THE MEGALOPA STAGE OF THE GULF STONE CRAB, *MENIPPE ADINA* WILLIAMS AND FELDER, 1986, WITH A COMPARISON OF MEGALOPAE IN THE GENUS *MENIPPE*

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ABSTRACT

The laboratory-reared megalopa stage of the Gulf stone crab, *Menippe adina*, is described and illustrated and compared with megalopae of three other species of *Menippe*. The megalopa of *M. adina* differs from that of *M. nodifrons* in having serrate spines on the ventral margin of the dactylus of pereiopod 5 and from that of *M. rumphii* in having spines on the dactyli of pereiopods 2–5 and a more quadrate carapace. The megalopa of the morphologically similar *M. mercenaria* was also reared in the laboratory, and selected characters are described and compared with the megalopa of *M. adina*; megalopae of the two species differ only slightly. Megalopae of *M. adina* taken from field collections made off South Texas, U.S.A., were compared with and were found to be consistent with laboratory-reared *M. adina* megalopae.

Stone crabs of the genus *Menippe* are large xanthid crabs common along the eastern coasts of the United States and Mexico from North Carolina to Yucatan, the Bahamas, Cuba, and Jamaica (Rathbun 1930; Felder 1973; Williams 1984; Williams and Felder 1986). Recently the "common" stone crab, *Menippe mercenaria* (Say, 1818), was divided into two species: *Menippe mercenaria* (Say) (restricted), known from the east coast of the United States, the Caribbean, and the west coasts of Florida and Yucatan, and *Menippe adina* Williams and Felder, 1986, known from the northwestern Gulf of Mexico; hybridization of the two species occurs in northwest Florida (see Williams and Felder 1986). These two species (primarily *M. mercenaria*) support an important stone crab fishery in the southern United States and Mexico (Williams and Felder 1986) and consequently have been the subject of numerous investigations. Despite this interest, the complete larval developments of both commercial species of *Menippe* remain unknown. For *M. mercenaria* (Say), Hyman (1925) described a prezoea and first zoeal stage, and Porter (1960) described six zoeal stages reared in the laboratory. Unfortunately, Porter did not describe the megalopa stage, presumably because he considered it a postlarva and not a true larval stage. An unpublished but often-cited report by Kurata[4] included descriptions of the zoeal stages of *M. mercenaria* and a brief sketch of the megalopa; Kurata's description of the megalopa did not include morphology of the pleopods, pereiopods, or mouthparts.

Because of recent interest in the phylogenetic significance of the brachyuran megalopa (see Rice 1981a, in press; Martin in press) and postlarval stages (Martin et al. 1984; Felder et al. 1985), and because of the potential importance of stone crab larval biology to aquaculture, it is surprising that the megalopae of *M. mercenaria* and *M. adina* remain undescribed. The present paper describes the laboratory-reared megalopa of the Gulf stone crab, *Menippe adina* Williams and Felder, and compares it with field collections of the same species from south Texas, laboratory-reared megalopae of *M. mercenaria*, and all previously described megalopae of the genus *Menippe*: *Menippe mercenaria* (Say, 1818) (as described by Kurata fn. 4); *Menippe nodifrons* Stimpson, 1859 (as described by Scotto 1979); and *Menippe rumphii* (Fabricious, 1798) (as described by Kakati 1977).

