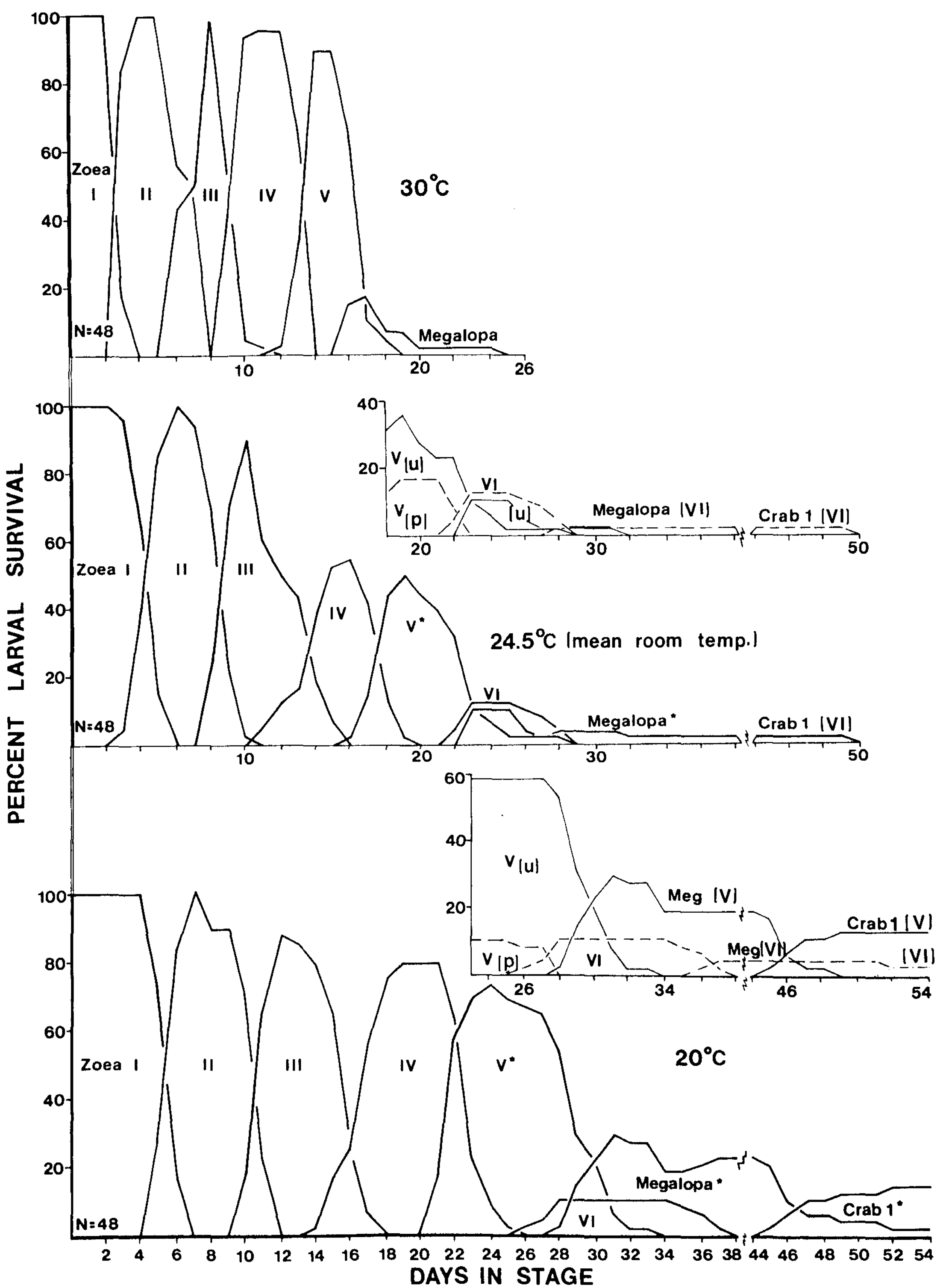

FIGURE 10.—Percentage survival and stage duration of *Menippe nodifrons* larvae reared under laboratory conditions. N = number of larvae cultured at each temperature; * = combined stages; u = ultimate stage; p = penultimate stage.

a dorsolateral spine not found in *M. nodifrons*. Additionally, in the first zoeal stage several differences (Table 2) include: antennular aesthetasc number, maxillulary coxal endite setation, and segmentation of the exopodites of the first and second maxillipeds. Setation differences in other stages are relatively minor (Table 3), and include: setation of the first maxilliped, in zoeal stage 2; setation of the maxillary basal endite and endopodite of the second maxilliped, in zoeal stage 3; and setation of the maxillulary basal endite, in zoeal stage 4.

