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THE COMPLETE LARVAL DEVELOPMENT IN THE LABORATORY OF  
*MICROPANOPE SCULPTIPES* (CRUSTACEA, DECAPODA, XANTHIDAE)  
WITH A COMPARISON OF LARVAL CHARACTERS IN  
WESTERN ATLANTIC XANTHID GENERA<sup>1</sup>

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ABSTRACT

The larval development in the laboratory of *Micropanope sculptipes*, a western Atlantic deepwater xanthid crab which inhabits encrusted and coralline substrates, is completely described and illustrated. Development proceeds from a prezoal stage of brief duration through four zoal stages and one megalopa stage. Survival of larvae was poor under experimental conditions of diel illumination, 36‰ salinity, and temperatures of 20°, 25°, and 25°-30° C. Development to megalopa occurred only at 25° C. Morphological characteristics of *M. sculptipes* zoeae and megalopa are compared with larval characteristics of several other western Atlantic xanthid species.

Crabs of the family Xanthidae are both numerous and diverse with species inhabiting a great variety of marine and estuarine environments (Rathbun 1930). The genus *Micropanope* was erected by Stimpson in 1871 with the type-species *Micropanope sculptipes*. This genus consists of small (12 mm carapace width) xanthid crabs with a known range from the Bahamas and Florida Keys to Brazil and Bermuda in deeper offshore oceanic water (Rathbun 1930; Guinot 1967). *Micropanope* was originally noted to resemble *Pilumnus*, and to be allied with *Panopeus*, but was supposedly distinct in being a sublittoral to bathyal group and not littoral as was *Panopeus*. However, subsequent collections yielded *Micropanope* species which were more littoral in distribution and, through time, the genus was considered to be a heterogeneous mixture of several distinct generic groups which were yet to be defined (Guinot 1967). This author emended the genus *Micropanope* to contain only two western Atlantic species: viz. *M. sculptipes* Stimpson, the type-species, and *M. lobifrons* A. Milne Edwards. The remaining species within *Micropanope* sensu lato have either

been placed by Guinot in several other genera, or await placement in genera yet to be named.

Larvae of many species of xanthid crabs from several different genera have been described based on laboratory rearing, but there have been no published descriptions of a complete larval development for any species of *Micropanope* sensu lato thus far. A study on the larval development of *M. barbadensis* Rathbun has recently been completed (Gore et al. 1981), but this species will ultimately be assigned to a separate, and as yet undefined, genus close to *Coralliope* (fide Guinot 1967). A knowledge of the larval morphology of *Micropanope*, when compared with larval characteristics of previously described xanthid species, especially those species once placed in the genus *Micropanope*, may be of some utility in recognizing the evolutionary relationships among such species within the Xanthidae. Accordingly, in this report we describe the complete larval development of *M. sculptipes* from hatching to megalopa stage based on specimens raised in the laboratory, and compare these larval and postlarval stages with those from other xanthid crabs in the western North Atlantic.

MATERIALS AND METHODS

A small (9.3 mm carapace width) ovigerous female *M. sculptipes* was collected 14 June 1978 by the crew of the Harbor Branch Foundation RV *Sea Diver* (cruise SD23, station #007), with a 20 ft (6.1 m) otter trawl. The trawl sample was taken off the

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coast of central eastern Florida between lat. 27°14.8' N, long. 79°56.7' W and lat. 27°15.1' N, long. 79°58.0' W from depths of 115.2-96.9 m. The specimen, collected from a substrate consisting of encrusted shell hash and *Oculina* coral, carried approximately 80 pale fuchsia eggs which darkened slightly before hatching on 20 June in the laboratory. After yielding larvae, this specimen was compared with specimens of *M. sculptipes* deposited in the National Museum of Natural History, Washington, D.C., which had been illustrated by Rathbun (1930: USNM 20719, 60777) and was found to agree in all important respects.

Three groups of 24 larvae were isolated, one each in 24 compartmented plastic boxes, and placed into controlled temperature units (CTU) at 20°, 25°, or 25°-30° C ( $\pm 0.5^\circ$  C) under diel illumination. Surf zone seawater (of 36‰) was filtered through glass wool fiber, stored in large Nalgene<sup>4</sup> bottles in the laboratory, and used to culture larvae.

Larvae received fresh seawater and were fed freshly hatched San Francisco brand *Artemia* nauplii daily. Molts and deaths of each larva and color notes of representative larval stages under refracted and reflected white light were recorded. Dead individuals and molts were preserved in 70% ethanol and were measured with a microscope fitted with an eyepiece micrometer. Measurements given are the arithmetic mean values of the number of specimens examined in each stage. Larvae were cleared in 50% lactic acid solution to which lignin pink stain was added to aid in drawing larval characters. Whole mounts (50 $\times$ ) and dissected appendages (drawn at 200 $\times$  and checked for details at 400 $\times$ ) were mounted in CMCP mounting medium and drawn with Wild M5 and M20 microscopes equipped with camera lucidas.

The spent female and a complete series of larval stages are deposited in the United States National Museum, USNM 171393.

## RESULTS OF REARING EXPERIMENT

*Micropanope sculptipes* larvae hatched as pre-zoeae of short, but not precisely determined, duration. They developed through four zoeal stages, after which metamorphosis to a megalopa occurred.

Figure 1 and Table 1 indicate that survival was poor and was apparently influenced by temperature. Most successful development occurred at 25° C; survival was notably lower at 20° C, and no larvae developed beyond first zoeae at 25°-30° C. Even at the "optimum" temperature of 25° C, 50% mortality occurred during the first zoeal stage and only one individual survived to the megalopa stage. At this temperature developmental duration was 26 d from hatching to megalopa; no crab stage was attained.

The duration of larval stages was variable. First stage zoeae generally required 6 or 7 d to successfully molt to second stage zoeae; however, one individual at 20° C required 15 d and another individual at 25° C persisted for 10 d before molting. These two zoeae did not survive beyond the second zoeal stage. Second and third zoeal stages generally remained as such 5 d before molting, although 20° C larvae took slightly longer than 25° C larvae. Fourth zoeal stages survived between 6 and 8 d before either molting or dying. The one fourth stage zoea at 25° C remained in stage 6 d before molting to megalopa.

Larval development was apparently regular and no larvae were observed to either skip a developmental stage or molt without developing into a more advanced stage. One zoea in the first stage at 25° C was grossly deformed when it molted to second stage at age 6 d and it died 7 d later without molting again. All other zoeae possessed similar morphological characters, so that temperature difference produced no variations. Many zoeae died during preecdysis or in ecdysis to the next larval stage. Five of the nine fourth stage zoeae died while attempting the molt to megalopae. Megalopal telsons, antennae, and chelipeds were observed beneath the transparent fourth zoeal exoskeletons of these specimens, indicating a terminal larval stage. No fifth zoeal stage larvae were observed.

The results of this study indicate that *M. sculptipes* larvae progress through four larval stages and thus are similar to the majority of xanthid species. Four zoeal stages have been considered characteristic in Xanthidae (Hyman 1925; Lebour 1928) and include many species, e.g., *Panopeus herbstii* (Costlow and Bookhout 1961a), *Eurypanopeus depressus* (Costlow and Bookhout 1961b), *Rhithropanopeus harrisi* (Chamberlain 1962), *Hexapanopeus angustifrons* (Costlow and Bookhout 1966), *Leptodius* [= *Pseudomadaeus*] *agassizii* (Costlow and Bookhout 1968), *Neopanope*

<sup>4</sup>Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

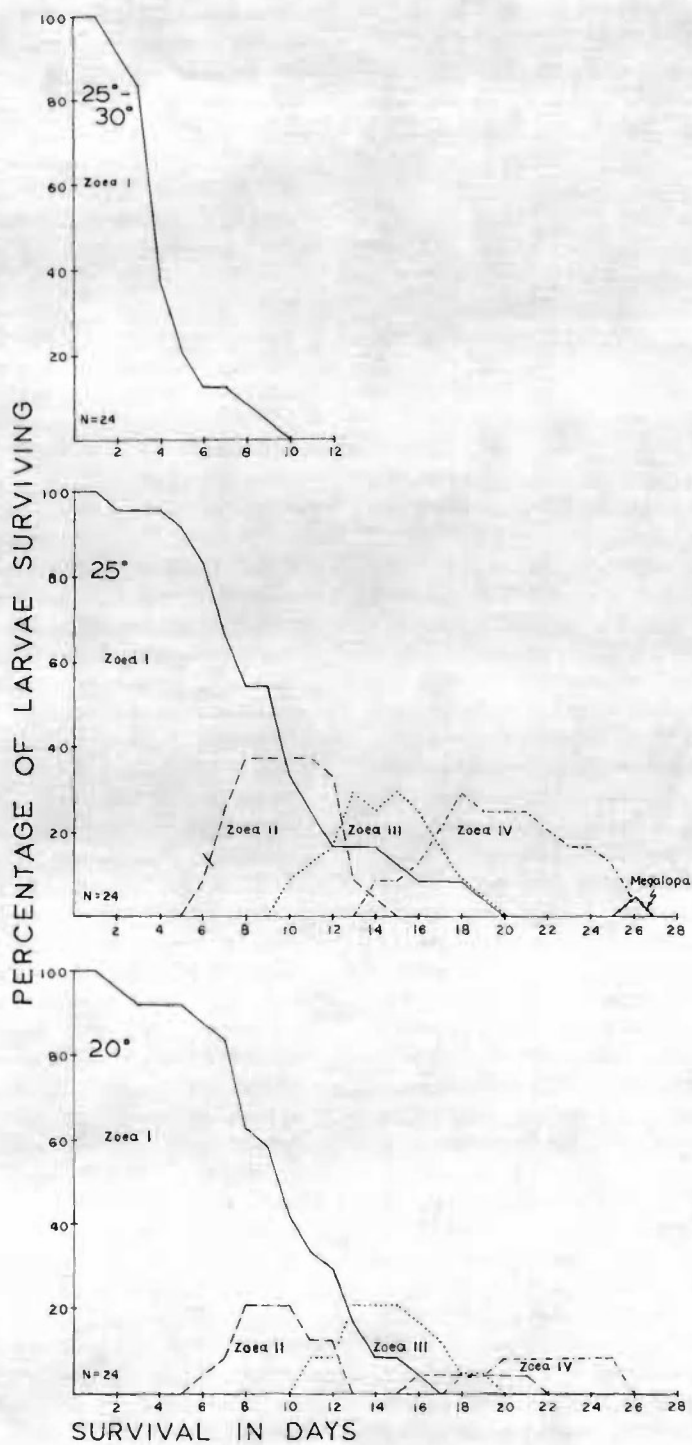


FIGURE 1.—*Micropanope sculptipes*. Percentage and duration of survival of larvae reared at three laboratory temperatures. N = number of larvae reared at each temperature in the series.

