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STUDIES ON DECAPOD CRUSTACEA FROM THE INDIAN RIVER REGION OF FLORIDA. XX. *MICROPANOPE BARBADENSIS* (RATHBUN, 1921): THE COMPLETE LARVAL DEVELOPMENT UNDER LABORATORY CONDITIONS (BRACHYURA, XANTHIDAE)

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ABSTRACT

The complete larval development of *Micropanope barbadensis* (Rathbun, 1921), a small, western Atlantic, coral-inhabiting xanthid crab, is described and illustrated based on larvae reared in the laboratory. The species passed through 3 or 4 zoeal and one megalopal stage over a 24–32 day period at 20°C. At 15 and 25°C the larvae did not survive beyond the first or second stage, respectively. The duration of abbreviated and normal development periods is discussed. Zoeae of *Micropanope barbadensis* exhibit an antennal exopod:protopod ratio intermediate in length and are therefore not assignable to any of the four categories delineated by Aikawa. A fifth category, Group E, is proposed. Criteria used to distinguish larvae of the genus *Micropanope* from other xanthid genera, as well as the taxonomic position of *M. barbadensis*, are considered. This is the first species in the genus *Micropanope sensu lato* for which the complete larval development in the laboratory has been obtained.

The genus *Micropanope* is a widely distributed, essentially tropical taxon of very small crabs, many species of which are associated with coral or coralline substrata. Rathbun (1930) listed about 9 or 10 species from the western Atlantic, but the systematics of the genus requires revision, so the ultimate number remains presently in doubt. Towards this end, Guinot (1967, 1968, 1969) in a continuing series of re-examination and revision of genera within the family Xanthidae, has split the genus *Micropanope* into several taxa and restricted to the nominate genus but two western Atlantic species, *M. sculptipes* Stimpson, 1871 (type) and *M. lobifrons* (Guinot, 1967). In the same paper (Guinot, 1967: 353 ff), she established the genus *Coralliope* for some very small forms previously assigned to *Micropanope* but having affinities more toward the genera *Domecia* and *Maldivia*. At the same time, Guinot stated that three species, one of which was *M. barbadensis*, were related to the new genus *Coralliope*, but were sufficiently distinct to be placed in a separate, and as yet undefined, genus of their own. Consequently, until this last genus is established we will continue to refer to the species of this study as *Micropanope barbadensis*.

Micropanope barbadensis is not a common species, and was previously known from a very small series of specimens collected from Tortugas, Florida, and the island of Barbados. All previously recorded specimens came from coral heads or a coral reef biotope. During a sampling program established in 1977 to investigate the decapod crustacean community associated with the *Oculina* coral biotope off the central eastern Florida coast, several specimens of *M. barbadensis* were collected. One of these was an ovigerous female from which larvae were subsequently cultured in the laboratory. This paper is a report on the complete larval development of *M. barbadensis* and constitutes the first time the larvae of any species of *Micropanope sensu lato* have been reared from hatching to megalopa in the laboratory, as well as being a range extension of the species from Tortugas, Florida, to off Ft. Pierce, Florida, a distance of approximately 600 km northward along the central Florida coastline.

MATERIALS AND METHODS

The ovigerous female was collected on 19 May 1977 in approximately 80 m of water from Jeff's Reef, 17 nautical miles (27 km) northeast of Ft. Pierce, St. Lucie County, Florida, 27°32.8'N, 79°58.8'W, by lockout diver from the R/S Johnson-Sea-Link of the Harbor Branch Foundation, Inc. Larvae were obtained on 1 June and cultured under laboratory temperatures of 15°C in a Controlled Temperature Unit, and about 20°C (±1°C) and "25°C" (24–29, mean 24.9°C) room temperature, using methodology previously described by Gore (1973). The three series of 24 larvae each were fed *Artemia* nauplii and received a change of 35–36‰ seawater every day; illumination was diel (12L–12D) in the CTU, and ambient in the room temperature series. Illustrations, measurements, and examinations of stages followed previous methodology, and the meristics provided for each stage are the arithmetic average of the specimens examined in that stage. Following re-establishment of laboratory routine after the passage of Hurricane David in September, 1979, it was discovered that several vials containing whole zoeal stages had been broken or the seal damaged, resulting in loss of specimens through dehydration. Consequently, examination of material in some zoeal stages was confined to molted carapaces, thus accounting somewhat for the obvious distortion in the illustrated specimens and their appendages. Measurements and drawings were made as carefully as the limitations of this material would allow, and we believe the resultant figures to be reasonably accurate renditions of the zoeal stages. The descriptions and illustrations that follow are based primarily on specimens from the 20°C series, the only one in which megalopae were obtained. The spent female and a complete larval series are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. USNM 180234. The remaining larvae and postlarvae are deposited in the Indian River Coastal Zone Reference Museum, Smithsonian Institution, Ft. Pierce, Florida IRCZM 89:4614.

RESULTS

Micropanope barbadensis passes through 3 or 4 zoeal stages and one megalopal stage before completing its development. Whether a prezoeal stage exists is uncertain, because the eggs hatched early in the morning and by the time the culture trays were started only first zoeae were seen. Prezoeal cuticles could not be distinguished among the debris from *Artemia* nauplii in the hatching bowl, but if *M. barbadensis* is similar to other xanthid species, a prezoeal stage of short duration probably occurs.

The number of days required to complete larval and postlarval development in the laboratory is unknown, because none of the megalopae held at 20°C completed this stage. One megalopa at this temperature remained as such 22 days before dying without molting. None of the other megalopae showed any indication of ensuing molt when examined, so that the only positive data on larval development comes from the zoeal stages. As seen in Table 1, at 20°C it required from 24 to 32 days for larvae to attain megalopal stage, and this duration was further conditional on whether three zoeal stages were passed through, or four. The elimination of the fourth stage, contrary to what might have been expected, did not shorten zoeal development time, but prolonged it. This was because the first and last zoeal stages in those specimens showing abbreviated development each lasted one day longer than in those undergoing "normal" development. Furthermore, in the abbreviated series the penultimate (=second) stage took the same amount of time (11 days) as did the ante- and penultimate (second and third) stages in the normal series. It can, of course, be speculated that the resultant megalopal stages might have been shortened in the abbreviated series, but with only a single "normal series" megalopa surviving for any duration (22 days as noted above) the data do not warrant further consideration. It can be surmised, however, that planktonic development in *M. barbadensis* is probably on the order of 40 days or more at 20°C. Development at cooler or warmer temperatures was unsuccessful (Fig. 1).