Setation on the larval appendages of *M. nodifrons* becomes particularly variable in the fifth stage; because of this, distinguishing characters between *M. nodifrons* and *M. mercenaria* in this stage are not discussed. However, in *M. nodifrons* there are several differences between ultimate fifth stage zoeae [ZV(u)] that molt directly to megalopae and penultimate fifth stage zoeae [ZV(p)] that molt to sixth stage. These include (Table 4): coxopodal setation of the first maxilliped, antennular aesthetasc number, exopodal setation of the third maxilliped, and setation on the first abdominal somite. In addition, the antennal endopodite bud reaches the tip of the protopodite in ZV(u); in ZV(p) it is less elongate, reaching only to distal end of protopodite process spinules.

Differences between the sixth zoeal stages of *M. nodifrons* and *M. mercenaria* concern setation of the maxillary scaphognathite and first maxillipedal basipodite (Table 5). Other distinguishing characters include evidence of antennular exopodite and antennal endopodite segmentation, also observed in *Callinectes sapidus* (Costlow and Bookhout 1959).

Kurata[4] described the complete larval development, including the megalopal stage, of *M. mer-*

[4]Kurata, H. 1970. Part III. Larvae of decapod Crustacea of Georgia. *In* Studies on the life histories of decapod Crustacea of Georgia. Unpubl. manuscr., 274 p. University of Georgia, Marine Institute, Sapelo Island, GA 31327.

TABLE 2.—Taxonomically important first zoeal characters in three species of *Menippe*.[1]

Character	*M. nodifrons*	*M. rumphii* (Prasad and Tampi 1957)	*M. mercenaria* (Porter 1960)
Carapace:			
Rostrum	Straight, unarmed	Straight, unarmed	Straight, unarmed
Dorsal spine	Posteriorly curved	Posteriorly curved	Posteriorly curved
Lateral spine	Ventrally curved	Ventrally curved	Ventrally curved
Margin	Unarmed	Unarmed	Unarmed
Antennule	Conical rod	Conical rod	Conical rod
Exopodite	4 aesthetascs	4 aesthetascs	6 aesthetascs
Antenna	Exopodite ¾ protopodite	Exopodite = protopodite	Ratio not given
Exopodite	Tapered, long subterminal spine	Tapered, single spine	Tapered, 1 long heavy spine
Mandible	Scoop-shaped, incisor and molar processes indistinctly dentate and serrate, no palp	Cutting edge serrate, no palp	Lateral and posterior cutting edge indistinct teeth, no palp
Maxillule:			
Endopodite	Two-segmented 1, 4 setae	Two-segmented 1, 4 setae	Two-segmented 1, 4 setae
Basal endite	5 hirsute setae	5 hirsute setae	5 stout hairy setae
Coxal endite	7 hirsute setae	6 hirsute setae	6 stout hairy setae
Maxilla:			
Endopodite	Bilobed 3,3 setae	Bifid 3,3 setae	Bilobed 3,3 setae
Basal endite	Bilobed 5,4 setae	Bifid 5,4 setae	Bilobed 5,4 setae
Coxal endite	Bilobed 5,4 setae	Bifid 5,4 setae	Bilobed 5,4 setae
Scaphognathite	4 plumose setae, distal plumose process	4 plumose setae, posterior plumose process	4 plumose setae, distal plumose process
Maxilliped 1:			
Coxopodite	1 seta	1 seta	Not given
Basipodite	10 setae, 2,2,3,3,	6 setae	10 setae
Endopodite	Five-segmented 3,2,1,2,5	Five-segmented 2,2,1,2,4	Five-segmented 2,2,1,2,5
Exopodite	Two-segmented, 4 natatory setae	4 natatory setae	Partially bisegmented, 4 natatory setae
Maxilliped 2:			
Coxopodite	Naked	Not given	Not given
Basipodite	4 setae	Few setae	4 setae
Endopodite	Three-segmented 0,1,4 setae	Three-segmented 0,2,4 setae	Three-segmented 0,1,4 setae
Exopodite	Two-segmented, 4 natatory setae	4 natatory setae	Partially bisegmented, 4 natatory setae
Abdomen	Somites 2 to 5 with 2 posterodorsal setae; somite 4 without spines in all stages	Somites 2 to 4 with a pair of short hairs; somite 4 without spines	Somites 1 to 5 with 2 posterodorsal setae; somite 4 with pair of dorsolateral spines in all stages

[1]Characters taken from authors descriptions and illustrations.