TABLE 1.—*Micropanope sculptipes*, relative duration of larval life in days at three temperatures. (Number of larvae started at each temperature = 24.)

Temp °C	Larval stage	Duration				Total no. molting to next stage
		Minimum	Mean	Mode	Maximum	
20	Zoea I	5	8	7	15	6
	Zoea II	4	—	5	5	5
	Zoea III	5	6	—	7	2
	Zoea IV	1 <sup>6</sup>	—	—	1 <sup>8</sup>	0
25	Zoea I	5	7	8	10	12
	Zoea II	4	—	5	5	9
	Zoea III	4	—	5	5	9
	Zoea IV	1 <sup>1</sup>	6	6	1 <sup>8</sup>	1
25-30	Did not survive beyond first zoeal stage					

<sup>1</sup>Died in stage without further molt.

*texana* (McMahan 1967), *N. sayi* and *N. packardii* (Costlow and Bookhout 1967), *Pilumnus dasyopodus* (Sandifer 1974), and *P. sayi* (McDonald and Lang 1976). However, crabs of the genus *Menippe* develop through 5 or 6 zoeal stages prior to metamorphosis (e.g., Porter 1960; Ong and Costlow 1970; Scotto 1979), *Heterozius rotundifrons* and *Epixanthus dentatus* have two zoeal stages, and *Pilumnus lumpinus* has only one zoeal stage (Saba et al. 1978). The latter three species live in specialized and restricted habitats which may account for the differences in number of developmental stages. However, *Ozius truncatus* (four zoeal stages) and *Heteropanope (Pilumnopeus) serratifrons* (probably four zoeal stages) are also species which live in restricted habitats (Wear 1968), so other factors besides environment may influence developmental time. *Micropanope barbadensis* develops through either three or four zoeal stages (Gore et al. 1981), and the elimination of the "terminal" stage may be an adaptive response to food supply, nutritional deficiencies, or an inherited response from adult genotypes, according to several hypotheses considered by these authors.

It is therefore difficult to directly compare the duration of larval development for *M. sculptipes* (about 26 d at 25° C) with larval development times for other xanthid species. Species of *Menippe* (5 or 6 zoeal stages) required at least 17-21 d at 25° C to develop into megalopa (summarized by Scotto 1979). The duration of larval development seems to be largely dependent on temperature, and the experimental temperature conditions employed by different researchers may vary considerably for a number of reasons. Larval development time decreased for *Micropanope sculptipes* as tempera-

ture increased. This inverse relationship between temperature and duration of larval development is consistently observed for the larvae of different xanthid species (Costlow et al. 1962; Costlow and Bookhout 1971; Scotto 1979). Based on these data and at 25° C, we may postulate a planktonic development time on the order of 1 mo before metamorphosis to first crab in *M. sculptipes*.

## LARVAL DESCRIPTION

### First Zoea

Carapace length (anterior margin of orbit to median posterodorsal edge of carapace): 0.47 mm.

Number of specimens examined: 14.

**Carapace** (Figure 2A, B). Typically brachyuran, possessing rostral, dorsal, and 2 lateral spines. Eyes sessile. Rostrum straight, naked, sharply pointed, slightly shorter than carapace length. Dorsal spine about equal in length to carapace, curving gently posteriad, bearing a few scattered minute tubercles. Lateral spines short, naked, projecting perpendicular to sagittal plane. Carapace elliptical, naked except for 2 small dorsolateral setae originating midway between dorsal and lateral spines; mediodorsal knob [= "forehead protuberance" Yang 1967] naked.

**Antennule** (Figure 2C). Flabellate rod with 3 aesthetascs, 2 naked setae at tip.

**Antenna** (Figure 2D). Protopodite long, tapering to point; spirally arranged spines present along distal three-fourths length with spines larger, longer toward tip. Exopodite one-sixth to one-fifth protopodite length, naked throughout length, with 1 short apical spine, 1 long and 2 short apical nonplumose setae.

**Mandibles** (Figure 2E). Well-developed incisor and molar processes; no palp.

**Maxillule** (Figure 2F). Coxal endite with 7 stout, plumose setae. Basal endite with 5 denticulate spines, about 20 minute hairs on lateral surface. Endopodite two-segmented; proximal segment with 1 long, nonplumose seta; distal segment with 2 subterminal, 4 terminal, sparsely plumose setae.

**Maxilla** (Figure 2G). Coxal endite bilobed with 4 proximal, 3 distal plumose setae. Basal endite bilobed with 4 (occasionally 5) proximal and 4 distal plumose setae. Endopodite bilobed; 3 terminal sparsely plumose apical setae on proximal lobe, 5 terminal (appearing as 3 apical, 2 slightly lower) sparsely plumose setae on distal lobe; this setal formula holds for remainder of stages.

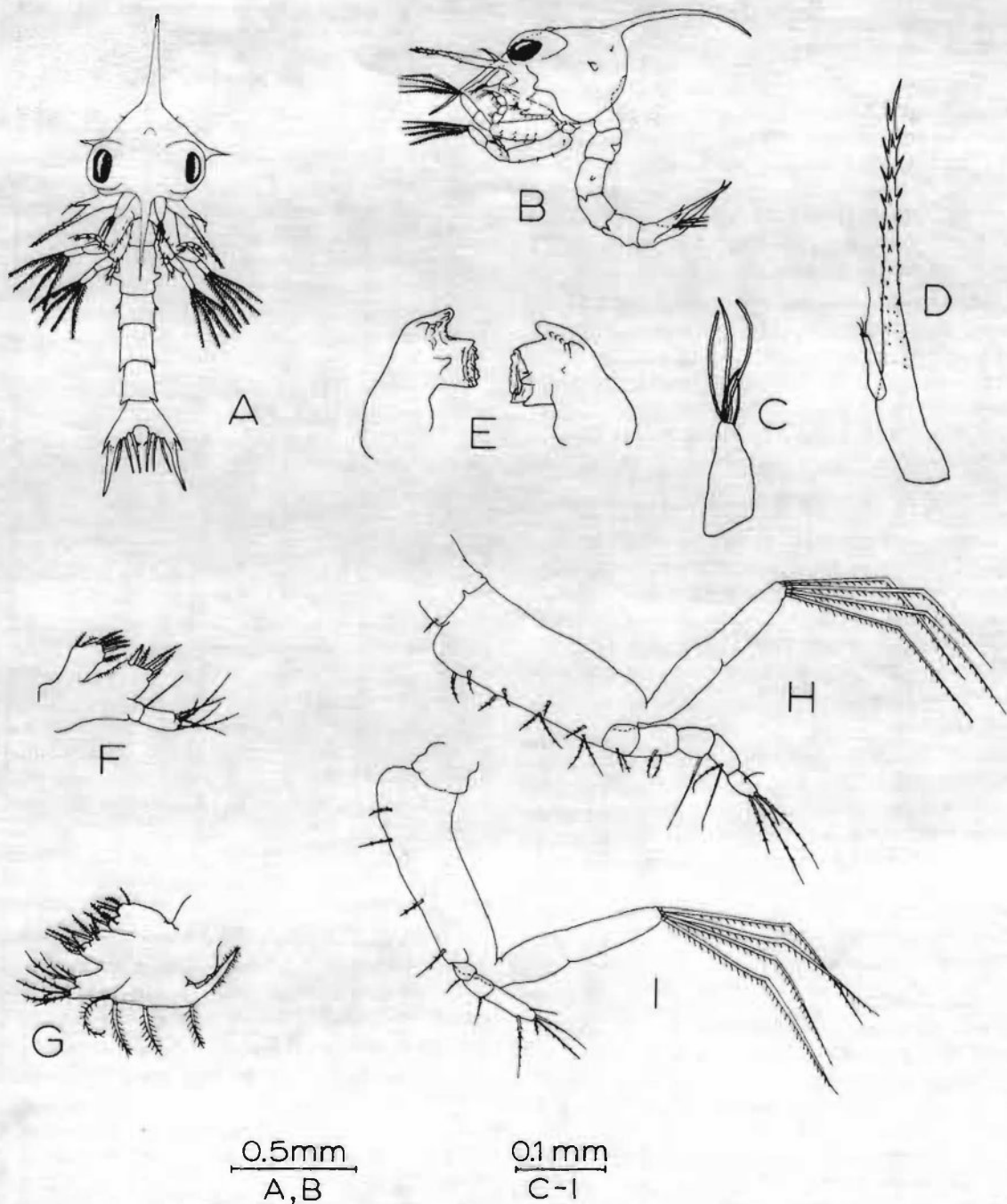


FIGURE 2.—*Micropanope sculptipes*, first zoea. A, ventral view; B, lateral view; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, maxilliped 1; I, maxilliped 2.

Scaphognathite with 4 marginal plumose setae and elongate sharp process bearing numerous minute hairs laterally.