MATERIALS AND METHODS

A large ovigerous *M. adina* was collected from

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

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shallow waters of the northern Gulf of Mexico near Grande Terre, LA, in May 1982 and held in a small aquarium at room temperature. After the eggs hatched, the zoeal larvae were given fresh seawater and newly hatched *Artemia* nauplii daily. Exuviae as well as dead and some living megalopae were preserved in 70% ethanol. Drawings were made with the aid of a Wild[5] M-5 stereoscope and a Wild M-11 compound stereoscope, both with camera lucida; accuracy was verified with a Nikon Optiphot. Measurements were made with an ocular micrometer. Ten laboratory-reared megalopae were examined, measured, dissected, and compared with megalopae from field collections made in 1973 off south Texas. Comparisons with *M. mercenaria* are based on laboratory-reared *M. mercenaria* megalopae from two females collected on 13 August 1987 from the Indian River system, north of Ft. Pierce, FL. Eggs of these two females hatched on 21 August 1987, and the megalopa stage was first reached after 17 days in mass culture aquaria (30‰ salinity, 25°C, 12h:12h light/dark regime). Descriptions of setation for all appendages proceed from proximal to distal. Specimens examined under the scanning electron microscope (SEM) were prepared according to procedures outlined by Felgenhauer (1987) but without postfixation in osmium tetroxide and with 100% ethanol, rather than amyl acetate, as the transitional fluid. Sibling megalopae and field collections have been deposited in the U.S. National Museum of Natural History, catalogue No. USNM 229962 (laboratory-reared *M. adina*), USNM 229961 (field-collected *M. adina*), and USNM 229963 (laboratory-reared *M. mercenaria*).

RESULTS

Carapace (Figs., 1A, B, C, 3A).—Length 1.67 mm, width 1.45 mm ($N = 10$). Subquadrate, with 2 lateral prominences on each side; dorsoventrally thick, with minute tubercle centrally located. Posterior border fringed with numerous short setae; lateral margin with few scattered setae. Rostrum ventrally deflexed, nearly vertical, with deep medial depression, rounded anteriorly. Angular interorbital prominences extend ventrally between orbit and antennule. Chromatophores variable in placement, but almost always found in areas indicated in Figure 1B.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Eyes (Figs. 1A, B, C, 3A).—Large, exposed; eyestalks sometimes with 2 or 3 short, simple anterior setae, always with posterodorsal chromatophore.

Abdomen (Fig. 1A, B).—Subequal in length to carapace. All pleura with rounded posterolateral angles. All somites with sparse setae dorsally; somites 2–5 always with elongated chromatophores.

Telson (Fig. 1G).—Broadly rounded with variable setation, occasionally with pair of small posterior spines (as in Figure 1B).

Antennule (Fig. 1K).—Biramous; peduncle 3-segmented, with variable setation. Basal segment of peduncle large, bulbous, always with large chromatophore; middle segment subcylindrical with 0–2 distal setae; distal segment ovoid with scattered short setae. Lower ramus 1-segmented with 6–8 setae; upper ramus 5-segmented with aesthetascs arranged in tiers, usually 0, 7, 8, 6, 4 subterminal plus 3 terminal, with short setae sometimes present on segments 2 and 4 (note: all aesthetascs not illustrated).

Antenna (Fig. 1J).—Flagellum 12-segmented (sometimes 11), with 3 peduncular articles and 8 or 9 flagellar articles (see Rice, in press, for correct number of antennal segments in megalopae); setation variable, usually 2, 3, 2, 0, 0, 2, 4, 0, 4 or 5, 1, 4, 4.

Mandibles (Fig. 2F).—Asymmetrical, with broadly rounded spade-shaped cutting edges; palp 2-segmented with setation 0, 11–14.

Maxillule (Fig. 2E).—Protopodite with 1 or 2 long plumose setae on posterodorsal margin; endopodite 2-segmented with setation 1, 2 subterminal plus 2 terminal; basal endite with 29–35 spines and setae; coxal endite with 13–16 spines and setae.

Maxilla (Fig. 2D).—Scaphognathite with 70–78 fringing setae and 0–6 setae on blade; endopodite unsegmented with 0 or 1 distolateral seta and 4 or 5 basal plumose setae; basal endite bilobed with setation variable, usually 8–10, 9–11; coxal endite bilobed with setation usually 7, 9 or 10.