Figure 1 plots percent survival of larvae in the 3 series, and reiterates the now widely accepted fact that cooler temperatures delay, and warmer temperatures increase, the speed of development. At 15°C and 20°C the point of 50% survival

Table 1. Duration of the larval stages of *Micropanope barbadensis* at various temperatures.

Temperature (°C)		Duration in days				Number molting to next stage
		Minimum	Mean	Mode	Maximum	
15°C	Zoeae I	4*	—	—	19*	0
20°C	Zoeae I	6	7.6	7	10	13
	II	5	8	5	12	7
	III	6	6.8	7	8**	6
	IV	6	7	7	8	4
	Megalopa	1*	—	—	22*	0
	Zoeae I	7	7.5	—	8	2
	II	11	11.5	—	12	2
	III	7	7	7	7	2
	Megalopa	3*	—	—	9*	0
25°C	Zoeae I	6	6.3	6	8	6
	II	3*	—	—	6*	0

Minimum number of days Zoea I–II–III–IV (Megalopa) = 24; maximum = 32
Minimum number of days Zoea I–II–III (Megalopa) = 26; maximum = 26

* Died in stage.
** Died immediately after molting.

occurred about day 10, but the zoeae remained in stage I at the former temperature, whereas they were about 30% through stage II at the latter. The precipitous decline in survival at "25°C" was probably a consequence of two events: the entry of many of the zoeae into the premolt or actual ecdysis of the second stage, and the rapid rise in room temperature in the laboratory due to breakdown in an air-conditioning unit on the day of molting, day 7 in the series. The data obtained from numerous studies on decapod larval development have all previously indicated that the period prior to and immediately after a molt is a critical period for the larvae with survival tending to decline drastically if conditions prove unfavorable (see e.g., Yang, 1967).

One further consequence should be noted. The 20°C series, although clearly the most successful in terms of larval survival and completion of stages, also suffered problems, primarily caused by agglutination of *Artemia* nauplii and their castes to the zoeal carapaces and appendages. We have experienced this condition before and believe it a result of bacterial growth on dead *Artemia* within the culture water and not a direct consequence of the brand name or geographical origin of the brine shrimp, especially because the same *Artemia* has been used successfully in other cultures of decapod larvae in our laboratory.

Abbreviated Development Versus Normal Development

The majority of xanthid crabs whose larval development has been studied usually undergo four zoeal stages before molting to megalopa. *Micropanope barbadensis* fits this category, but also may have only three zoeal stages on occasion and thus differ from the norm. There are other xanthid species which differ, too, including species of *Menippe* (five–six zoeal stages; Scotto, 1979), *Epixanthus* (two zoeal stages; Saba *et al.*, 1978b), *Pilumnus* (one or no zoeal stages; Wear, 1967), and if *Heterozius* remains classified as a xanthid, it also exhibits two zoeal stages (see Wear, 1967, 1968). Wear (1968) inferred more than three zoeal stages in the New Zealand xanthid *Heteropanope* (*Pilumnopeus*) *serratifrons*