TABLE 3.—Taxonomically important zoeal characters in two species of *Menippe*. Data on *M. mercenaria* taken from Porter (1960).

	Stage II		Stage III		Stage IV	
Character	*M. nodifrons*	*M. mercenaria*	*M. nodifrons*	*M. mercenaria*	*M. nodifrons*	*M. mercenaria*
Carapace:						
Margin	3 setae	Several setae	8 setae	5 setae	11-12 setae	12 setae
Antennule aesthetascs	5-6	5	4	5	Base swollen, 7-8	Base swollen, 7
Antenna:						
Endopodite	Small hump	Not given	Bud	Hump	Bud terminal tip at mid-point of antenna	Terminal tip bud at mid-point of antenna
Maxillule setation:						
Endopodite	1,4	1,4	1,4	1,4	1,4	1,4
Basal endite	7 + 1 laterally	7 + 1 laterally	8 + 1 laterally	8 + 1 laterally	12 + 1 laterally	12 + 2 laterally
Coxal endite	7	7	7	7	8	8
Maxilla setation:						
Endopodite	3,3	3,3	3,3	3,3	3,3	3,3
Basal endite	5,4	5,4	5,5	5,4	6,5	6,5
Coxal endite	5,4	5,4	5,4	5,4	6,4	6,4
Scaphognathite	11 plumose	11-12 plumose	19-20 plumose	18 plumose	25-29 plumose	27-28 plumose
Maxilliped 1 setation:						
Coxopodite	1	Not given	1	Not given	2	Not given
Basipodite	2,2,3,3, (10)	10	2,2,3,3, (10)	10	2,2,3,3, (10)	10
Endopodite	3,2,1,2,5	2,2,1,2,5	3,2,1,2,6	3,2,1,2,5	3,2,1,2,6	3,2,1,2,6
Exopodite	6 natatory	6 natatory	8 natatory	8 natatory	10 natatory	10 natatory
Maxilliped 2 setation:						
Coxopodite	Naked	Not given	Naked	Not given	Naked	Not given
Basipodite	4	4	4	4	4	4
Endopodite	0,1,4	0,1,4	0,1,4	0,1,4	0,1,4	0,1,4
Exopodite	6 natatory	6 natatory	8 natatory	8 natatory	10 natatory	10 natatory
Maxilliped 3					Bilobed bud	Bud
Abdomen					Pleopod buds	Pleopod buds
First somite	1-2 setae	1 setae	3 setae	3 setae	5-7 setae	5-7 setae
Sixth somite			2 dorsal setae	Unarmed	2 dorsal setae	Unarmed

cenaria. His data show that differences between megalopae of the two species are exhibited chiefly in the spination of the pereiopods. *Menippe mercenaria* has 5 or 6, 2 or 3, and 1 small spine on the ischia of walking legs, one, two, and three, respectively; and 2 small spines on the proximal inner edge of the merus of the first walking leg. *Menippe nodifrons* exhibits variable setation on these same segments but lacks spines. Kurata also stated that the ischium of the third maxilliped of *M. mercenaria* has 9 small spines; in *M. nodifrons* variable setation occurs, but 25 setae are usually found.

Among other species of *Menippe* only the first zoeal stage of the Indo-Pacific *M. rumphii* has been described (Prasad and Tampi 1957). As indicated in Table 2, the three congeners have a similar first stage, but differ in antennular aesthetasc number, setation of the maxillary coxal endite, setation of the basi- and endopodite of the first maxilliped, and endopodite setation of the second maxilliped. As noted in the introduction, there is some question as to whether *M. rumphii* is synonymous with *M. nodifrons*. The complete larval development of *M. rumphii* is needed to establish the status of this species and its taxonomic relationship to *M. nodifrons*.