*Maxilliped 1* (Figure 2H). Coxopodite with 1 seta. Basipodite ventral margin with 10 sparsely plumose setae arranged (proximally to distally) 2, 2, 3, 3; this setal formula holds for remainder of stages. Endopodite five-segmented with proximal to distal segment setation of 2, 2, 1, 2, 4+I. (Roman numeral denotes dorsal seta.) Exopodite with 4 terminal natatory setae.

*Maxilliped 2* (Figure 2I). Coxopodite without setae. Basipodite ventral margin with one row of 4 sparsely plumose setae; this setal formula holds for remainder of stages. Endopodite three-segmented with proximal to distal segment setation of 1, 1, 4+I. Exopodite with 4 terminal natatory setae.

*Maxilliped 3 and Pereiopods.* Not apparent.

*Abdomen* (Figure 2A, B). With five somites. Somite 1 unornamented; somite 2 with anteriorly curved lateral hooks; somite 3 with smaller posteriorly curved lateral hooks. Somites 3-5 with small posterolateral spines overlapping following somite. Somites 2-5 with pair of minute posterodorsal setae.

*Telson* (Figure 2A, B). Bifurcate; each furca smooth, possessing one larger lateral spine near its midlength and one smaller dorsal spine originating near apex of lateral spine. Inner telson margin with 3 pairs of articulated spines, each armed throughout length with minute spinules, center pair of spines with 2 longer interior spinules and 1 longer exterior spinule located at proximal one-third of spine. Inner telson margin with pronounced medial sinus.

*Color.* Zoea mainly colorless with exception of localized pigment concentrations. Dorsal area of orbit pale mint green, color fading into interorbital area; interorbital protuberance faint orange. Gastric region pale orange extending along gut through first two abdominal segments (this color not due to ingested *Artemia*); diffused pale mint green surrounds orange of gastric region. Mandible incisor and molar surfaces scarlet, blending into pale orange within mandible. First and second maxillipeds with diffuse pale orange at junction of basipodite and exopodite. Proximal region of telson furcae on either side of median telson sinus tinted with diffused pale orange.

## Second Zoea

Carapace length: 0.61 mm.

Number of specimens examined: 10.

*Carapace* (Figure 3A, B). Eyes faceted, stalked. Rostrum base with small, lateral preorbital protuberances perpendicular to longitudinal axis. Dorsal spine usually with 2 small proximal setae, occasionally with a few small widely spaced setae and tubercles. Lateral spines with 2 to 4 minute dorsal tubercles. Carapace ventral margin with 3 or 4 fringing setae; mediodorsal knob now with 4 integumental sensillae arranged into rectangle on crest, one pair setae anterior and posterior to knob.

*Antennule* (Figure 3C). Four aesthetascs, 2 naked setae at tip.

*Antenna* (Figure 3D). Unchanged except for incipient endopodite primordium near exopodite base.

*Mandibles* (Figure 3E). As illustrated, without palp.

*Maxillule* (Figure 3F). Coxal endite unchanged from first zoea. Basal endite apex with 6 denticulate spines, 1 naked seta; lateral surface with 1 plumose seta,  $\approx$ 20 minute hairs. Endopodite unchanged from first zoea. Protopodite now with 1 distal plumose seta.

*Maxilla* (Figure 3G). Coxal endite bilobed with 4 proximal, 4 distal plumose setae. Basal endite bilobed with 5 proximal, 4 distal plumose setae. Scaphognathite with 11 or 12 marginal plumose setae.

*Maxilliped 1* (Figure 3H). Coxopodite with 1 (rarely 2) seta. Endopodite unchanged from first zoea. Exopodite with 6 terminal natatory setae.

*Maxilliped 2* (Figure 3I). Coxopodite without setae. Endopodite three-segmented with proximal to distal segment setation of 1, 1, 4 or 5+I. Exopodite with 7 terminal natatory setae.

*Maxilliped 3 and Pereiopods.* Not apparent.

*Abdomen* (Figure 3A, B). With five somites. Somite 1 with 1 posterodorsal seta; somites 2-5 generally unchanged from first zoea, but posterolateral spines of somites 3-5 slightly longer relative to body size.

*Telson* (Figure 3A, B). Generally unchanged from first zoea. An additional minute lateral furcal spine may occasionally be present within the fork created by the major lateral spine where it originates from the furca. This spine (when present) may be readily apparent, reduced to a lump,

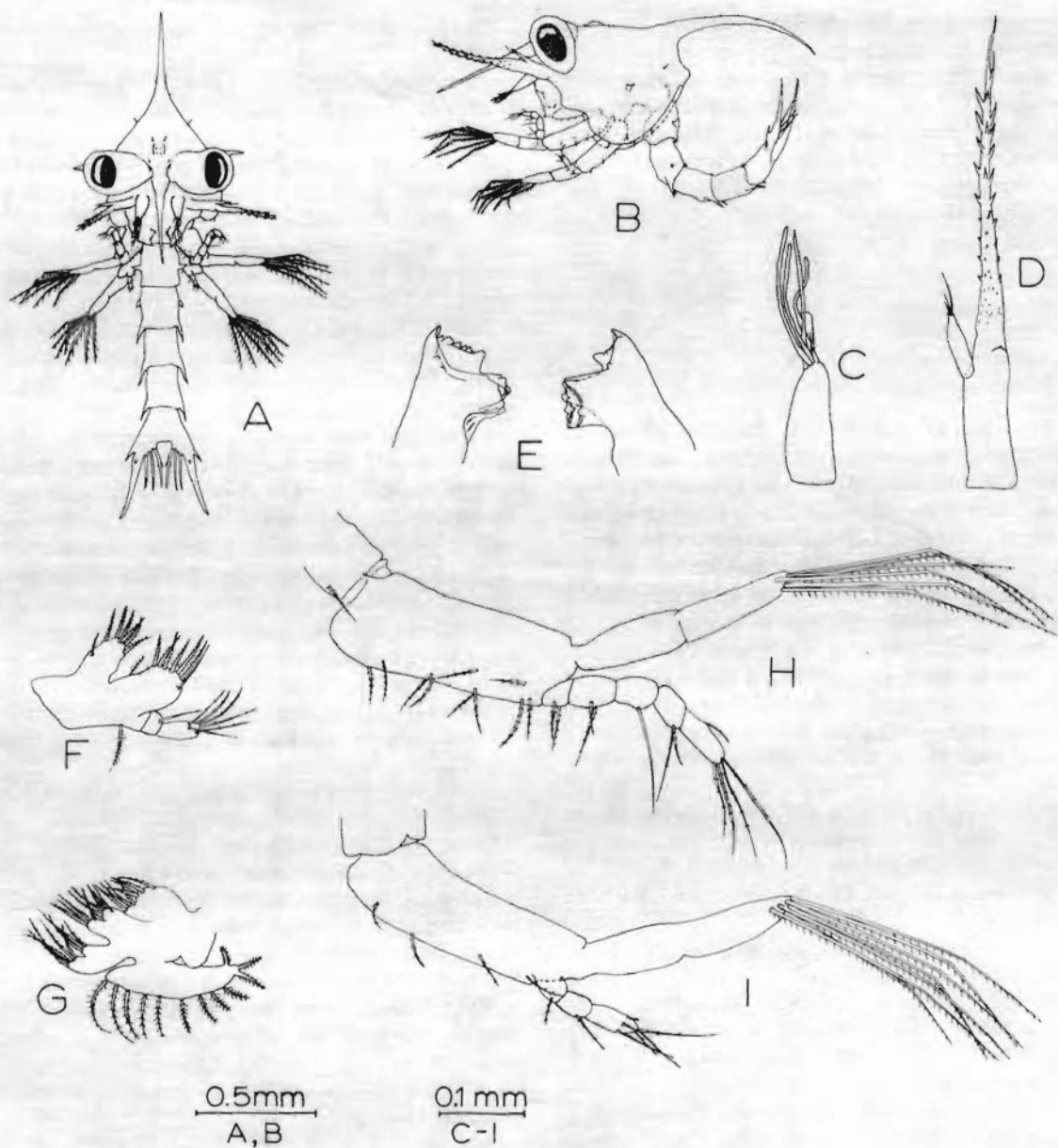


FIGURE 3.—*Micropanope sculptipes*, second zoea. A, ventral view; B, lateral view; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, maxilliped 1; I, maxilliped 2.

or present on one furca while absent from the other on the same individual.

*Color*: Similar to that of first zoea, but noticeably intensified. Pale orange highlights distal three-fourths of rostrum, dorsal spine, antennae, and antennules. Gut color more burnt orange, extending through abdominal somite 4. Mandibles most pronounced in burnt orange, outer surfaces scarlet.

### Third Zoea

Carapace length: 0.76 mm.

Number of specimens examined: 8.

*Carapace* (Figure 4A, B). Rostrum preorbital protuberances pronounced, angular. Dorsal spine with 3 (occasionally 2 or 4) small, scattered proximal setae with some scattered distal setae and minute tubercles. Lateral spines with 3 or 4 minute dorsal tubercles. Carapace ventral margin with 2 or 3 setae. Mediodorsal knob with 2 or 3 additional smaller integumental sensillae located within rectangular region previously demarcated by 4 sensillae of second zoea; 6 setae anterior, 4 setae posterior to mediodorsal knob.

*Antennule* (Figure 4C). With 3 aesthetascs and 1 naked seta at tip, 1 subterminal budlike projection.

*Antenna* (Figure 4D). Similar to earlier stage, endopodite more developed, with pointed tip slightly exceeding exopodite length.

*Mandibles* (Figure 4E). As illustrated, without palp.

*Maxillule* (Figure 4F). Coxal endite with 8 thick, plumose setae. Basal endite with 5 pectinate spines, 3 long sparsely plumose setae, 1 subterminal plumose seta, almost no minute hairs. Endopodite as in first zoea. Protopodite with 1 distal plumose seta.