Maxilliped 1 (Fig. 2C).—Exopodite 2-segmented, with setation 2 or 3, 5–7. Endopodite

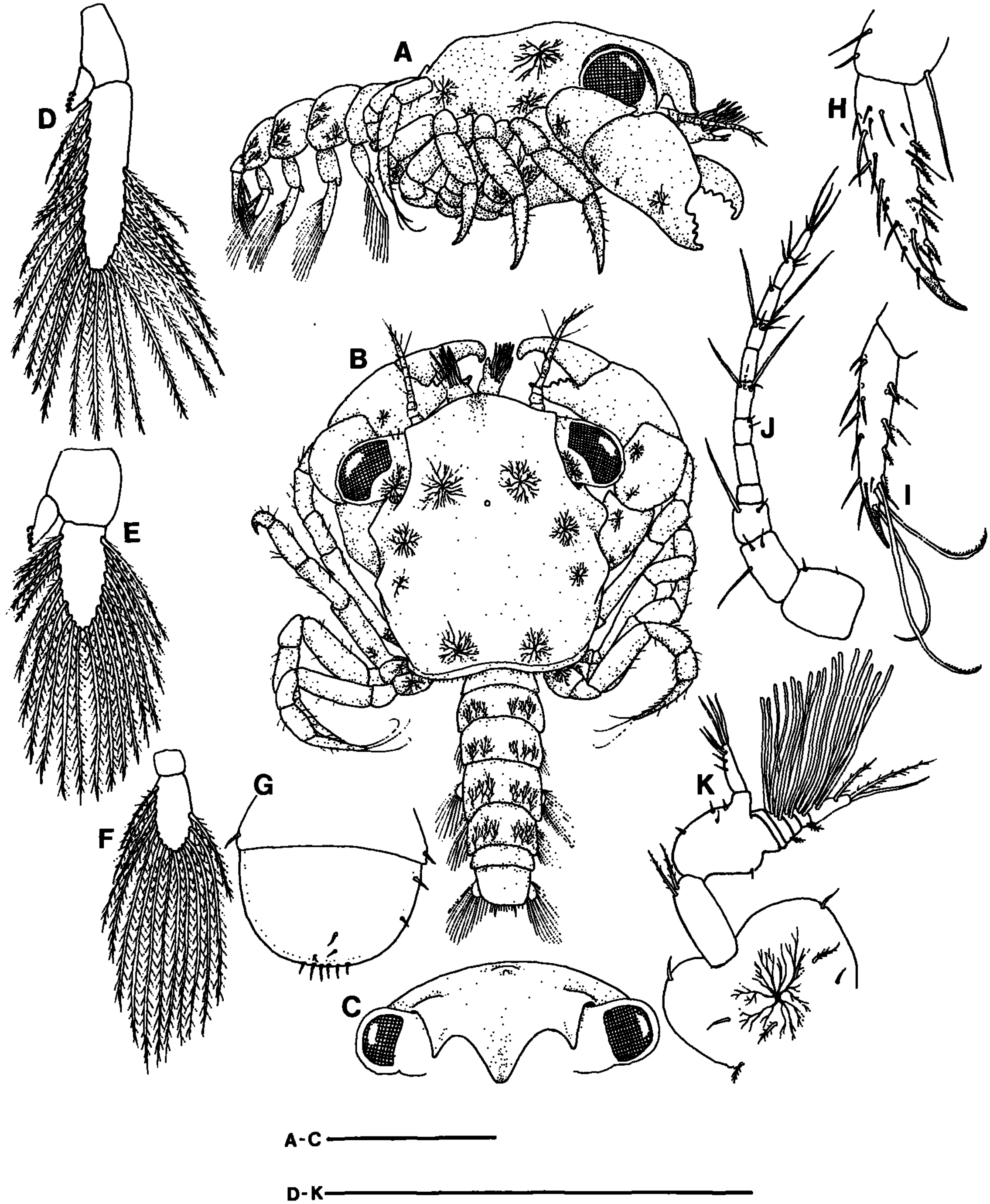

FIGURE 1.—Megalopa of the Gulf stone crab, *Menippe adina*. A, entire animal, lateral view; B, same, dorsal view; C, frontal view of rostrum and eyes; D, pleopod 1; E, pleopod 4; F, pleopod 5; G, telson and posterior part of sixth abdominal segment; H, dactylus of pereiopod 3; I, dactylus of pereiopod 5; J, antenna; K, antennule, Both scale bars = 1.0 mm.