Distinguishing Morphology of Xanthidae Larvae

According to Lebour (1928), larvae of the family Xanthidae exhibit the following characters:

1. One prezoeal and four zoeal stages.
2. Carapace with dorsal, rostral, and one pair of smaller lateral spines.
3. Antenna with rudimentary exopodite, or with one nearly as long as the spinous protopodal process.
4. Abdomen with lateral knobs on somites 2 and 3, somites 3-5 or 6 with lateral spines in all stages.
5. Telson furcae with 3 lateral spines or with 1 tending to disappear in later stages.

Wear (1970) reviewed the diagnostic characters of certain xanthid larvae and enumerated several conclusions about *Menippe*. Known larvae of the genus *Menippe*, reared under laboratory con-

TABLE 4.—Taxonomically important characters of the fifth zoeal stage in two species of *Menippe*.

Character	*M. nodifrons* (ultimate)	*M. nodifrons* (penultimate)	*M. mercenaria* (Porter 1960)
Carapace:			
Margin	15-20 setae	15-16 setae	20-22 setae
Antennule:			
Endopodite	Bud	Bud less elongate	Bud elongate
Exopodite	7,7,1,5	3-7,7,1,5	2-7,6-8,1,4-5
Antenna:			
Endopodite	Bud elongate	Bud less elongate	Bud elongate
Mandible	Palp present	Palp smaller	Palp present
Maxillule setation:			
Endopodite	1,4	1,4	1,4
Basal endite	16+2 laterally	16+2 laterally	14-17+2 laterally
Coxal endite	11+1 basally	11+1 basally	11-12
Maxilla setation:			
Endopodite	3,3	3,3	3,3
Basal endite	7,7	7,7	8,7
Coxal endite	8-9, 4-5	8-9, 4-5	6-10, 4-5
Scaphognathite	36-45 plumose	34-42 plumose	36-39 plumose
Maxilliped 1 setation:			
Coxopodite	5	4	Not given
Basipodite	2,2,3,3 (10)	2,2,3,3 (10)	10
Endopodite	3,2,1,2,6	3,2,1,2,6	3,2,1,2,6
Exopodite	11+1 natatory	11 or 11+1 natatory	11+1 natatory
Maxilliped 2 setation:			
Coxopodite	1	1	Not given
Basipodite	4	4	4
Endopodite	0,1,4	0,1,4	0,1,4
Exopodite	12+1 natatory	12 or 12+1 natatory	12+1 natatory
Maxilliped 3 setation:			
Endopodite	Indistinctly 4-5 segmented	Reduced	Partially five-segmented
Exopodite	Two-segmented 0, 0-6	Naked	Unsegmented
Epipodite	Unsegmented, naked	Reduced	Unsegmented, naked
Abdomen setation:			
First somite	Usually 10	Usually 8	8-9
Pleopoos	Pair 1 to 4 with exopod and rudimentary endopod; pair 5 a bud	Pair 1 to 4 with exopod and rudimentary endopod; pair 5 a bud	Pair 1 to 4 with protopod, exopod, and endopod; pair 5 a bud

ditions, are distinguished from other xanthid genera by attaining five and atypically six zoeal stages; other xanthid larvae exhibit only four zoeal stages. Larvae of the genus *Menippe* (and *Eriphia*) are distinguished from other xanthids by antennal development, i.e., the larval exopodite is about 0.75× the length of the spinous protopodal process (see Aikawa 1937; Porter 1960; Sandifer 1974). *Menippe* (and *Sphaerozius*) larvae are distinguished from other closely related xanthid genera by the absence of setae on the basal segment of the second maxillipedal endopodite (Aikawa 1937; Porter 1960).

Number of Zoeal Stages

According to descriptions to date, every genus of xanthid crab has four zoeal stages except *Menippe*. In this study, *M. nodifrons* attained five zoeal stages, occasionally a sixth, and a prezoeal stage occurred. These stages also appeared in the larval development of *M. mercenaria* (Porter 1960). The prezoeal stage exhibited by both *M. mercenaria* and *M. nodifrons* was never observed to molt to a first stage zoea. Larvae of both species, collected within seconds after hatching, were almost always found to be in the first stage, indicating that the observed *M. nodifrons* prezoeae were those zoeae too weak to molt to stage I. Porter also indicated that *M. mercenaria* prezoeae, which were seen most often when subsequent survival was poor, may not be a normal stage in planktonic existence of the larvae. However, Lebour (1928), Chamberlain (1957), and Wear (1970) established that larvae of other xanthid genera hatch from the egg as prezoeae. Based on data obtained in this experiment, it seems possible that the prezoeal stage of *M. nodifrons* may occur in nature under certain conditions, as may the sixth zoeal stage.