*Maxilla* (Figure 4G). Coxal endite bilobed with 5 proximal, 4 distal plumose setae. Basal endite bilobed with 5 proximal, 4 distal plumose setae. Endopodite as in first zoea except all setae naked. Scaphognathite with 17 to 20 marginal plumose setae.

*Maxilliped 1* (Figure 4H). Coxopodite with 1 (rarely 2) seta. Five-segmented endopodite setation now 2, 2, 1, 2, 5+I. Exopodite with 8 terminal natatory setae.

*Maxilliped 2* (Figure 4I). Coxopodite without setae. Three-segmented endopodite setation now 1, 1, 6. Exopodite with 9 terminal natatory setae.

*Maxilliped 3*. Present as small, unbranched lobe.

*Pereiopods* (Figure 4B). Apparent as small rudiments beneath carapace.

*Abdomen* (Figure 4A, B). Sixth somite present, lacking posterolateral spines and posterodorsal setae. Somite 1 with 2 or 3 posterodorsal setae; somites 2-5 as in second zoea, but with posterolateral spines of somites 3-5 progressively longer; somites 2-6 developing small pleopod buds; those of somite 6 barely apparent.

*Telson* (Figure 4A, B). Median sinus with 2 small plumose setae. Secondary minute lateral furcal spines may or may not be present as in second zoea.

*Color*: Rostrum, dorsal spine, antennules, antennae nearly colorless. Maxillipeds with pale orange spreading through much of basipodites. Mandibles slightly darker burnt orange. Orbits pale mint green blending into faint sky blue at interorbital region. Sky-blue stellate chromatophore at dorsal spine base. Vandyke-brown stellate chromatophore fringed in olive, mint green, sky blue at lateral spine bases. Pereiopod buds light orange. Gut burnt orange through somite 3, with small spots of pale orange highlighting pleopod buds on somites 3-5.

### Fourth Zoea

Carapace length: 0.84 mm.

Number of specimens examined: 9.

*Carapace* (Figure 5A, B). Rostrum preorbital protuberances recurved into anteriorly directed hooks. Dorsal spine with 4 small proximal setae, few scattered minute tubercles. Lateral spines as in third zoea. Carapace ventral margin with 6-11 (usually 9) setae. Mediodorsal knob with 4 outer sensillae (arranged as rectangle) surrounding 4 smaller inner sensillae; 10 setae anterior, 4 setae posterior to knob.

*Antennule* (Figure 5C). Biramous. Endopodite half exopodite length, naked, pointed at tip. Exopodite two-segmented with 12 aesthetascs arranged proximally to distally (2, 6) (1, 3 apical) plus 1 naked seta at tip. Protopodite swollen proximoventrally, supporting 2 minute plumose setae.

*Antenna* (Figure 5D). Endopodite at least one-half protopodite length.

*Mandibles* (Figure 5E). As illustrated; palp present.

*Maxillule* (Figure 5F). Coxal endite with 11 or 12 setae (small proximal seta occasionally absent).



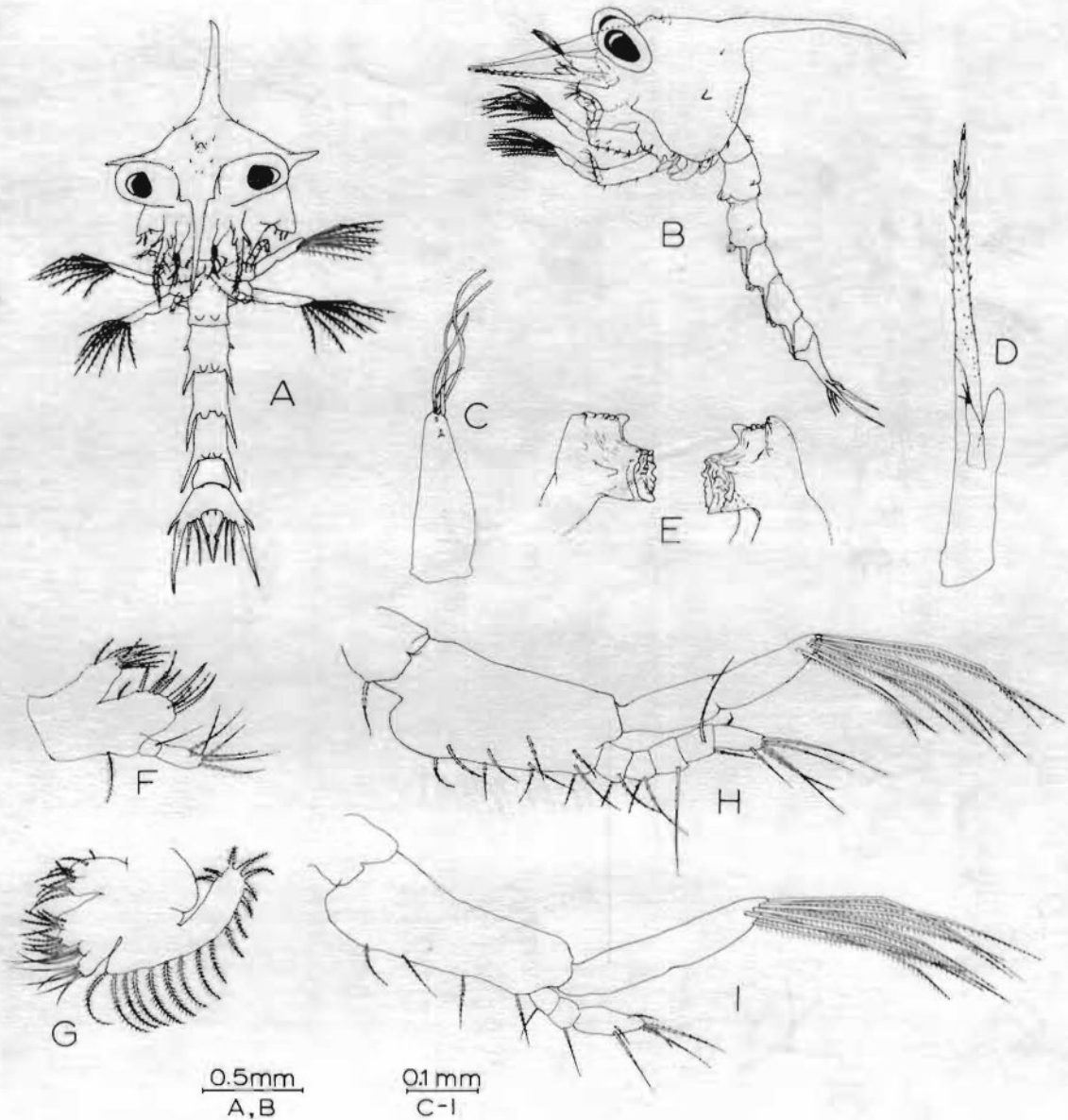


FIGURE 4.—*Micropanope sculptipes*, third zoea. A, ventral view; B, lateral view; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, maxilliped 1; I, maxilliped 2.

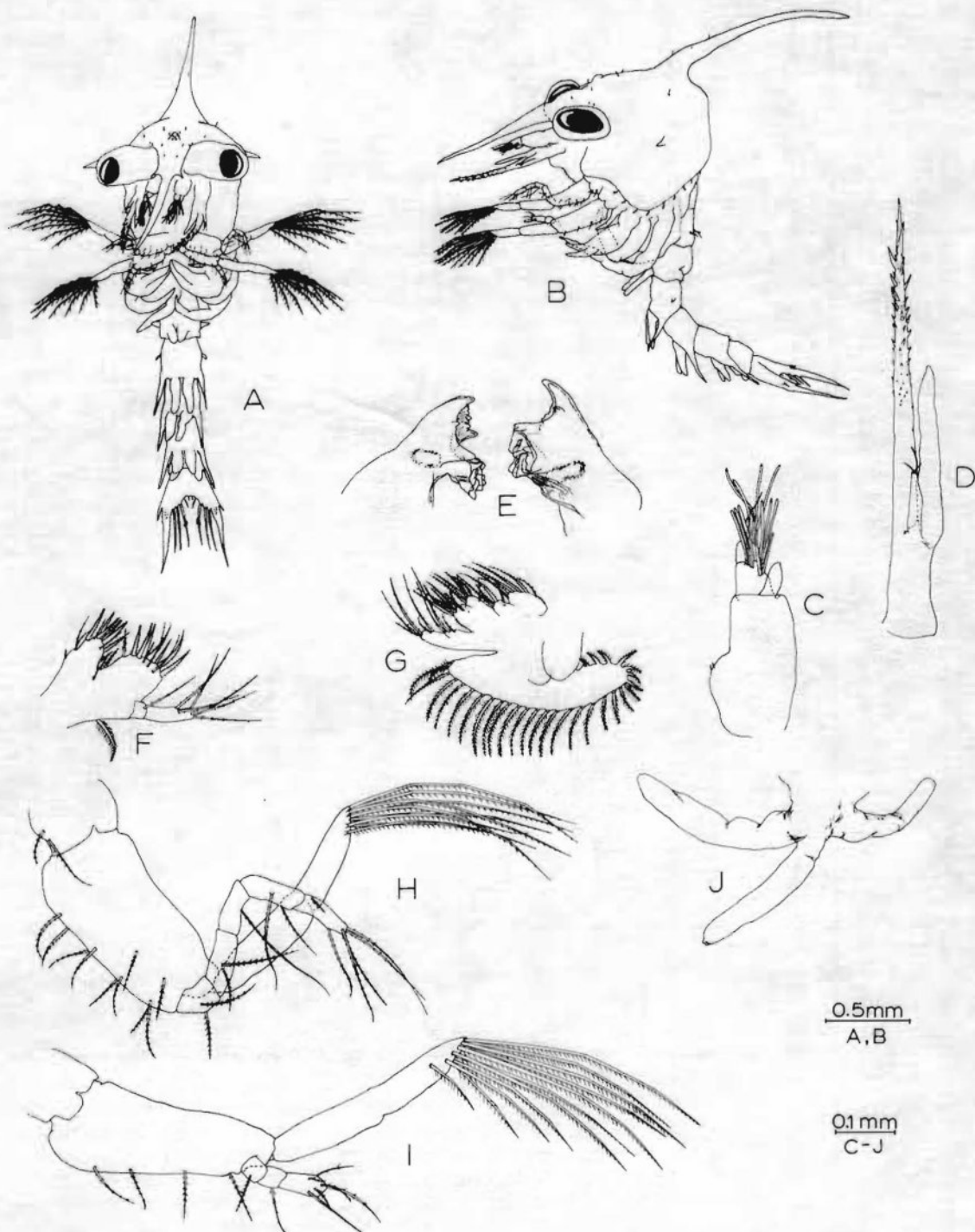


FIGURE 5.—*Micropanope sculptipes*, fourth zoea. A, ventral view; B, lateral view; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, maxilliped 1; I, maxilliped 2; J, maxilliped 3.