FIGURE 2.—Megalopa of *Menippe adina*, mouthparts. A, third maxilliped; B, second maxilliped; C, first maxilliped; D, maxilla; E, maxillule; F, mandible. Scale bar = 0.5 mm.

unsegmented with 6–8 setae arranged as shown. Basal endite setation 28–33; coxal endite setation 15–17. Epipodite with 22 or 23 long, minutely plumose setae, appearing simple under low magnification.

Maxilliped 2 (Fig. 2B).—Exopodite 2-segmented, with setation 3, 5–8. Endopodite 4-segmented, with setation usually 5, 2 or 3, 5 or 6, 9 or 10; distal segment with 4 or 5 stout serrate setae. Epipodite with 9 or 10 long minutely plumose setae.

Maxilliped 3 (Fig. 2A).—Exopodite 2-segmented, with setation 0 or 1, 6–8. Endopodite 5-segmented, with variable setation, usually 18–20, 15 or 16, 5–9, 6–8, 7–10; ischium with scalloped medial border. Epipodite with 18 long minutely plumose setae on distal two-thirds plus 8–12 plumose setae on proximal one-third. Protopodite setation variable.

Pereiopods (Figs. 1A, B, H, I, 3B, C, D).—Chelipeds long, stout, subequal; dactylus with 4 irregular teeth; immovable finger with 3 teeth (Fig. 3B); tips of fingers overlap distally when approximated. No recurved hook on basi-ischium (Fig. 3B). Second to fourth pereiopods similar; dactylus with 5 (rarely 4) serrate spines ventrally (e.g., Figs. 1H, 3C, D); propodus with long ventrodistal spine (Fig. 1H). Fifth pereiopod dactylus (Fig. 1I) with 3 long pectinate setae, 1 markedly toothed and concave (Fig. 3E), on distal ventral border and 3 or 4 serrate spines ventrally.

Pleopods (Fig. 1D, E, F).—Decreasing in size posteriorly. Pleopod 1 (Fig. 1D) with 19–22 plumose setae; endopodite with 3 or 4 hooked setae. Pleopod 4 (Fig. 1E) with 19–21 plumose setae; endopodite with 3 or 4 hooked setae (Fig. 3F). Pleopod 5 (uropod) (Fig. 1F) with 12–14 plumose setae; basal segment lacking setae or with 1 or 2 setae (field collections); endopodite absent.

Color.—Overall coloration rose-orange, with dark blue-black chromatophores located as shown in Figure 1A, B.

DISCUSSION

The genus *Menippe* de Haan, 1833, presently contains about 8 species, only 3 of which occur in North America. The megalopa stage is now known for 3 species in the genus: *M. rumphii* (Fabricious, 1798), *M. nodifrons* Stimpson, 1859, and *M. adina* Williams and Felder, 1986. In addition, selected characters of *M. mercenaria* (Say, 1818) are presented here for comparison; some characters of that species are also obtainable from an unpublished report by Kurata (fn. 4) (see Table 1).

Laboratory-reared megalopae of *M. adina* were virtually identical to megalopae presumed to belong to *M. adina* that were collected off south Texas. Even meristic counts of the mouthpart setation agreed exactly, with the only observed differences being that field-collected megalopae were slightly larger and occasionally bore 1 or 2 setae on the basal segment of the uropod. Thus, we feel that our laboratory conditions have not adversely affected development or introduced abnormal characters, and we have used these field collections for the SEM figures of *M. adina* megalopae (Fig. 3).