Porter (1960) suggested that, based on the variability of morphological characters and the fact that no stage VI zoeae molted to megalopae, the sixth stage in *M. mercenaria* may not be a true stage but an advanced fifth stage. As noted in the rearing results, the observation of temperature-dependency in relation to number of zoeal stages

TABLE 5.—Taxonomically important characters of the sixth zoeal stage in two species of *Menippe*. Data on *M. mercenaria* taken from Porter (1960).

Character	*M. nodifrons*	*M. mercenaria*
Carapace:		
Margin	20-22 setae	20-22 setae
Antennule:		
Endopodite	Bud elongate, 0-3 setae	Bud elongate, occasional setae
Exopodite	Five-segmented, 0, 6-11, 9-10, 7-9, 2 subterminal + 5 terminal	Unsegmented, 4-6 6-8, 1, 4-5
Antenna:		
Endopodite	Five-segmented, 0-1, 0-3, 0-3, 0-3, 0-3	Unsegmented
Mandible	Palp elongate, 0-3 setae	Palp as in stage 5
Maxillule setation:		
Endopodite	1,4	1,4
Basal endite	22-23 + 2 laterally	23-29 + 2 laterally
Coxal endite	13	11-12
Maxilla setation:		
Endopodite	3,3	3,3
Basal endite	8(8-9), 10(8-10)	9-11, 8-9
Coxal endite	11,7	8-11, 4-5
Scaphognathite	43-50 + 2 plumose	39-44 plumose
Maxilliped 1 setation:		
Coxopodite	6	Not given
Basipodite	12-4	10
Endopodite	3,2,1,2-3,6	3,2,1,2,6
Exopodite	11 + 1 natatory	11 + 1 natatory
Maxilliped 2 setation:		
Coxopodite	1	Not given
Basipodite	4	4
Endopodite	0,1,5	0,1,4
Exopodite	12 + 2 natatory	12 + 1 natatory
Maxilliped 3 setation:		
Endopodite	Unsegmented, naked	Not given
Exopodite	Two-segmented, 0-8	0-8
Epipodite	Unsegmented, 0-6	Not given
Abdomen setation:		
First somite	11-14	9-11
Pleopods	Exopodite setae only partially extruded	Exopodites with setae on all or only last pair

indicates that his supposition may not hold for all members of the genus, notably for *M. nodifrons*.

Regardless of whether a sixth zoeal stage is a laboratory artifact, the appearance of which seems to be temperature-dependent, it is apparent that larvae of at least two species of *Menippe* undergo at least five zoeal stages. The ramifications of this fact will be discussed below.

Few other brachyuran species exhibit an inconsistent number of instars in their larval development. Boyd and Johnson (1963) reported that out of 20 species of brachyuran crabs observed by Costlow, only two species, both Portunidae, exhibited variation in the number of zoeal stages. The phylogenetically primitive Portunidae have at least seven and sometimes eight zoeal stages (Bookhout and Costlow 1974, 1977). The extra stages resulted in reduced viability, with only a few zoeae developing to megalopae. Boyd and Johnson (1963) also suggested that the sixth stage in some normally five-staged Brachyura is a result of laboratory conditions because the extra stage has never been found in the plankton. This supports Gurney's (1942) and Porter's (1960) contentions that laboratory conditions produce aberrant larval forms. However, Boyd and Johnson (1963) also stated that extra stages might possibly occur in nature under certain conditions. Now that larvae of *M. nodifrons* are known it should be relatively easy to identify a sixth stage zoea of this species in the plankton based on criteria produced earlier in my study.

Plesiomorphy and Larval Development

Lebour (1928) set forth the genus *Portunus* as the most primitive of the Brachyrhyncha, based on the following characters: many zoeal stages (up to eight, Bookhout and Costlow 1977); telson with 6 long internal setae plus 3 lateral spines on each furca, making 7 spines on each side, with 2 extra pair of internal setae in later stages; knobs on the second and third abdominal somites, those on the third disappearing in later stages; and antenna with a well-developed exopodite, about one-half as long as the spinous protopodital process.