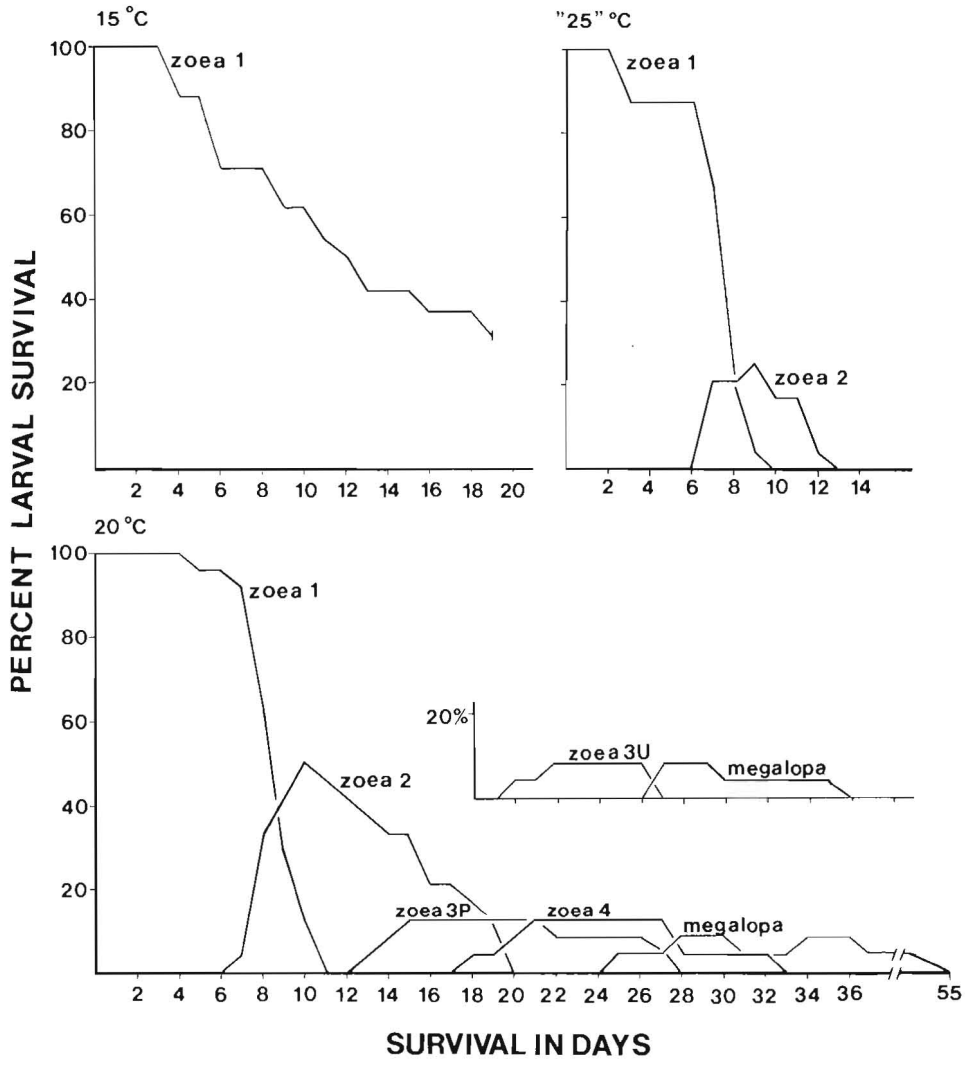

Fig. 1. Percentage survival and stage duration of *Micropanope barbadensis* larvae reared under laboratory conditions; 24 larvae at each temperature. U = ultimate stage; P = penultimate stage. (See text for details.) 15°C series terminated on day 20.

(Kinahan) stating that few species developed through only three stages. However, three zoeal stages are known to occur in several brachyuran families, including species in the Grapsidae (Cano, 1891; Costlow and Bookhout, 1962), Pinnotheridae (Roberts, 1975), Hymenosomatidae (Lucas, 1972), Portunidae (Fielder and Greenwood, 1979), and Calappidae (Hong, 1976). *Micropanope barbadensis* differs from all of these in that it exhibits three zoeal stages apparently only rarely, with four stages being more normal. The elimination of the fourth zoeal stage, as noted earlier, would suggest that development time is considerably shortened, but such is not the case in *M. barbadensis*. This species, moreover, would not seem to fit the general concept which considers elimination of such stages to be an adaptive response by a species, shortening the time spent as larvae in the

plankton either to avoid continued predation, or prevent removal by oceanic currents from an accessible and utilizable habitat already colonized by adults of the species (e.g., Wear, 1968). Alternatively, Sulkin (1978) postulated reduced nutritional vulnerability as an adaptive response to shortened planktonic development time, i.e., if the larvae may not encounter sufficient prey at specific points in their ontogeny, the evolutionary response may be to reduce the number of ontogenetic stages. Such nutritional deficiencies, either through lack of food, or lack of properly nutritious food, are known to affect duration and number of zoeal stages (e.g., Sulkin and Norman, 1976). Makarov (1968) had already postulated a combination of factors that might affect developmental duration in those species (especially caridean shrimp) in which the planktonic existence is made difficult because of insufficient food, predation, or being swept from optimally colonizable areas by oceanic currents. Yet another hypothesis advanced by Sandifer and Smith (1979) is that variation in duration of larval stages, and in numbers of instars as well, may be inherited. Presumably, this mechanism would aid in the dispersal of larvae from "successful" parental genotypes, as well as increasing recruitment to established populations.

Thus, several mechanisms might be applicable toward the reduction of larval stages in nature, and be equally manifest in larvae cultured in the laboratory as well. This, of course, circumvents the question as to whether laboratory food supplies (*Artemia,* rotifers, and others) are nutritionally deficient in some way, so that the number of developmental stages observed in the laboratory is not necessarily that which occurs in nature.

The differences exhibited in the ultimate third zoeal stage of *M. barbadensis,* compared to the penultimate third stage are not great, and are more differences of degree than of kind. They consist primarily of variation in setal counts, although some variation in development of antennal and uropodal buds is evident. These differences are decidedly less dramatic than those seen in, for example, *Menippe nodifrons* ultimate or penultimate fifth, or the intercalated sixth stages (Scotto, 1979). In the latter species, stages can be added, whereas in *M. barbadensis* it appears that stage IV is being eliminated. As will be seen in the larval description that follows, the megalopa stages obtained from either the third or fourth zoeal stages exhibit few distinguishing differences.

Whether any of the hypotheses discussed above are applicable to changing developmental duration in *M. barbadensis* is uncertain. The *Oculina* coral biotope inhabited by adults of the species undergoes some fluctuation in physical parameters (Reed, 1980), but whether these may be considered sufficiently "stressful" on either adults or larvae remains unknown.

The postulated planktonic developmental time of at least 40 days or longer may not necessarily be disadvantageous to the species. Although there are no long-term current gyres in the area of the *Oculina* pinnacles which might return the larvae to these reefs upon completion of development, there is a seasonal onshore deflection of the colder lower layers of the Florida Current during the months of June–August. This upwelling system moves more or less toward shore at about one nautical mile per day. In addition, the net longshore nontidal transport along the central eastern Florida coast is southerly, at a rate of about two nautical miles per day. This longshore current diffuses in the area of Jupiter Inlet, the mouth of the Indian River lagoon, where the Floridan continental shelf becomes extremely narrow, and the Florida Current may lie as close as 10 km offshore or less (Smith, unpubl.). If larvae were entrained in the cold water upwelling and transported shoreward, they might enter the longshore southerly current in about 10 days. Once entrained in the longshore current, larvae might reach Jupiter Inlet

area in about 30 days. Here, swept up by the northward flowing Florida Current, they could easily be transported back to the general point of origin in as little as three days, assuming a minimum speed of this current system of 24 nautical miles per day. By this method, central Floridan larvae may recolonize the oculinid reefs. Moreover, by starting larval life in colder waters (ca. 8–12°C on the oculinid reefs, Reed 1980), and being carried shoreward in cool upwelling waters (15–18°C), the developmental duration would be slowed, thereby extending larval lifetime in the plankton. Once into the longshore and Florida Currents, the prevailing warm temperatures of these systems (22–28°C) would tend to hasten further development so that the species could presumably arrive over the oculinid reefs as megalopae, perhaps even ready for metamorphosis to crabs. Although the ability to eliminate a zoeal stage may not shorten the overall time spent in the plankton by *M. barbadensis,* it does push the animal into the metamorphic stage which is far more able to take up a benthic existence than the zoeae, once the coralline habitat is attained. It may also be that the megalopae from fourth stage zoeae have a far longer duration-in-stage than those obtained from third stage zoeae, thereby enhancing the recruitment potential of that stage. We must, however, await for additional data from both laboratory and *in situ* studies for confirmation of these intriguing possibilities.