We expected to find that characters of the megalopa of *M. adina* are similar to those described by Kurata (fn. 4) for the morphologically similar (in adulthood) *M. mercenaria*, a species known to hybridize with *M. adina* (see Williams and Felder 1986). In general this is true. However, some characters reported by Kurata differ from our observations on *M. adina* and from our laboratory-reared megalopae of *M. mercenaria* (Fig. 4). Kurata mentioned (but did not illustrate)

TABLE 1.—Comparison of characters in megalopae of the genus *Menippe*. Dash (—) indicates information not available from reference.

			Setation				Spination			
	Size[1] (mm)		Palp of	Epipod of			Dactylus of		Setation	
Menippe	CL	CW	mandible	Maxilliped 1	Maxilliped 2	Maxilliped 3	Pereiopods 2–4	Pereiopod 5	pleopod 5	Reference
adina	1.67	1.45	0, 11–14	22–23	9–10	18	5	4	12–13	Present study
mercenaria	1.70	1.55	0, 11–13	20–23	7–10	18–20	4	4	11–13	Present study
mercenaria	1.7–8	—	—	—	—	—	4–5	0	11–12	Kurata[3]
nodifrons	1.50	1.31	0, 10–13	12–20, [2]26	up to 10	18	5	0	11	Scotto 1979
rumphii	1.60	1.55	0, 0, 9	22	8	18	0	0	12	Kakati 1977

[1]CL = carapace length; CW = carapace width.
[2]From a megalops hatched from a stage 6 (rather than the typical stage 5) zoea.
[3]See text footnote 4.