Larvae of the western North Atlantic species of *Menippe* also exhibit these characters, differing only in the number of larval stages (up to six) and in the retention of the knob on the third abdominal somite. Larvae of the Cancridae, considered to be more primitive than the Xanthidae (Rathbun 1930; Gurney 1939) and by some authors (Borradaile 1907; Lebour 1928; Glaessner 1969) than the Portunidae, also exhibit the primitive characters enumerated by Lebour for the Portunidae, differing mainly in number of zoeal stages (five), armature of the telson (2 lateral spines on each furca), and possession of a knob only on the second abdominal somite.

Based on the assumption that a greater number of zoeal stages is a primitive character, I agree with the phylogenetic arrangement of Rathbun (1930) and Gurney (1939), both of whom placed the Cancridae primitive to the Xanthidae but more advanced than the Portunidae. However, in comparing the number of larval stages, the genus *Menippe* shows a closer relationship to the Cancridae than to the Xanthidae. This relationship is discussed below in light of additional larval characters.

Excluding *Menippe*, the laboratory cultured genera of xanthids have four zoeal stages (e.g., *Pilumnus dasypodus*, Sandifer 1974; *Eurypanopeus depressus*, Costlow and Bookhout 1961a). These xanthids usually possess 8 or 9 natatory maxillipedal setae in the third zoeal stage and pleopod buds first appear in this instar. However, third zoeae of *Menippe*, which also possess 8 natatory maxillipedal setae, lack pleopod buds and the latter do not appear in known *Menippe* larvae until the fourth stage (10 natatory maxillipedal setae). *Menippe* larvae, as do other xanthid larvae, otherwise attain the sixth abdominal somite in the third stage.

A similar situation is found among known larvae of the Cancridae (e.g., *Cancer borealis*, Sastry 1977b; *C. irroratus*, Sastry 1977a), which exhibit 8 natatory maxillipedal setae but no pleopod buds in the third zoeal stage, while 10 natatory maxillipedal setae and pleopod buds are exhibited in the fourth stage, as in *Menippe*. Thus *Menippe* again shows, in this respect, a closer relationship to the Cancridae than to the Xanthidae.

Another heterochronic feature is the mandibular palp, which appears in the fourth (i.e., last) zoeal stage in all xanthid genera except *Menippe*. Fourth stage *Menippe* larvae in the western North Atlantic may thus be distinguished from other stage IV xanthid larvae in lacking a mandibular palp as well as in possessing 10 natatory maxillipedal setae, as noted above. In all other laboratory cultured xanthid genera with 9 or 10 natatory maxillipedal setae the mandibular palp is present. Again, *Menippe* larvae seem closer to cancrid larvae than to xanthid larvae, in that the mandibular palp appears in the fifth (usually the last) zoeal stage.

Comparison of *M. nodifrons* maxillipedal coxopodal setation with that of other xanthid and cancrid larvae, which may be a significant feature, was not analyzed because of the lack of descriptions and illustrations of this larval character. The coxopodal setation has been described for only one other xanthid, *Neopanope texana* (McMahan 1967). Setal number of *M. nodifrons* agreed with that of *N. texana* for the first four zoeal stages, increasing in the fifth and sixth stages of *M. nodifrons*.

Assuming then, that data just presented are evidence of retained, primitive features, it can then be postulated that *Menippe* larvae are recapitulating, in the sense of retarded heterochronic maturation (Gould 1977), a larval development now accelerated in other xanthid larvae. The presence of the fifth zoeal stage, the irregular occurrence of the sixth stage, the delayed appearance of mandibular palp and pleopod buds, and retention of coxopodal setation in cultured species of *M. nodifrons* and *M. mercenaria* are all evidence which indicates this might have happened. Evolution has apparently acted in the larvae of other xanthid genera to reduce the number of zoeal stages.