Description of the Larvae

First Zoea

RCL (Rostral-carapace length) 1.05–1.31 (1.13) mm; 5 specimens examined.

Carapace (Fig. 2A).—Smooth, inflated, rostral, dorsal and lateral carapace spines present; RS (rostral spine)::CL 0.6–1.1 (0.83); posteriorly curving dorsal spine and lateral spines each with widely spaced minute tubercles; median dorsal protuberance present in all stages, placed about midway between bases of dorsal and rostral spines; single seta above each lateral spine, paired setae on posterodorsal margin; eyes sessile.

Antennule (Fig. 2B).—Elongate pyriform rod, 0.2–0.35 × length of antennal protopod, 2–3 aesthetascs, 0–2 terminal setae.

Antenna (Fig. 2C).—Protopodal spine elongate, slender, distinctly and circularly spinose distally, spinules smaller proximally, tip more or less daggerlike and bifid; protopod 4.5–6.1 × length of exopod; latter tapered, short, 2–3 terminal setae plus minute spinule.

Mandible (Fig. 2D).—Asymmetrically dentate processes, each with blunt, massive molar lobe; no palp.

Maxillule (Fig. 2E).—Endopod two-segmented, setal formula progressing proximally 4, 2, 1, remaining essentially unchanged throughout zoeal development; basal endite usually with 4 strong spines, 1 seta (rarely 2 setae), plus marginal fine hairs; coxal endite with 3–4 terminal spines, 2 strong setae, 1 lateral seta.

Maxilla (Fig. 2F).—Endopod unsegmented, setal formula progressing proximally 3, 2, 3; basal endite distal and proximal lobes each with 3 terminal, 1 subterminal setae; coxal endite distal lobe with 2–3 terminal, 1–2 subterminal setae, proximal lobe 2–3 terminal, 1–2 marginal setae; scaphognathite with 4 marginal setae plus elongate thicker terminal seta.

Maxilliped 1 (Fig. 2G).—Coxopod in all zoeal stages with 1–2 setae; basipodal setal formula in all zoeal stages progressing distally as 2, 2, 3, 3; endopod five-

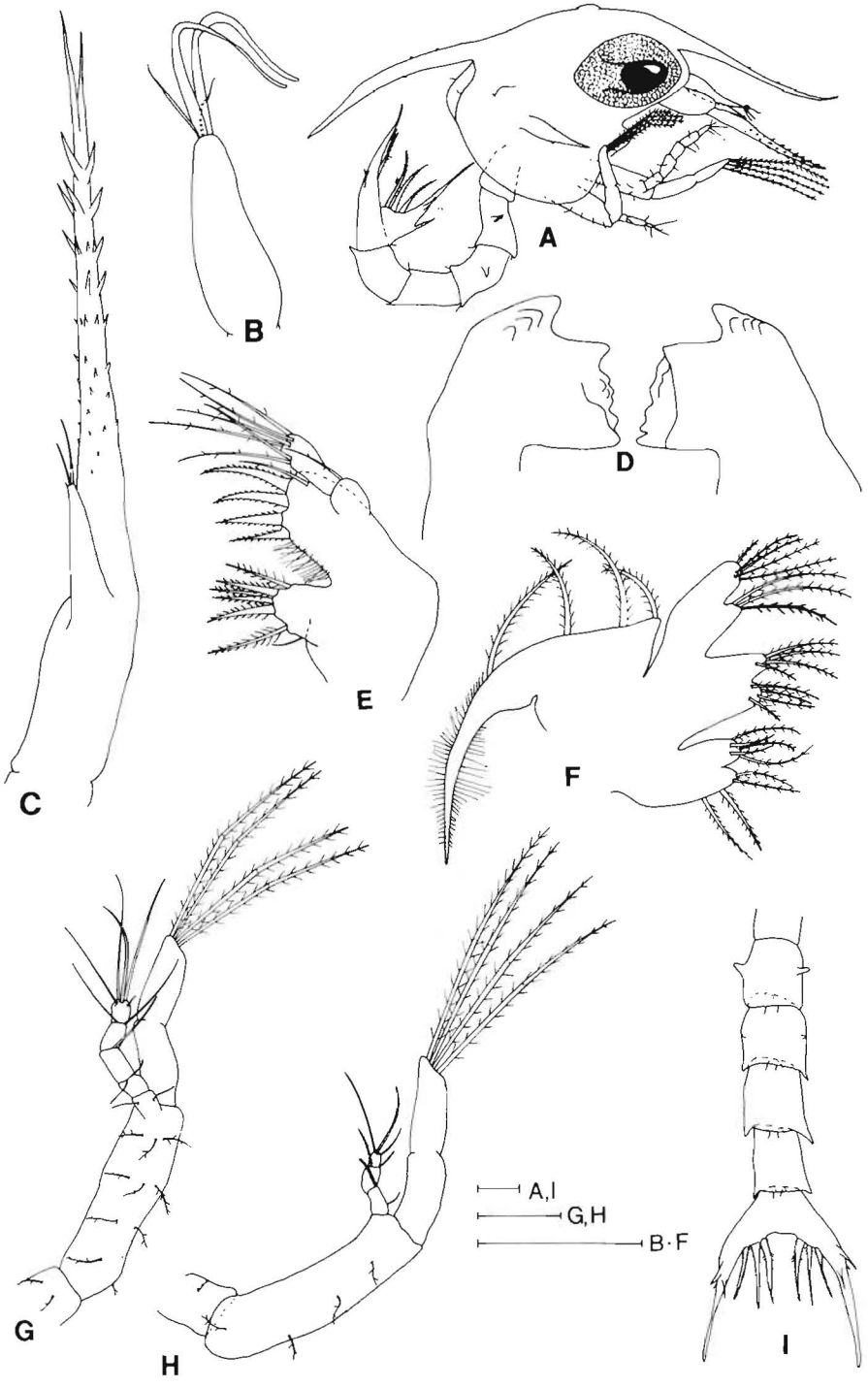

Fig. 2. *Micropanope barbadensis*, first zoea: A, Lateral view; B, Antennule; C, Antenna; D, Mandibles; E, Maxillule; F, Maxilla; G, Maxilliped 1; H, Maxilliped 2; I, Abdomen and telson, dorsal view. Scale lines in 0.1 mm.

segmented throughout zoeal development, setal formula in stages I–III regular, progressing distally 2, 2, 1, 2, 4, + I dorsally; exopod with 4 natatory setae.