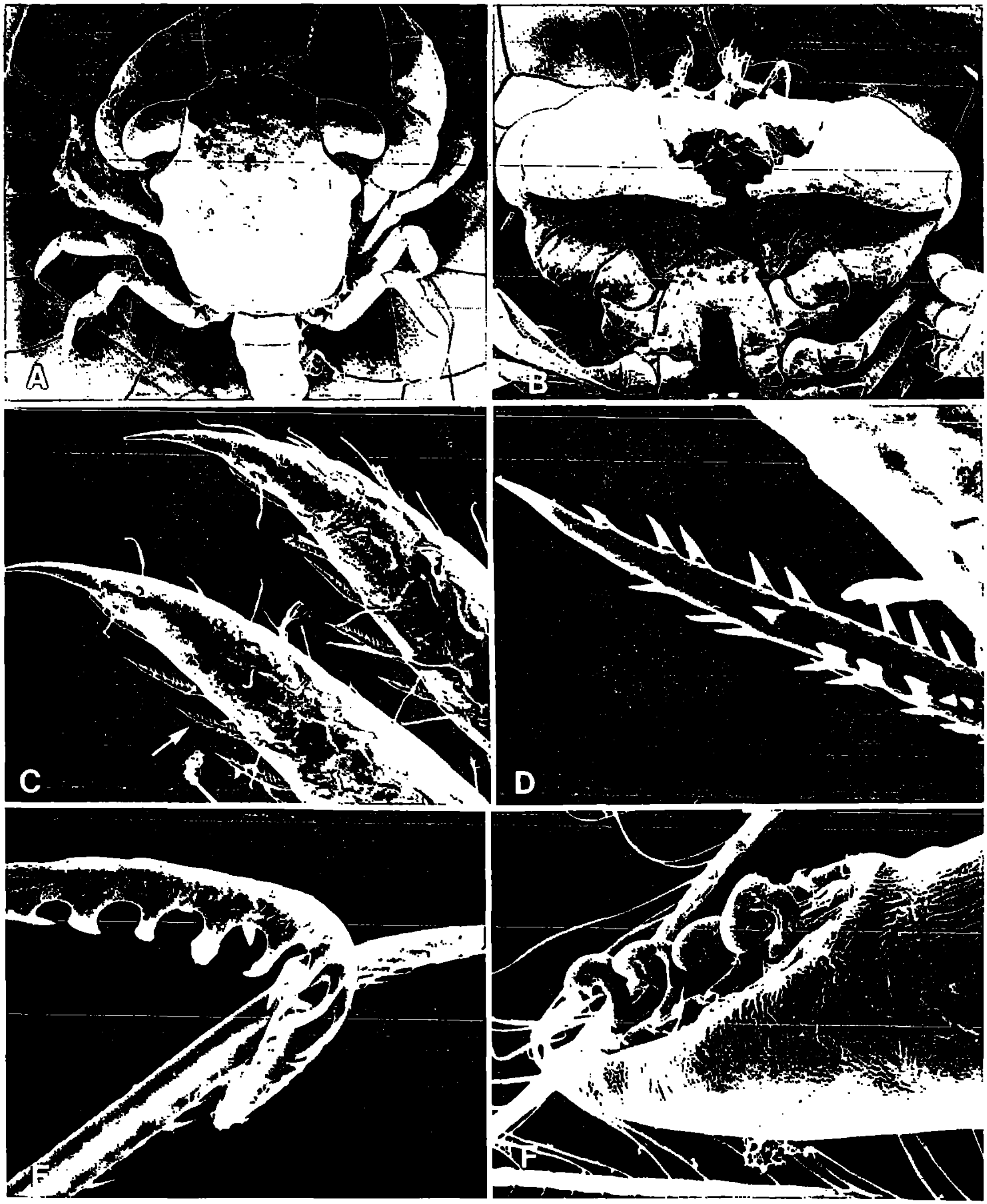

FIGURE 3.—Scanning electron micrographs (SEM) of selected characters of *Menippe* megalopae (presumably *M. adina*) collected in south Texas. A, dorsal view of carapace (× 25); B, ventral view of chelipeds showing dentition of the fingers and lack of recurved hook on ischium (× 37); C, dactyli of second (upper figure) and third pereiopods (× 230); D, higher magnification of ventral dactylar spine indicated by arrow in C (× 1,900); E, endopod of third abdominal pleopod showing 4 dentate hooklike setae (× 2,200); F, serrate setae (only 2 of 3 shown) of dactylus of pereiopod 5 (× 2,300).