In summary, because of the greater number of zoeal stages and the tardy appearance of both pleopod buds and mandibular palp, *Menippe* may be the most primitive genus of the family Xanthidae. Whether the genus is transitional between the Cancridae and the Xanthidae remains speculative. As noted above, larvae of the family Cancridae, phylogenetically primitive to the Xanthidae, also exhibit five zoeal stages and pleopodal and mandibular features which appear in a similar developmental sequence to those of *Menippe*. The more advanced xanthid larvae, on the other hand, pass through only four zoeal stages and exhibit sequential features typical of larvae of the family Goneplacidae, a group considered to be more advanced than xanthids (Lebour 1928; Kurata 1968).

Carapacial Armature

Menippe larvae have well-developed dorsal, rostral, and smaller lateral spines, a feature found in all cancrid and most xanthid larvae. Thus, little can be inferred regarding phylogenetic relationships using these features.

The reason for such spines remains conjectural. Lebour (1928) stated that these well-developed carapacial spines were used "in directing movement and keeping up [the larvae in] the surface-layers, and their reduction appears to be associated with habits near the bottom." Her supposition may be correct. *Menippe nodifrons* larvae reared in this study were active swimmers near the surface in earlier stages. Their locomotion was usually in a forward direction with the dorsal spine pointed anteriorly.

Antennal Morphology

In considering antennal features, xanthid larvae were first divided into either two (Hyman 1925) or three (Lebour 1928) groups. In the former, both authors noted that the length of the antennal exopodite is either about equal to the protopodite (primitive) or rudimentary (advanced). In the third group, also considered primitive, the antennal exopodite is about three-fourths the length of the protopodal process (this group was established by Lebour to include *Menippe* and *Eriphia*). Therefore, regardless of classification scheme (Hyman's or Lebour's), larvae of the genus *Menippe* exhibit a primitive antennal morphology. However, as will be seen, the degree of primitiveness is relative.

Aikawa (1929) classified four types of antennae (A, B, C, and D) based on the ratio of length of peduncle to that of exopodite. In the A type antenna the exopodite and peduncle (= protopodal process) are nearly equal in length. Aikawa also considered this to be the most primitive condition because other authors (e.g., Calman 1909) have noted that the long exopodite is homologous with the antennal scale of the Caridea.

Xanthid larvae exhibiting A type antennae are *Pilumnus* (considered by Hyman 1925 to be the most primitive xanthid), *Heteropanope*, and *Actumnus* (Aikawa 1929, 1937; Lebour 1928).

The typical B type antenna occurs most frequently in brachyuran larvae. The exopodite is about one-half to three-fourths the length of the peduncle. Type B antennae are found in the larvae of the xanthids *Menippe*, *Eriphia*, *Sphaerozius*, and *Trapezia* (Aikawa 1937). This antennal morphology, primitive by Hyman's standards, is considered by Aikawa (1929) to be intermediate in development, but less advanced than the following C type.

The C type antenna consists of a long peduncle and a very short spine (= exopodite). This highly advanced antenna is exhibited in the larvae of the xanthids *Panopeus* (considered by Hyman 1925 to be the most advanced xanthid), *Eurypanopeus*, and *Neopanope*, among others (Aikawa 1929).

Aikawa (1929) briefly described the D type antenna (seen in the oxystome crab *Philyra psium* (Leucosiidae)) as a simple, inconspicuous spiny process shorter than either the rostrum or the antennule, and considered it to be a deviation.

The cancrids exhibit the intermediate B type antenna seen in *Menippe*. Thus, in antennal features, larvae of both *Menippe* and the Cancridae would be more advanced than some of the xanthids, and equal to or less advanced than others.

Abdominal Morphology

A lateral knob occurs on the second abdominal somite of most brachyuran larvae also on the third somite of some xanthid larvae (Lebour 1928). Lebour did not attribute much significance to the abdominal processes and was ambivalent in regarding these as either a primitive or advanced feature. Later, Wear (1970), noted that "the posterior pair of papillae [knobs] may be absent" and that "lateral spines on the third to fifth abdominal segments is also a variable character, but these occur in a great majority of xanthid larvae." Both *M. nodifrons* and *M. mercenaria* exhibit the lateral papillae on the second and third abdominal somites, as well as ventrolateral spines on the third, fourth, and fifth somites, thereby agreeing with the great majority of xanthid larvae. As noted above, *M. mercenaria* larvae may be distinguished from *M. nodifrons* larvae by possession of a pair of dorsolateral spines on the fourth abdominal somite. In the more primitive Cancridae, lateral knobs only occur on the second abdominal somite, and lateral spines on the third to fifth somites are much smaller than those of the xanthid larvae (Aikawa 1937; Sastry 1977a, b). Thus *Menippe* larvae are more advanced than cancrid larvae if additional spines indicate apomorphy.