Basal endite with 7 denticulate spines, 5 or 6 sparsely plumose setae; few minute hairs. Endopodite and protopodites as in third zoea.

*Maxilla* (Figure 5G). Coxal endite bilobed with 6 proximal, 4 distal plumose setae. Basal endite bilobed with 6 proximal, 7 distal plumose setae, several minute lateral hairs on distal lobe. Scaphognathite with 25 to 30 (usually 28 or 29) marginal plumose setae.

*Maxilliped 1* (Figure 5H). Coxopodite with 2 (rarely 1) setae. Endopodite as in third zoea. Exopodite with 9 terminal natatory setae.

*Maxilliped 2* (Figure 5I). Coxopodite with no (rarely 1 very small) seta. Three-segmented endopodite setation 1, 1, 5+1 (rarely 4+1). Exopodite with 11 terminal natatory setae.

*Maxilliped 3* (Figure 5J). Greatly enlarged from third zoea, epipodite and endites well developed, not yet segmented.

*Pereiopods* (Figure 5A, B). Greatly enlarged from third zoea, with incipient segmentation and differentiation.

*Abdomen* (Figure 5A, B). Somite 1 with 3 posterodorsal setae, slight posterolateral projections. Somites 2-6 as in third zoea but pleopod buds enlarged and biramous on somites 2-5, small and uniramous on somite 6.

*Telson* (Figure 5A, B). Median sinus with 3 or 4 small plumose setae. Secondary minute lateral furcal spines may or may not be present as in second zoea.

*Color*. Rostrum, antennules, antennae pale orange. Maxilliped 1 and 2 basipodites proximally with prominent burnt-orange stellate chromatophores, diffused with pale mint green at basipodite-exopodite junction. Mandible incisor and molar surfaces fringed in dark Vandyke brown blending into scarlet and burnt orange. Orbits pale mint green. Sky-blue stellate chromatophore mixed with pale green and yellow at dorsal spine base. Lateral spines with burnt-orange and Vandyke-brown stellate chromatophores blending into mint green distally. Body (cephalothorax) generally pale yellow-orange mixed with faint mint green. Gastric region and gut burnt orange extending through abdominal somite 3. Abdominal somites 2-5 with paired patches of pale burnt orange lateral to pleopod bud origins, otherwise colorless. Telson entirely pale orange diffused with mint green in vicinity of lateral and dorsal furcal spines.

## Megalopa

Carapace length (rostrum tip to median posterior margin)  $\times$  greatest width: 1.25 mm  $\times$  1.20 mm.

Number of specimens examined: 1.

*Carapace* (Figure 6A-C). Slightly longer than wide, subrectangular, somewhat inflated. Frontal region produced, highly sculptured; rostrum prominent, acutely triangular, sharply rounded, becoming broader at base, recurving anteriorly into prominent anterolateral horns; latter one-half rostrum length, each with a small lateral spine bearing 2 small apical setae near base, oriented perpendicular to longitudinal axis of horn. Four prominent plumose setae equal in length to rostrum project anteriorly between rostrum base and base of each horn. Several smaller setae scattered in interorbital, gastric, and cardiac regions. One small tubercle projecting near median posterodorsal margin. Numerous setae fringe posterior and ventrolateral margins.

*Antennule* (Figure 6D). Biramous; peduncle three-segmented; proximal article with 2 small plumose setae and 1 naked seta, penultimate article with 1 naked seta, ultimate article with 2 small lateral setae and 6 nearly terminal, long, naked setae (arranged as 3 on either side of segmented flagellum). Ventral ramus with 3 terminal, 1 slightly subterminal, naked setae; dorsal ramus with aesthetascs progressing distally as follows: (8), (6, +1 plumose seta opposite), (3 lateral, +3 nonplumose setae near tip).

*Antenna* (Figure 6E). Peduncle with 3 lateral setae, a distal lobe; setation (proximally to distally) on flagellar articles 1, 1, 0, 3, 4, 0, 0, 5. Articles 5 and 6 slightly constricted at midlength, may be partially segmented.

*Mandibles, maxillule, maxilla, and maxillipeds 1 and 2*. These were not dissected from the specimen to prevent the destruction of the only megalopa obtained.

*Maxilliped 3* (Figure 6F). Coxopodite and epipodite not exposed for examination. Basipodite partially exposed with at least 16 short setae. Endopodite five-segmented, setation progressing distally 16, 14, 8, 12, 8 (5 lateral, 3 apical). Exopodite two-segmented; proximal segment with 3 lateral setae, distal segment with 1 subterminal seta and 6 long, plumose terminal setae.

*Pereiopods* (Figure 6A-C, 6G-I). All bear numerous setae. Chelipeds (Figure 6G) similar, equal;

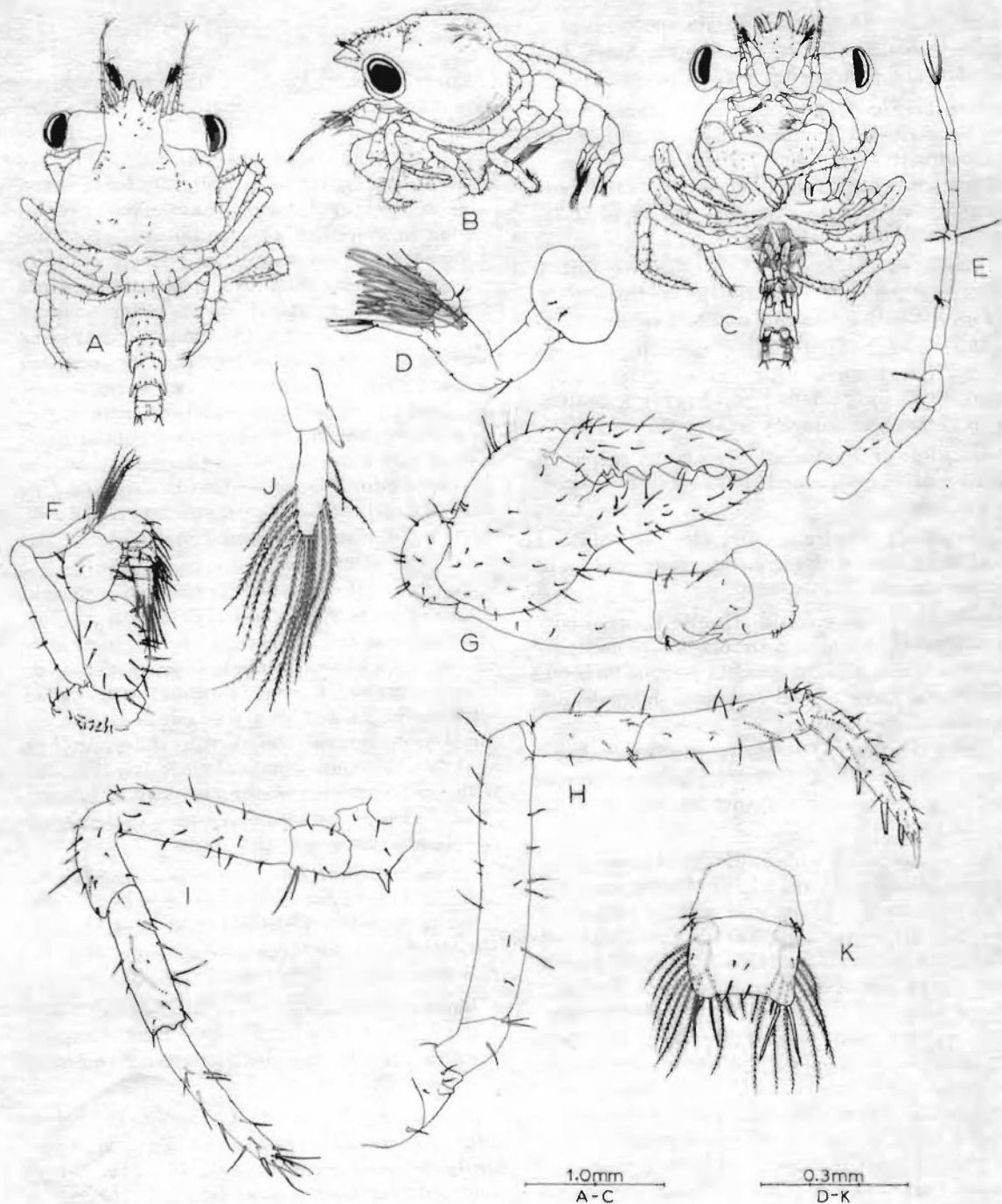


FIGURE 6.—*Micropanope sculptipes*, megalopa. A, dorsal view; B, lateral view; C, ventral view; D, antennule; E, antenna; F, maxilliped 3; G, cheliped; H, pereopod 3; I, pereopod 5; J, pleopod from abdominal somite 3; K, abdominal somite 6 with pleopods, telson.

coxa with small basal tubercle, ischium with large hooked spine and small dorsal tubercle. Bases of pereopods 2-5 (Figure 6H, I) with small median spine; dactyls of pereopods 2-4 with a row of 3 subterminal serrated spines, 1 terminal spine; dactylus of pereopod 5 with 1 subterminal serrated spine, 3 long subterminal setae, 1 terminal spine.