Maxilliped 2 (Fig. 2H).—Coxopod in all zoeal stages with 0–1 seta; basipod setal formula in all zoeal stages 1, 1, 1, 1; endopod three-segmented throughout development but setal formula variable; this stage 1, 1, 2 + 3 terminally, proximal and subdistal segments each bearing distinctly spinose seta; exopod with 4 natatory setae.

Abdomen (Fig. 2 A, I).—Five somites and telson; second through fifth somites with paired setae on dorsal and ventral posterior margins in all stages; second somite with blunt lateral spinule, third similarly armed but spinule smaller, these blunt spinules remain in all subsequent zoeae; posterolateral margins of somites 3–5 produced into blunt spinelike teeth.

Telson (Fig. 2I).—Furcae with paired spines, 2 laterally, 2 axillary, 2 medially; setal formula along posterior margin 3 + 3 stout spines, innermost of these with several short setae near base; medial rectangular sinus present.

Color.—Carapace generally translucent, spines with faint violet tinge; abdomen and telson faintly outlined in diffuse pale violet, color more pronounced at somite junctions; antenna with orange-red chromatophores basally; mandibulary mouthparts orange to orange-brown; maxillipedal articulations pale violet diffusing to pink; corneas of eyes light green in reflected light.

Second Zoea

RCL 1.34–1.46 (1.39) mm; 7 specimens examined.

Carapace (Fig. 3A).—Similar to first stage, but additional setae as follows: paired medially between eyes, plus several scattered along length of dorsal spine; RS::CL 0.9–1.3 (1.1); minute tubercles on spines as in previous stage; lateral spines substantially longer in this stage than in first; dorsal spine longer than rostral spine in this and subsequent zoeal stages; eyes stalked.

Antennule (Fig. 3B).—Form similar to first stage, 0.19–0.3 × length of antennal protopod, 4 terminal aesthetascs, 1–2 setae.

Antenna (Fig. 3C).—Spination as in first stage; endopodal primordium barely discernible; exopod setation unchanged; protopod 6.4–10.3× longer than exopod.

Mandible (Fig. 3D).—Processes stouter, more massive, otherwise unchanged from previous stage; no palp.

Maxillule (Fig. 3E).—Basal endite with 5 strong spines, 3 strong setae, single plumose seta basally; coxal endite with 4 strong spines, 3 strong setae.

Maxilla (Fig. 3F).—Endopod setal formula 3, 2, 3 progressing proximally and remaining as such throughout zoeal development; basal endite distal and proximal lobes with 3 + 1, 4 + 1 processes, respectively; both lobes of coxal endite with 3 + 1 processes; scaphognathite with 9–12 marginal setae, elongate apical seta lacking.

Maxilliped 1 (Fig. 3G).—As in previous stage; exopod with 6 natatory setae.

Maxilliped 2 (Fig. 3H).—Basipod rarely with extra seta as illustrated; endopod setal formula 1, 1, 4 + 1 smaller, laterally; exopod with 7 natatory setae.

Abdomen (Fig. 3A).—Similar to first stage but posterolateral spines more pronounced.

Fig. 3. *Micropanope barbadensis*, second zoea: A, Lateral view; B, Antennule; C, Antenna; D, Mandible; E, Maxillule; F, Maxilla; G, Maxilliped 1; H, Maxilliped 2. Scale lines in 0.1 mm.

Telson (Fig. 3A).—Unchanged from previous stage.

Color.—Carapace clear, small dark brown chromatophore laterally, ventral to lateral spine near posterior margin; rostral spine pale yellow; lateral spines clear with dark brown stellate chromatophore at base (this appearing dark reddish-violet at low magnification), plus small gold dot; dorsal spine with dark, almost black, band about ¼ distance from tip, followed about midway down length by small, dark coral-pink stellate chromatophore; mandibles reddish-violet with distal margins outlined in violet; maxillipedal articulations with faint darker violet banding, plus pale golden-yellow dotlike chromatophore; junctions of abdominal somites 2–3, 3–4 dorsally with small brown stellate chromatophores; telson faintly violet, more pronounced along margins, lateral spines diffused with pale gold; small dark brown stellate chromatophore midway on each furca dorsally.

Third Zoea (Penultimate)

RCL 1.84–1.96 (1.90) mm; 5 specimens examined.

Carapace (Fig. 4A).—Similar to previous stages but anterolateral and posterolateral margins not as convex; setation now more pronounced with additional paired hairs dorsally (Fig. 4B), plus 4 individual hairs along each posterolateral margin. Dorsal and rostral spines increased in length, RS::CL 0.9–0.96 (0.92); anterodorsal angles of carapace at rostral spine base produced into blunt teeth.

Antennule (Fig. 4C).—More inflated than in earlier stages; about 0.3–0.36 × length of antennal protopod, with 4 terminal, and usually 2 subterminal aesthetascs, plus terminal seta; incipient endopod a slight swelling laterally.

Antenna (Fig. 4D).—Spination remains more or less similar to earlier stages; endopod bud noticeably developed, 0.12–0.14 × length of protopod, 1.1× longer than exopod; protopod 6.3–7.5× longer than latter.

Mandible (Fig. 4E).—Heavily dentate but otherwise unchanged; no palp.