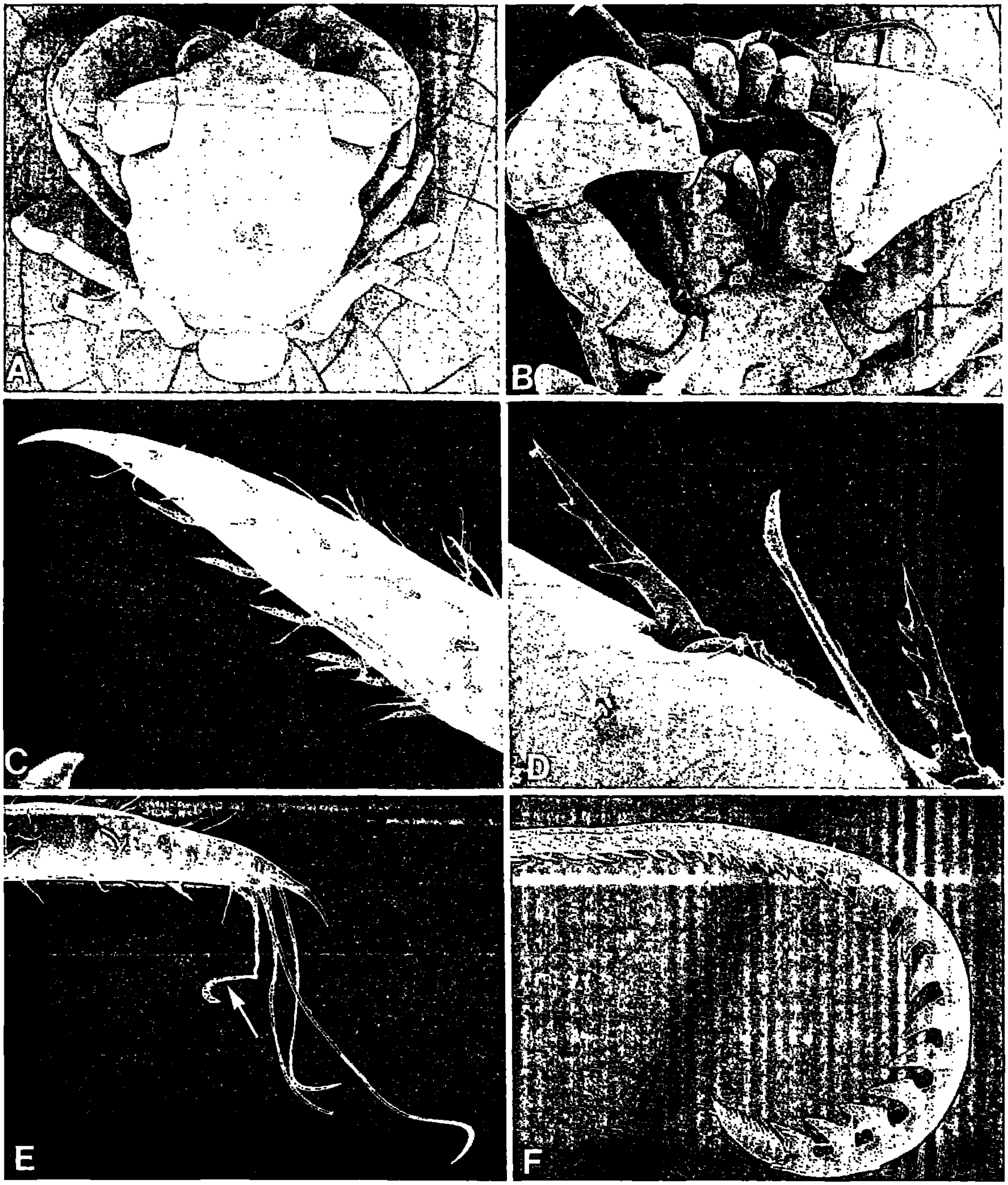

FIGURE 4.—Scanning electron micrographs (SEM) of selected characters of the laboratory-reared megalopa of *Menippe mercenaria*. A, dorsal view of carapace (× 37); B, ventral view of chelipeds and third maxillipeds (× 55); C, dactylus of second pereiopod showing ventral serrate spines (× 270); D, ventral spines on dactylus of fourth pereiopod with fewer spinules than anterior pereiopod spines (× 2,000); E, dactylus of fifth pereiopod showing four serrate "sensory" setae with one (arrow) more obviously serrate (× 190); F, higher magnification of concave serrate setae indicated by arrow in E (× 1,500).