**Abdomen** (Figure 6A-C). With 6 somites and telson. Lateral pleura of somites 2-5 slightly overlap following segment; lateral hooks of somites 2 and 3 absent. Numerous setae cover dorsal surfaces and posterodorsal margins of all somites. Pleopods biramous (Figure 6J) on somites 2-5, uniramous on somite 6 (Figure 6K); exopodites with plumose setae arranged (anteriorly to posteriorly) 15 or 16, 13 or 14, 13 or 14, 11, 7 or 8; endopodites of pleopods 2-5 with appendix interna consisting of 2 terminal curved hooks.

**Telson** (Figure 6K). Roughly rectangular with 2 pairs of dorsal setae. Lateral margins produced posteriorly, forming slightly extended lobes, each lobe bearing 3 serrated spines of variable length; posterior margin shallowly sinuous, with 3 plumose setae.

**Color.** The one megalopa died before color notes could be made.

## DISCUSSION

### Comparative Morphology of *Micropanope sculptipes* With Other Xanthid Larvae

The Xanthidae is a large and heterogeneous family containing many genera and numerous species. As a consequence, the larval stages of many such species from the Atlantic and Pacific Oceans have been studied over a long period (e.g., Lebour 1928; Aikawa 1929, 1937; Wear 1968; Saba et al. 1978). In the western Atlantic, larval development is reliably known either completely or in part for at least 10 genera and 15 species, in addition to several other genera and species which are less certain because identifications were based on planktonic material. As might be expected, there exist numerous characters, both shared and unshared, in the larval stages, so that comparison among the species and genera is often quite difficult. Readily observable morphological characters useful in distinguishing zoeae and megalopae of *M. sculptipes* from other western Atlantic xanthid species which may cooccur in the plankton include those of the rostral spine, antenna, anterodorsal

carapace setae, abdominal spination, telsonal furcae spination, and armature on basal segments of the pereopods.

Within the genus *Micropanope* (sensu lato), *M. sculptipes* exhibits extremely close morphological similarity (but not developmental similarity) with the larvae of *M. barbadensis* (Gore et al. 1981). Both species exhibit a type of antenna different from the four categories established by Aikawa (1929) necessitating the creation of a fifth category, Type E (Gore et al. 1981). This grouping contains those larvae (presently only the two species here considered) in which the antennal exopodite is from one-fourth to one-seventh total protopodite length. Other features allowing distinction between the two species include (in *M. sculptipes*) the unadorned rostral carapace spine, shorter lateral spines, unpaired lateral spines on the telsonal furcae, a less lunate telson, more distinct spination on the antennal protopodite, a single coxal seta on maxilliped 1, and the general distribution of fine hairs on the anterodorsal area of the carapace. The position and number of integumentary sensillae may prove to be of some value, but this feature in the genus has only been described for *M. sculptipes*. Gore et al. (1981) worked with molted carapaces in describing *M. barbadensis* and were unable to distinguish these sensory pits clearly.

A comparison of the larvae of *M. sculptipes* with those in other western Atlantic xanthid species is summarized in Table 2. The following differences appear salient. The preorbital rostral hooks of *M. sculptipes*, which are fully formed in the fourth zoeal stage, are similar to, yet larger than, those described for *Panopeus herbstii*. *Pseudomedaeus* [ex *Leptodius*] *agassizii* also possesses similar "secondary rostral spines," but these are much more prominent from its second through fourth zoeal stages. The rostrum of the other species noted (see Table 2) remains generally straight and unarmed throughout development.

The antenna of *M. sculptipes* consists of a spinous protopodite and has an exopodite which is one-sixth the protopodite length. The species in other genera possess an antennal protopodite which is either nonspinous or noticeably less spinous than that of *Micropanope*. The antennal exopodite of these xanthid zoeae fall into three general categories as described by Lebour (1928): equal to protopodite length or Type A (*Pilumnus sayi*, *P. dasypodus*); one-half to three-fourths protopodite length or Type B (*Menippe mercenaria*, *M.*

TABLE 2.—Comparison of morphologically important zoeal characters for distinguishing *Micropanope sculptipes* larvae from other western Atlantic species of Xanthidae based on descriptions and illustrations from different sources (only the first four zoeal stages of *Menippe mercenaria* and *M. nodifrons* are considered).

Species (source of description)	Rostrum	Antenna	Anterodorsal carapace setae	Abdomen spination	Telson furca spination
First zoea					
<i>Micropanope sculptipes</i>	Straight, unarmed, ≈ carapace length	Protopodite: spinous distal 3/4 Exopodite: 1/6-1/5 protopodite length, 3 apical setae	None	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine, 1 lateral spine
<i>Neopanope sayi</i> (Chamberlain 1961)	Straight, unarmed, 2 × carapace length	Protopodite: unarmed Exopodite minute, apical seta	None figured	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine
<i>Neopanope texana</i> (McMahan 1967)	Straight, unarmed, ≈ carapace length	Protopodite: unarmed Exopodite minute, apical seta	None	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine
<i>Neopanope packardii</i> (Costlow and Bookhout 1967)	Straight, unarmed, ≈ carapace length	Protopodite: sparsely spinous tip Exopodite: minute spine	None figured	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine
<i>Panopeus herbstii</i> (Costlow and Bookhout 1961a)	Straight, unarmed, ≈ carapace length	Protopodite: spinous tip Exopodite minute, apical spine	None figured	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine, 2 lateral spines
<i>Eurypanopeus depressus</i> (Costlow and Bookhout 1961b)	Straight, unarmed, 1.5 × carapace length	Protopodite: spinous distal 1/3 Exopodite minute, apical spine	None figured	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine
<i>Hexapanopeus angustifrons</i> (Costlow and Bookhout 1966)	Straight, unarmed, 1.5 × carapace length	Protopodite: unarmed Exopodite minute	None figured	Lateral hooks somites 2,3	Furca smooth
<i>Rhithropanopeus harrisi</i> (Chamberlain 1962)	Straight, unarmed, 2.5 × carapace length	Protopodite: minute spinules distal 1/4 Exopodite minute	None figured	Posterolateral spines somites 4, 5 prominent Lateral hooks somite 2	Furca smooth: 1 dorsal spine
<i>Pseudomedeaeus agassizii</i> (Costlow and Bookhout 1968)	Straight, unarmed, ≈ carapace length	Protopodite: spinous distal 1/2 Exopodite: 1/10 protopodite length, 2 apical setae	None figured	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine, 2 lateral spines
<i>Eurytium limosum</i> (Kurata <sup>1</sup> )	Straight, unarmed, ≈ carapace length	Protopodite: spinous distal 1/3 Exopodite minute, apical seta	None figured	Posterolateral spines somites 3-5 smooth, subequal Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine, 1 lateral spine, 1 minute lateral seta
<i>Pilumnus sayi</i> (Kurata <sup>1</sup> )	Unarmed, 1/3 carapace length	Protopodite: spinous distal 1/2 Exopodite → protopodite length, spinous distal 1/2, 2 mid- lateral spines	None figured	Posterodorsal margins somites 2-5 serrated Lateral hooks somites 2-5	Furca spinous: 1 dorsal spine, 2 lateral spines
<i>Pilumnus dasypodus</i> (Sandifer 1974)	Unarmed, 1/3 carapace length	Protopodite: spinous distal 1/2 Exopodite → protopodite length, spinous distal 1/2, 2 mid- lateral spines	None figured	Posterodorsal margins somites 3-5 serrated Lateral hooks somites 2,3	Furca spinous: 1 dorsal spine, 2 lateral spines
<i>Menippe mercenaria</i> (Porter 1960)	Straight, unarmed, ≈ carapace length	Protopodite: spinous distal 1/2-1/5 Exopodite: 3/4 protopo- dite length, apical spine 1/2-3/5 exopo- dite length	None figured	Dorsolateral spines somites 4, 5 Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine, 1 lateral spine
<i>Menippe nodifrons</i> (Scotto 1979)	Straight, unarmed, ≈ carapace length	Protopodite: spinous distal 1/2-1/5 Exopodite: 3/4 protopodite length, apical spine 2/5 exopodite length	None	Dorsolateral spines somite 5 Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine, 2 lateral spines

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TABLE 2.—Continued.