Maxillule (Fig. 4F).—Basal endite now bearing 6 strong spines, 3–4 strong setae; coxal endite with 5 strong spines, 2 strong setae; plumose seta retained basally.

Maxilla (Fig. 4G).—Basal endite lobes both with 4 + 1 processes; coxal endite distal lobe as in previous stage, proximal lobe with 2 terminal, 4 subterminal setae progressing in row down side; latter endite remains unchanged in following stage; scaphognathite with 18–20 marginal setae.

Maxilliped 1 (Fig. 4H).—Endopodal terminal segment occasionally with extra lateral hair; exopod with 8 natatory setae.

Maxilliped 2 (Fig. 4I).—Endopod terminal segment rarely with additional seta; exopod with 9 natatory setae.

Abdomen (Fig. 4A, J).—Six somites and telson; second through fifth with paired pleopod primordia; sixth with 2 dorsal setae but no posterolateral spines; lateral spinules and posterolateral spines longer and stronger than previous stages.

Telson (Fig. 4A, J).—Furcae more elongate compared to previous stage; paired lateral, axillar and dorsal spines remain quite strong, not reduced; inner pair of marginal setae often locked together by stout setules proximally; setal formula remains 3 + 3.

Color.—Similar to earlier stages; carapace now overall more noticeably violet, lateral surface and associated spines more heavily diffused with gold; single or-

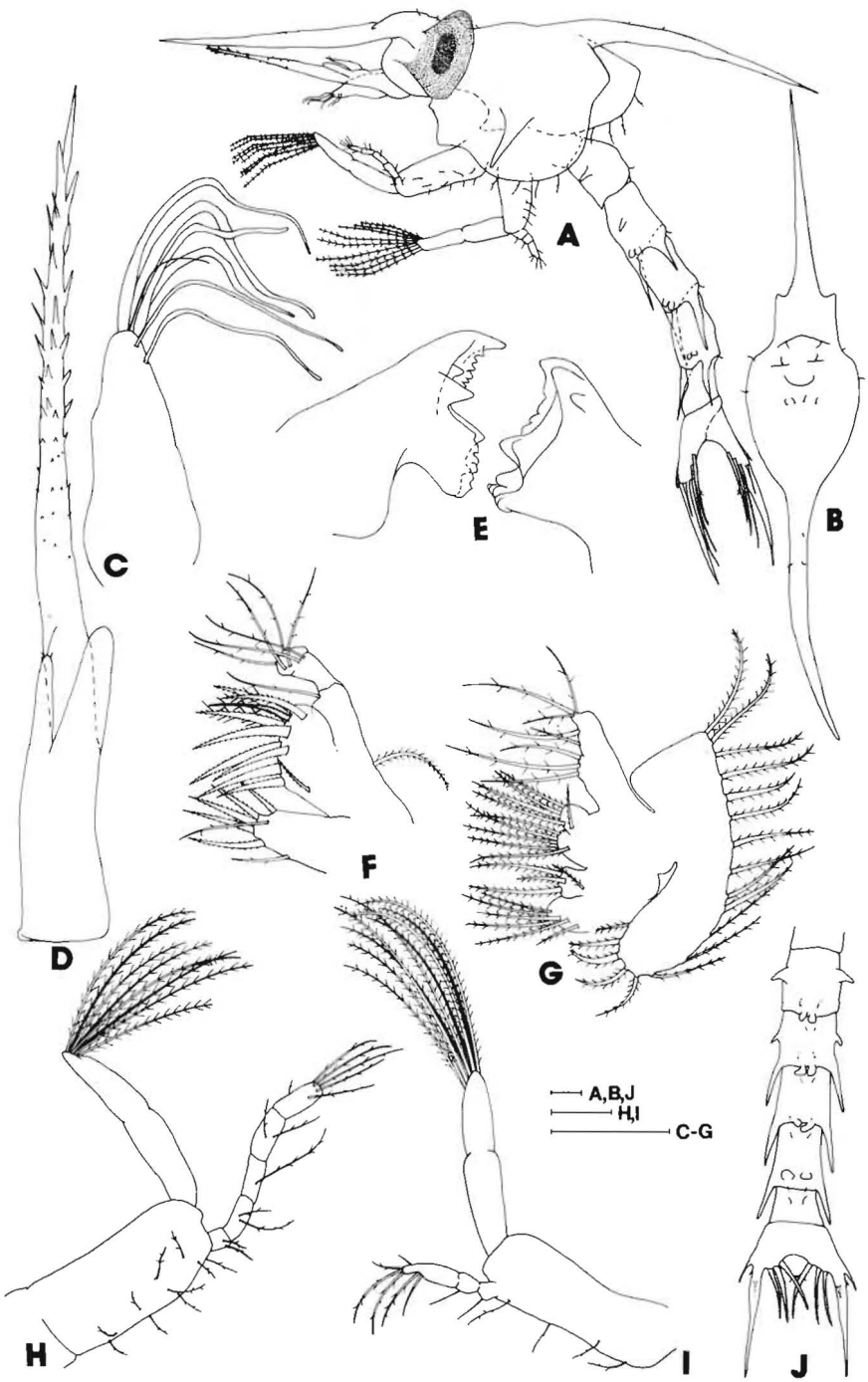

Fig. 4. *Micropanope barbadensis,* third (penultimate) zoea, exuvium: A, Lateral view; B, Carapace—dorsal view; C, Antennule; D, Antenna; E, Mandibles; F, Maxillule; G, Maxilla; H, Maxilliped 1; I, Maxilliped 2; J, Abdomen and telson, ventral view. Scale lines in 0.1 mm.

ange stellate chromatophore between and slightly posterior to each eye; antennule and antenna pale violet; maxillipeds 1 and 2 with penultimate segments of endopods each with brown chromatophore; telson pale violet with minute red chromatophore laterad to base of proximal lateral spine.

Remarks.—This stage, which always molted to a subsequent zoeal stage IV, was distinguished from the advanced third stage described below by having fewer antennular aesthetascs and maxillipedal natatory setae, no endopodal bud on the antennule and that of the antenna less developed, no mandibular palp buds, by the less developed pleopod primordia on the abdominal somites, and the absence of uropod buds.