Telsonal Armature

Menippe nodifrons larvae have a typically forked brachyuran telson with 6 setae anterior to the furcae. However, 3 setae which become reduced in later stages, appear on the median portion of the furcae, and one to three pair of extra, shorter setae occur in posterior telsonal margin. Lebour (1928) suggested that this type of telson is "most near the embryonic form, and therefore probably nearest the primitive form . . . ." The extra internal setae along the posterior telsonal margin first appear in the second zoeal stage of both the xanthid *M. nodifrons* and the cancrid *Cancer borealis* (Sastry 1977b). These internal setae, if present in other xanthid larvae, do not appear until the third zoeal stage, e.g., in *Panopeus herbstii* (Costlow and Bookhout 1961b), *Eurypanopeus depressus* (Costlow and Bookhout 1961a), and *Hexapanopeus angustifrons* (Costlow and Bookhout 1966), all more advanced forms than *Menippe*. These data lend further support to the primitive status of *Menippe* as compared with other xanthid genera.

In summary, using larval characters suggested by Lebour (1928) to determine the primitive or advanced status of decapod larvae, the genus *Menippe* is phylogenetically more primitive than most of the Xanthidae. It appears to be closer, in most features, to the family Cancridae.

Status of the Family Menippidae

Ortman (1894) established the family Menippidae, which included the subfamilies Menippinae, Myomenippinae, and Pilumninae, based on the following adult characters: a) the second segment of each antenna is short, not overreaching the frontal region; and b) the palate is with or without a ridge. However, because of the reigning taxonomic confusion in this group, this familial rank was not recognized by other authors of that time. Indeed, many present day xanthid species were placed under differing familial and subfamilial names (e.g., Pilumnidae, Cancridae) before the taxon Xanthidae became firmly established (Rathbun 1930). Later authors notwithstanding, Aikawa (1929, 1937), using Lebour's larval characters (with emphasis on antennal development), again recognized the family Menippidae, considering it to be more primitive than the Xanthidae. Subsequent study of the larval development of *Menippe*, reported by Porter (1960) and in this paper, supports Aikawa's phylogenetic arrangement based on larval morphology, as well as adding evidence using larval development, i.e., the fact that *Menippe* attains up to six zoeal stages (more stages = primitive). The establishment by Ortmann (1894) of the Menippidae as a family, although based only on adult characters, seems to be supported also by larval traits.

Guinot (1977) proposed a new classification scheme for brachyuran decapods based on placement of female and male genital openings. She divided the brachyurans into three sections as follows: 1) Podotremata—female and male openings coxal, a primitive condition (i.e., Homoloidea); 2) Heterotremata—female openings sternal, male openings either sternal or coxal, an intermediate condition (i.e., Xanthoidea); 3) Thoracotremata—female and male openings sternal, an advanced condition (i.e., Gecarcinoidea). Guinot[5] listed the family Menippidae under the superfamily Xanthoidea, based on adult characters emphasizing genital opening placement. Thus she provided additional evidence, based on adult gonopore/gonopod characters, for the reestablishment of the family Menippidae. Investigations of the larval development of other species of *Menippe* could provide further support warranting reestablishment of the family.

[5]Guinot, D. 1977. Project d'une *nouvelle classification* des Brachyoures. Unpubl. tables. Museum National d'Histoire Naturelle, Labortoire de Zoologie (Arthropodes), Paris, Fr.

NOTE ADDED IN PROOF

After this paper was sent to the printer, a publication—Larval development of *Epixanthus dentatus* (White) (Brachyura, Xanthidae) by M. Saba, M. Takeda, and Y. Nakasone published 1978 in Bulletin of the National Science Museum (Tokyo), Series A (Zoology) 4(3):151-161—was received indicating that three genera of xanthids developed through less than four zoeal stages. *Epixanthus dentatus* and *Heterozius rotundifrons* attain two larval stages, while *Pilumnus lumpinus* attains only one larval stage. These three species live in specialized and restricted habitats.

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