Species (source of description)	Rostrum	Antenna	Anterodorsal carapace setae	Abdomen spination	Telson furca spination
Second zoea					
<i>Micropanope sculptipas</i>	Small preorbital proluberances	Protopodite, exopodite unchanged <sup>2</sup>	4	Unchanged <sup>2</sup>	Furca smooth: 1 dorsal spine, 1 or 2 lateral spines
<i>Naopanope sayi</i> (Chamberlain 1961)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Naopanope texana</i> (McMahan 1967)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Neopanope packardii</i> (Costlow and Bookhout 1967)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Panopeus herbstii</i> (Costlow and Bookhout 1961a)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Eurypanopeus depressus</i> (Costlow and Bookhout 1961b)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Hexapanopeus angustifrons</i> (Costlow and Bookhout 1966)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Posterolateral spines somites 3-5 equal, smooth Lateral hooks unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Rhithropanopeus harrisii</i> (Chamberlain 1962)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Pseudomedeus agassizii</i> (Costlow and Bookhout 1968)	Secondary rostral spines	Protopodite: spinous distal 1/3 Exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Eurytium limosum</i> (Kurata <sup>1</sup> )	Unchanged <sup>2</sup>	Protopodite smooth, Exopodite unchanged <sup>2</sup>	Not given	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Pilumnus sayi</i> (Kurata <sup>1</sup> )	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	Not given	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Pilumnus dasypodus</i> (Sanditer 1974)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Menippe mercenaria</i> (Porter 1960)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Posteroventral spines somites 3-5; otherwise unchanged <sup>2</sup>	Unchanged <sup>2</sup> ; spines minute
<i>Menippe nodifrons</i> (Scotto 1979)	Unchanged <sup>2</sup>	Protopodite: unchanged <sup>2</sup> Exopodite: spine slightly longer	4	Posteroventral spines somites 3, 4; posteroventral tooth somita 5; otherwise unchanged <sup>2</sup>	Unchanged <sup>2</sup> ; spines minute
Third zoea					
<i>Micropanope sculptipas</i>	Angular preorbital proluberances	Protopodite: spinous distal 2/3 Exopodite unchanged <sup>2</sup>	10	Unchanged <sup>2</sup>	Unchanged <sup>3</sup>
<i>Neopanope sayi</i> (Chamberlain 1961)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Neopanope texana</i> (McMahan 1967)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Neopanope packardii</i> (Costlow and Bookhout 1967)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Panopeus herbstii</i> (Costlow and Bookhout 1961a)	Small preorbital proluberances	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Eurypanopeus depressus</i> (Costlow and Bookhout 1961b)	Unchanged <sup>2</sup>	Protopodite: spinous tip Exopodite miniscule	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Hexapanopeus angustifrons</i> (Costlow and Bookhout 1966)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>3</sup>	Unchanged <sup>2</sup>
<i>Rhithropanopeus harrisii</i> (Chamberlain 1962)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Pseudomedeus agassizii</i> (Costlow and Bookhout 1968)	Secondary rostral spines 1/3 rostrum length	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Eurytium limosum</i> (Kurata <sup>1</sup> )	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>1</sup>	Not given	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Pilumnus sayi</i> (Kurata <sup>1</sup> )	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	Not given	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Pilumnus dasypodus</i> (Sanditer 1974)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Menippe mercenaria</i> (Porter 1960)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>3</sup>	Unchanged <sup>3</sup>
<i>Menippe nodifrons</i> (Scotto 1979)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	4	Unchanged <sup>3</sup>	Unchanged <sup>3</sup>

TABLE 2.—Continued.

Species (source of description)	Rostrum	Antenna	Anterodorsal carapace setae	Abdomen spination	Telson furca spination
		Fourth zoea			
<i>Micropanope sculptipas</i>	Praeorbital hooks	Protopodite: spinous distal 1/3	14	Unchanged <sup>2</sup>	Unchanged <sup>3</sup>
<i>Neopanope sayi</i> (Chamberlain 1961)	Unchanged <sup>2</sup>	Exopodite unchanged <sup>2</sup> Protopodite, exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Neopanope texana</i> (McMahan 1967)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Neopanope packardii</i> (Costlow and Bookhout 1967)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Panopeus herbstii</i> (Costlow and Bookhout 1961a)	Small preorbital hooks	Protopodite: unchanged <sup>2</sup> Exopodite miniscule	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Eurypanopeus depressus</i> (Costlow and Bookhout 1961b)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Hexapanopeus angustifrons</i> (Costlow and Bookhout 1966)	Unchanged <sup>2</sup>	Protopodite: unchanged <sup>2</sup> Exopodite miniscule	None figured	Unchanged <sup>3</sup>	Unchanged <sup>2</sup>
<i>Rhithropanopeus harrisi</i> (Chamberlain 1962)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Pseudomedaeus agassizii</i> (Costlow and Bookhout 1966)	Unchanged <sup>4</sup>	Protopodite, exopodite unchanged <sup>3</sup>	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Eurytium limosum</i> (Kurata <sup>1</sup> )	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>3</sup>	Not given	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Pilumnus sayi</i> (Kurata <sup>1</sup> )	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Pilumnus dasypodus</i> (Sandifar 1974)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	1(?) figured	Unchanged <sup>2</sup>	Unchanged <sup>2</sup>
<i>Menippe mercenaria</i> (Porter 1960)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	None figured	Unchanged <sup>3</sup>	Unchanged <sup>3</sup>
<i>Menippe nodifrons</i> (Scotto 1979)	Unchanged <sup>2</sup>	Protopodite, exopodite unchanged <sup>2</sup>	8	Posterolateral spines somites 3, 4, dorso- lateral spines somite 5 longer	Unchanged <sup>4</sup>

<sup>1</sup>Kurata, H. 1970. Studies on the life histories of decapod Crustacea of Georgia. Unpubl. rep., 274 p. Univ. Georgia Mar. Inst., Sapelo Island.

<sup>2</sup>Character unchanged from first zoea.

<sup>3</sup>Character unchanged from second zoea.

<sup>4</sup>Character unchanged from third zoea.

*nodifrons*); minute or Type C (*Neopanope sayi*, *N. texana*, *N. packardii*, *Panopeus herbstii*, *Eurypanopeus depressus*, *Hexapanopeus angustifrons*, *Rhithropanopeus harrisi*, *Pseudomedaeus agassizii*, *Eurytium limosum*). The antennal exopodite of *Micropanope sculptipes* (Type E) is thus distinctive from other xanthid larvae both in its length relative to the protopodite length, and in its armature. Although the antenna of *P. agassizii* closely resembles that of *M. sculptipes*, the protopodite is less spinous and the exopodite is one-tenth the protopodite length with two apical setae.

The anterodorsal carapace (anterior half of the dorsal carapace surface) setae of *M. sculptipes* zoeae first appear in the second stage (2), and number 10 and 14 in the third and fourth stages, respectively. Anterodorsal carapace setae are not described for most of the other xanthid species; one seta is illustrated in the fourth stage of *Pilumnus dasypodus*, and *Menippe nodifrons* develops 4 setae during its second and third stages and 8 setae in its fourth stage. These setae are present in

stage II zoeae of *Micropanope barbadensis* (1-2), stage III (4), and stage IV (12-14).

*Micropanope sculptipes* zoeae have abdominal spination characteristics which consist of lateral hooks on the second and third abdominal somites, and smooth posterolateral spines on the third through fifth abdominal somites. The posterolateral spines increase in length with each succeeding zoeal stage. This pattern of abdominal spination is similar to that observed for most other xanthid species, but some species vary. *Hexapanopeus angustifrons* does not possess posterolateral spines in the first stage, but develops them in subsequent stages in a manner similar to *M. sculptipes*. *Rhithropanopeus harrisi* possesses lateral hooks only on the second somite and conspicuously long posterolateral spines on the fourth and fifth somites. *Pilumnus sayi* has serrated posterodorsal margins and lateral hooks on the second through fifth somites, and *P. dasypodus* has serrated posterodorsal margins on the third through fifth somites and lateral hooks on the



second and third somites. *Menippe mercenaria* and *M. nodifrons* possess lateral hooks on the second and third somites. *Menippe mercenaria* has a large pair of dorsolateral spines on the fourth and fifth somites, and develops posteroventral spines on the third through fifth somites in its second and subsequent zoeal stages. *Menippe nodifrons* has a large pair of dorsolateral spines only on the fifth somite, and develops posteroventral spines only on the third and fourth somites in its second and subsequent zoeal stages.

Spination of the zoeal telson furca is varied among xanthid species. *Micropanope sculptipes* first zoeae have smooth telson furcae with 1 dorsal and 1 lateral spine. Second and subsequent zoeal stages have furcae with 1 dorsal spine, and 1 or 2 lateral spines. *Neopanope sayi*, *N. texana*, *N. packardii*, *Eurypanopeus depressus*, and *Rhithropanopeus harrisi* have smooth telson furcae with only 1 dorsal spine. *Panopeus herbstii* and *Pseudomedeus agassizii* have smooth telson furcae with 1 dorsal spine and 2 lateral spines. *Hexapanopeus angustifrons* has smooth telson furcae without dorsal or lateral spines. *Pilumnus sayi* and *P. dasypodus* have spinous telson furcae with 1 dorsal spine and 2 lateral spines. The telson furcae of *Menippe* are smooth and bear minute spines; *M. mercenaria* has 1 dorsal and 1 lateral furcal spines, and *M. nodifrons* has 1 dorsal and 2 lateral furcal spines.

*Micropanope sculptipes* megalopae may be quickly distinguished from those of *M. barbadensis*, because the latter is presently the only species within the genus which bears spines on the coxal bases and ischia; in *M. sculptipes* only the bases are so armed.

*Micropanope sculptipes* may be separated from other xanthid megalopae by examining the frontal region ornamentation and telson structure (Table 3). The frontal region of *M. sculptipes* is ornamented with a prominent rostrum and lateral horns; each lateral horn has a small lateral spine near its base. Four long, plumose setae lay between the rostrum and each lateral horn. *Panopeus herbstii*, *Neopanope packardii*, and *Pseudomedeus agassizii* have pointed, depressed rostrums. The lateral spines (horns) of *N. packardii* are short, and the frontal region is devoid of setae. *Panopeus herbstii* and *Pseudomedeus agassizii* have conspicuous lateral spines with 1 seta and 2 setae, respectively, between the rostrum and each lateral spine. The remaining species discussed herein have rostrums which are reduced,

broad, and generally rounded. The lateral spines of *Neopanope sayi* and *N. texana* are short and there are 5 setae and 2 setae, respectively, between the rostrum and each lateral spine. *Hexapanopeus angustifrons* and *Eurytium limosum* have prominent lateral horns which equal or exceed the rostrum length. Five setae and two setae are present between the rostrum and each lateral spine in *H. angustifrons* and *E. limosum*, respectively. No lateral horns are found in *Rhithropanopeus harrisi* or *Eurypanopeus depressus*; 2 setae are found lateral to the rostrum in the former species while no setae are present in the latter species. No lateral horns are found in *Pilumnus sayi* or *P. dasypodus*, and 3 setae are present on either side of the rostrum in both species. The rostrums of *Menippe mercenaria* and *M. nodifrons* are broad and have a distinct median cleft. No lateral horns or setae are present in *M. mercenaria*, but bluntly angular interorbital protuberances and a few small, scattered setae are found in the frontal region of *M. nodifrons*.