Third Zoea (Ultimate)

RCL 1.9–2.1 (2.0) mm; 2 specimens examined.

Carapace (Fig. 5A).—Larger, anterodorsal margins slightly more produced; paired hairs ventrally beneath insertion of rostral spine; RS::CL 1.0–1.1.

Antennule (Fig. 5B).—Aesthetascs progressing proximally 4 terminal, 3 subterminal (2 thin, 1 thick), 1 thin lateral, plus 2 other setae as illustrated; small endopod bud present; length about 0.34–0.37 antennal protopod.

Antenna (Fig. 5C).—Endopod 0.31–0.33 × length of protopod, about 2.2× longer than exopod; protopod 6.7–6.8 × length of latter; no noticeable spination differences.

Mandible (Fig. 5D).—Similar to penultimate stage but each with palp bud.

Maxillule (Fig. 5E).—Endopod appearing indistinctly three-segmented; basal endite with 11 strong processes, 2 lateral setae; coxal endite with 10 strong processes, 2 lateral setae.

Maxilla.—Scaphognathite with 27–30 marginal setae.

Maxillipeds 1 and 2.—Each with 9 and 11 natatory setae.

Pereopods.—Developed, with incipient segmentation in specimens examined.

Abdomen (Fig. 5F).—Somite 1 with 3 dorsal setae near posterior margin; pleopod buds elongate; uropod buds on somite 6.

Telson (Fig. 5F, G).—Posterior margin with additional setae as shown; mesial and outer margin of innermost pair of setae with stout setules. Color not recorded.

Remarks.—Zoeae in this stage invariably molted to megalopae. They differed from third stage penultimate zoeae as follows: the antennular aesthetascs appeared in rows, the associated setae were situated differently, and an endopodal bud was present, as were mandibular palp buds, the antennal exopod was greatly lengthened, the maxillipeds had increased numbers of natatory setae, the pleopod primordia were longer, uropod buds appeared on somite six, and the posterior telsonal margin carried additional setae.

Fourth Zoea

RCL 2.1–2.2 mm; 3 specimens examined.

Carapace (Fig. 6A).—Cephalothorax rather globose, enlarged, lower margin with about 10 widely spaced setae; several pairs of interocular setae placed as illus-

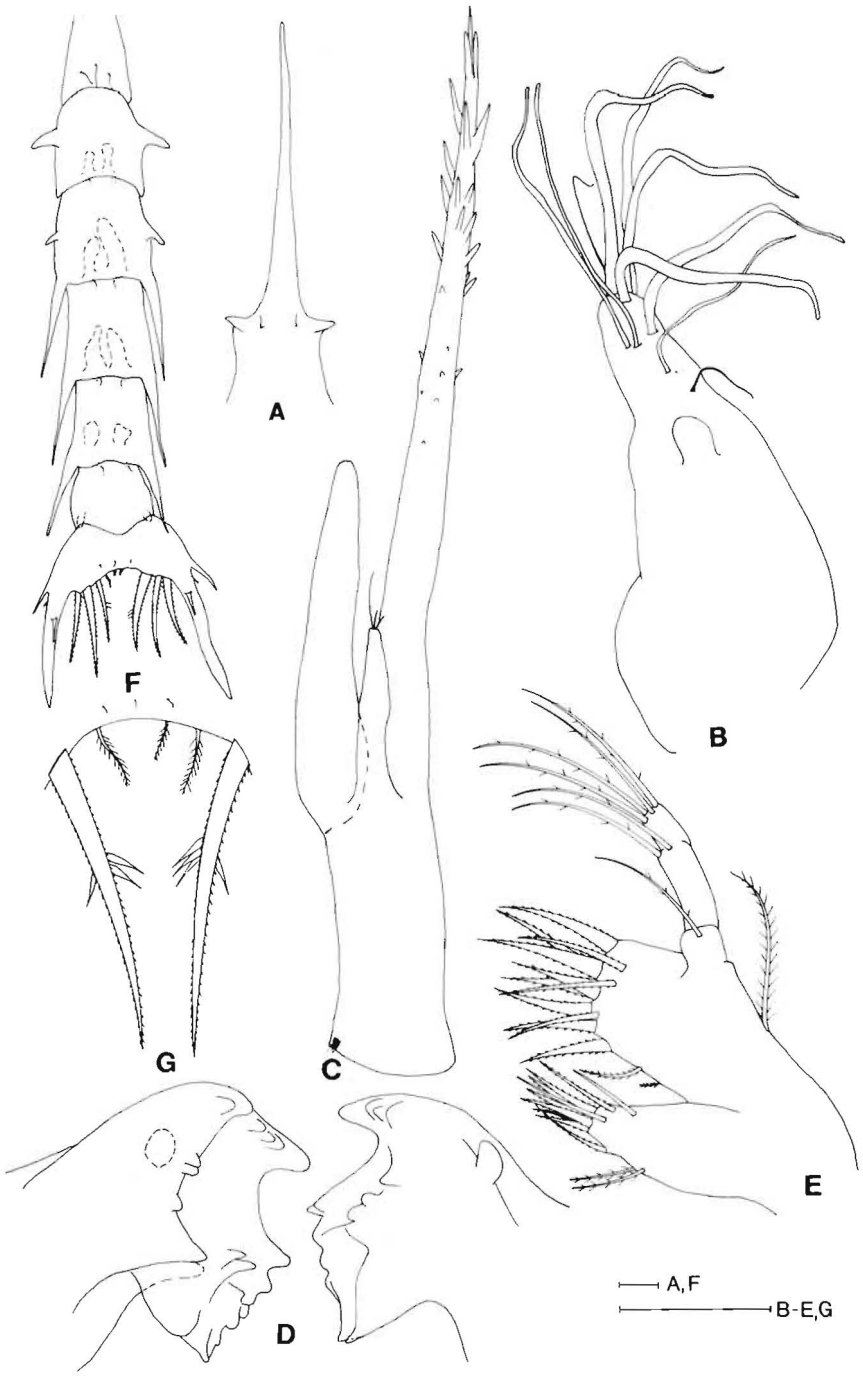

Fig. 5. *Micropanope barbadensis,* third (ultimate) zoea, exuvium: A, Rostrum, ventral view; B, Antennule; C, Antenna; D, Mandibles; E, Maxillule; F, Abdomen and telson, dorsal view; G, Telson detail, median posterior margin. Scale lines in 0.1 mm.