"about 9 small spines" on the ischium of the third maxilliped; we found no spines on *M. adina* or *M. mercenaria* (Figs. 3B, 4B), but it is possible that Kurata was referring to the acute borders of the scalloped medial margin (our Figure 2A), in which case the 2 species are similar. Spination of the ischium of pereiopods 1–3 differs also; Kurata described 5 or 6, 2 or 3, and 1 small spine on the ischia of pereiopods 1, 2, and 3, respectively, whereas we did not notice this condition in *M. adina* or *M. mercenaria* (see Figures 3B, 4B). Finally, Kurata (fn. 4: pl. 74, fig. E) illustrated no spines on the ventral surface of the fifth pereiopod dactylus of *M. mercenaria*; these spines are obvious on both species (Figs. 1I, 4E). We found few differences between megalopae of *M. adina* and *M. mercenaria*. General morphology of the carapace and chelipeds, spination of the dactylus of the pereiopods, and setation of the pleopods agreed almost exactly (compare Figures 3 and 4). Ventral dactylar spines on the posterior walking legs of *M. mercenaria* were not so serrate as in *M. adina* and were sometimes armed with only 2 or 3 large spinules rather than the numerous spinules seen in *M. adina* (e.g., Fig. 3D) and in the more anterior legs of *M. mercenaria* (see Figure 3C, D, 4C). Also, in all but 1 of the 9 megalopae of *M. mercenaria* examined there were 4 (rather than 3) long serrate setae on the dactylus of the fifth pereiopod (Fig. 4E). As in *M. adina*, one of these setae was more serrate and concave than were the other long setae (Fig. 4E, F). However, we have not examined mouthpart morphology of *M. mercenaria* in the detail in which we described *M. adina*, and so it is possible that additional characters will be found to separate these 2 species at the megalopa stage.

The megalopa of *M. adina* is very similar to that of *M. nodifrons* as described by Scotto (1979). Although the 2 species differ in setation of some of the mouthparts, this setation may differ from side to side in a given individual. The salient character that serves to separate megalopae of these 2 species is the presence in *M. adina* of 4 stout serrate spines on the dactylus of pereiopod 5. Scotto (1979) figured only setae (and no spines) on the dactylus of the fifth pereiopod in *M. nodifrons* and the dactylar spines on other pereiopods apparently are not serrate (Scotto 1979, fig. 9c, pereiopod 3).

The megalopa of *M. rumphii* described by Kakati (1977) differs from that of *M. nodifrons*, *M. mercenaria*, and *M. adina* in having a more ovoid carapace with the rostrum only slightly deflexed. Kakati did not describe the dactyli of pereiopods 2–5 for *M. rumphii*, but his figure of pereiopod 2 (1977:639, fig. 2, p. 50) does not show stout ventral spines on the dactylus. Possibly Kakati overlooked these spines; if not, the absence of these spines on pereiopod 2 would further serve to separate the megalopa of *M. rumphii* from those of *M. nodifrons*, *M. mercenaria*, and *M. adina*. All 4 species have been described as having a rose-orange coloration in life.

Although Rathbun (1930) and Monod (1956) synonymized *M. rumphii* with *M. nodifrons*, descriptions of the zoeal stages of *M. rumphii* and *M. nodifrons* by Kakati (1977) and Scotto (1979), respectively, show that larvae of the 2 species differ considerably. In the first zoeal stage, *M. rumphii* exhibits elongated posterolateral processes on abdominal segment 5 that extend posteriorly to more than half the length of the telsonal furcae, which lack spines. The first zoea of *M. nodifrons* has similar posterolateral processes but these do not extend posteriorly beyond the fork of the telson; the telsonal furcae bear 1 dorsal and 2 lateral spines each. These differences are not apparent in later zoeal stages, but their presence in the first zoeal stage and the differences noted in the megalopa stage may be reason to question the synonymy of these 2 species.

Xanthid larvae are known to be variable, and it is often difficult to reconcile larval and adult groupings based on morphology. Larvae of some morphologically disparate (as adult) species are very similar, whereas zoeal stages for species in some genera differ markedly in their morphology (see Martin 1984; Martin et al. 1984, 1985; Martin and Abelë 1986). Because of the known morphological variability of xanthid larvae, characters presented for taxonomic purposes here and elsewhere (e.g., Martin 1984) must be used with caution.

It is not our intent to promote descriptions of single stages in the life cycles of brachyuran crabs. However, in those cases where a description of a single stage adds appreciably to our knowledge of phylogeny (e.g., Rice 1981b) or fills a gap in the larval biology of a commercially important species complex (present study), we feel such a description is justified. A detailed comparison of zoeal stages of the two species is planned for the near future.

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