The telson of *Micropanope sculptipes* is rectangular with 2 pairs of dorsal setae, 3 serrated spines at each posterolateral angle, and 3 plumose setae along the shallow median telson sinus. Rectangular telsons are found in *E. depressus*, *H. angustifrons*, *Pseudomedeus agassizii*, and *R. harrisi*. *Eurypanopeus depressus* has 3 short caudal setae with 2 longer setae on either side. *Hexapanopeus angustifrons* and *P. agassizii* have 2 to 4 short setae and 4 short setae, respectively, along the posterior telson margin. *Rhithropanopeus harrisi* has a few short setae along its posterior telson margin. Rounded (convex) posterior telson margins are found in *N. sayi*, *M. texana*, *N. packardii*, *Panopeus herbstii*, and *Eurytium limosum*. *Neopanope texana* has 3 pairs of dorsal telson setae and 3 setae along the posterior telson margin, and *N. packardii* has 8 stiff spines along its telson caudal margin. *Panopeus herbstii* has 3 to 6 stiff caudal telson spines. The telsons of *Pilumnus sayi* and *P. dasypodus* are posteriorly rounded; *P. dasypodus* has 2 dorsal and 2 ventral setae, and a posterior border which is generally unarmed. *Menippe mercenaria* has a rounded and somewhat truncated posterior telson margin. The telson of *M. nodifrons* is subquadrate with 5 setae along its posterior margin; other telson setation is variable.

#### Plesiomorphy and Larval Development

Scotto (1979) provided a detailed discussion of

TABLE 3.—Comparison of morphologically important megalopal characters for distinguishing *Micropanope sculptipes* from megalopae of other western Atlantic species of Xanthidae based on descriptions and illustrations from different sources.

Species (description source)	Frontal region	Telson
<i>Micropanope sculptipes</i>	Rostrum prominent, sharply rounded Lateral horns prominent, 1/2 rostrum length, small lateral spines bearing 2 apical setae 4 long, plumose setae between rostrum and each lateral spine	Rectangular, 2 pairs dorsal setae, 3 serrated spines at each outer corner, 3 plumose setae along shallow median sinus
<i>Neopanope sayi</i> (Chamberlain 1961)	Rostrum square, depressed into blunt bifid tooth Lateral spines blunt 5 short setae between rostrum and each lateral spine	Rounded posteriorly
<i>Neopanope texana</i> (McMahan 1967)	Rostrum blunt, depressed, notched Lateral spines small, pointed 2 short setae between rostrum and each lateral spine	Rounded posteriorly, 3 pairs dorsal setae, 3 posterior setae
<i>Neopanope packardii</i> (Costlow and Bookhout 1967)	Rostrum long, pointed, depressed Lateral spines short, pointed No frontal setae figured	Caudal margin with 8 stiff spines
<i>Panopeus herbstii</i> (Costlow and Bookhout 1961a)	Rostrum stoutly pointed, depressed Lateral spines stout, pointed slightly less than rostrum length 1 stout seta between rostrum and each lateral spine	Rounded posteriorly, 3-6 stiff caudal spines
<i>Eurypanopeus depressus</i> (Costlow and Bookhout 1961b)	Rostrum blunt, broadly triangular, depressed No lateral spines or frontal setae	Rectangular, posterior margin with 3 short caudal setae, 2 longer setae on each side
<i>Hexapanopeus angustifrons</i> (Costlow and Bookhout 1966)	Rostrum broad, rounded, depressed Lateral horns prominent 5 short setae between rostrum and each lateral horn	Rectangular, posterior margin with 2-4 short setae
<i>Rhithropanopeus harrisi</i> (Chamberlain 1962)	Rostrum blunt, depressed bifid tooth No lateral spines 2 short setae on each side of rostrum	Rectangular, few short setae on posterior margin
<i>Pseudomedeus agassizii</i> (Costlow and Bookhout 1968)	Rostrum pointed, depressed Lateral spines stout, pointed, slightly shorter than rostrum 2 small setae between rostrum and each lateral spine	Rectangular, 4 short setae on posterior margin
<i>Eurytium limosum</i> (Kurata <sup>1</sup> )	Rostrum blunt, depressed bifid tooth Lateral horns prominent = rostrum length 3-4 setae between rostrum and each lateral horn, 1 outer lateral horn seta	Rounded posteriorly
<i>Pilumnus sayi</i> (Kurata <sup>1</sup> )	Rostrum short, blunt, depressed No lateral spines 3 short setae on each side of rostrum	Rounded posteriorly
<i>Pilumnus dasypodus</i> (Sandifer 1974)	Rostrum broad, rounded, depressed No lateral spines or frontal setae	Rounded, 2 dorsal, 2 ventral setae; posterior border unarmed (rarely with 1, 2 small medial spines)
<i>Menippe mercenaria</i> (Kurata <sup>1</sup> )	Rostrum broad, depressed, shallow median groove No lateral spines or frontal setae figured	Rounded, somewhat truncated posterior margin
<i>Menippe nodifrons</i> (Scotto 1979)	Rostrum strongly deflexed, blunt, rounded, distinct median cleft Interorbital prominences lateral to rostrum angular, blunt	Subquadrate, 5 setae on posterior margin, other setation variable

<sup>1</sup>Kurata, H. 1970. Studies on the life histories of decapod Crustacea of Georgia. Unpubl. rep., 274 p. Univ. Georgia Mar. Inst., Sapelo Island.

the importance of larval characters in determining phylogenetic relationships among brachyuran taxa, with special reference to the genus *Menippe*, and the families Xanthidae and Cancridae. Although Lebour (1928) enumerated several distinguishing morphological characters of xanthid larvae, including number of zoeal stages, carapacial armature, antennal morphology, abdominal morphology, and telson armature, Wear (1968, 1970) has shown that few of these are now valid. Even so, the larval characteristics of *Micropanope sculptipes* generally agree with Lebour's classical categorization of morphological characteristics of the Xanthidae. Moreover, the antennal structure of *M. sculptipes* differs in important respects, distinctive for the genus.

Hyman (1925) and Lebour (1928) divided the antennal morphology of xanthid larvae into two or

three distinctive groups: antennal exopodite either minute, nearly equal to protopodite length, or about three-fourths protopodite length. Shorter antennal exopodites were considered indicative of evolutionarily more advanced species.

Aikawa (1929) recognized four types of antennae (A, B, C, D), also based on the relative length of the peduncle (= protopodite) to that of the exopodite. In Type A the protopodite and exopodite are nearly equal in length, a condition considered most primitive; in Type B the exopodite is one-half to three-fourths of the protopodite length, a type characteristic of most brachyuran zoeae; in Type C the exopodite is minute, these are the most highly developed. Type D antennae have a simple, inconspicuous spiny process which is shorter than either the rostrum or the antennule, and is considered to be a deviation.

The antennal exopodite of larval *M. sculptipes* is one-sixth to one-fifth the length of the protopodite, and therefore may be considered an intermediate form in the antennal classification schemes of Hyman (1925), Lebour (1928), and Aikawa (1929). The antennal configuration of *M. sculptipes* has been shown here to be distinctive from many other xanthid larvae, and it may be a general characteristic of the genus *Micropanope* (sensu lato). This contention is supported by a nearly identical antennal configuration for zoeae of *M. barbadosis*. However, similar antennal morphological characteristics are seen in the larvae of *Paramedaeus noelensis* and *Heterozius rotundifrons*. This similarity in antennal morphology allows establishment of a separate antennal classification typed "Group E" for larvae of the Xanthidae (Gore et al. 1981). Larvae in this grouping might be considered more advanced than most xanthids, although *P. noelensis* has four zoeal stages and is otherwise similar in development to other members of the family. *Heterozius* has two zoeal stages but, as noted by Wear (1968), may not belong in the Xanthidae.

#### Status of *Micropanope* in Family Xanthidae

Guinot (1967) discussed systematic relationships among adults of the Xanthidae and considered the genus *Micropanope* to be a mixture of several distinct generic groups which were intermediate between the genera *Panopeus* and *Pilumnus*. She concluded *Micropanope* to be more closely related to *Panopeus* than to *Pilumnus*.

A comparison of the overall larval morphology of *M. sculptipes* with *Panopeus herbstii* and *Pilumnus dasypodus* (Table 2) reveals a much closer similarity between larvae of *M. sculptipes* and *Panopeus herbstii* than between *M. sculptipes* and *Pilumnus dasypodus*. Examination of the antennal structure for these three species shows that the length of the antennal exopodite relative to that of the antennal protopodite for *M. sculptipes* (exopodite one-sixth protopodite length) is intermediate between the advanced state seen in *Panopeus herbstii* (exopodite minute) and the primitive state seen in *Pilumnus dasypodus* (exopodite equals protopodite length), being more similar to *Panopeus herbstii*. Assuming that the antennal exopodite relative length is an indicator of the degree of relative primitiveness among xanthid species (Lebour 1928; Aikawa 1929), it can be concluded on this larval character that *Micro-*

*panope* is evolutionarily more closely related to *Panopeus* than to *Pilumnus*. This finding supports the contentions of Guinot (1967), and the apparent alliance between both larvae and adults of *Micropanope* and *Panopeus* emphasizes the importance which larval taxonomy may have in determining systematic and possible evolutionary relationships within the complex family Xanthidae.

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