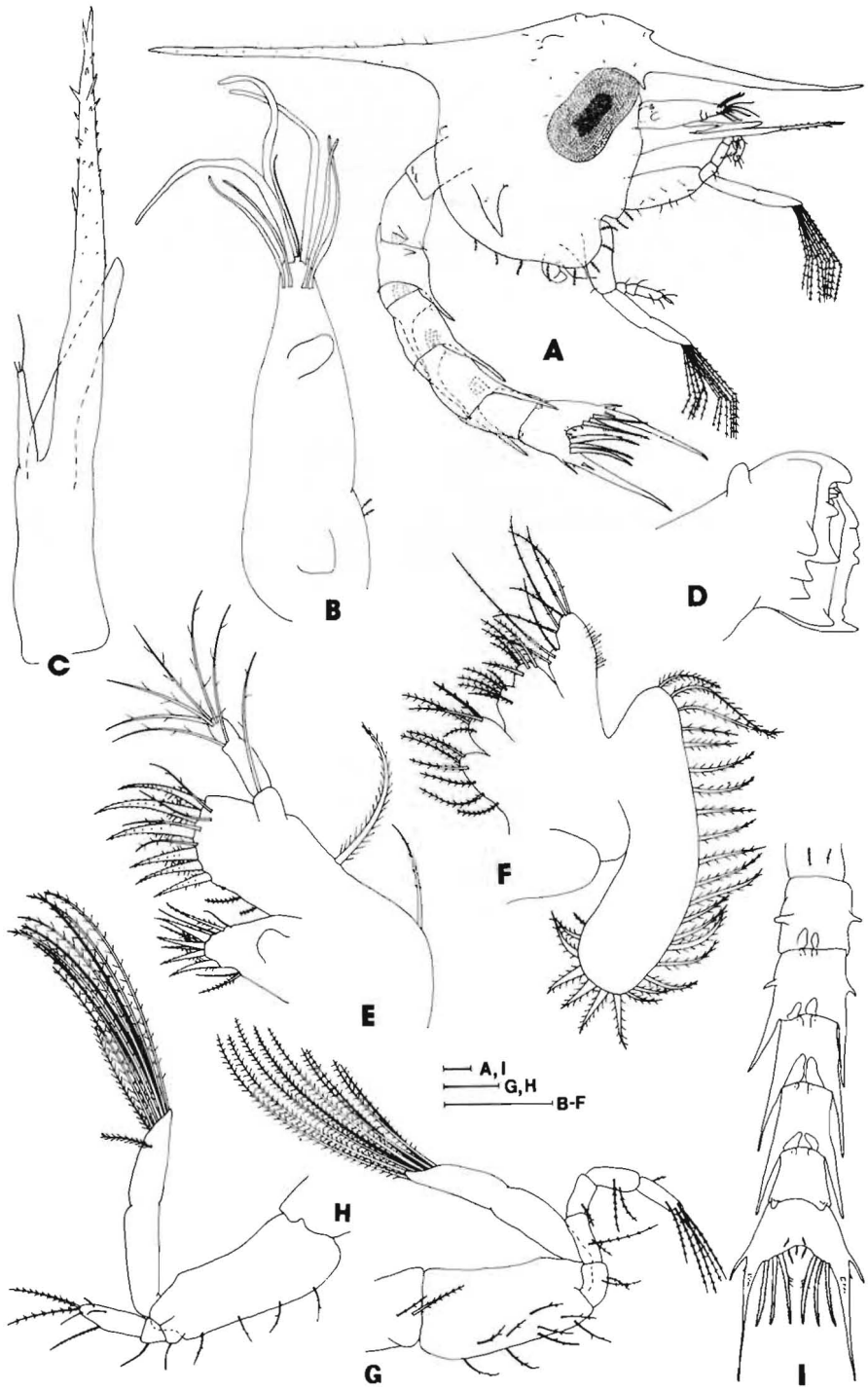

Fig. 6. *Micropanope barbadensis*, fourth zoea, exuvium: A, Lateral view; B, Antennule; C, Antenna; D, Mandible; E, Maxillule; F, Maxilla; G, Maxilliped 1; H, Maxilliped 2; I, Abdomen and telson, ventral view. Scale lines in 0.1 mm.

trated; dorsal spine bearing minute but noticeable tubercles along its length, those of lateral and rostral spines present but less distinct.

Antennule (Fig. 6B).—Length about 0.4 × antennal protopod; aesthetasc formula 3-4, 4, with 1–2 setae, these placed differently than in penultimate third stage (q.v.); endopod bud produced, second protuberance basally plus 2 thin hairs laterally, entire segment indistinctly two-segmented.

Antenna (Fig. 6C).—Endopod 0.34–0.4 × length of protopod, about 2.9 × length of exopod; protopod 6.6–8.7× longer than exopod; spination as illustrated.

Mandible (Fig. 6D).—Heavily dentate, rudimentary palp bud present.

Maxillule (Fig. 6E).—Basal endite with 6 stout spines, 4 strong setae, 2 lateral setae, and 2 elongate plumose setae basally; coxal endite with 11–13 processes, plus bluntly rounded protuberance laterally.

Maxilla (Fig. 6F).—Basal endite lobes with either 4 + 1 or 4 + 2 processes; coxal endite unchanged from penultimate third stage; scaphognathite with 23–27 marginal setae.

Maxillipeds 1 and 2 (Figs. 6G, H).—Exopods with 9 and 11 natatory setae, respectively.

Maxilliped 3 (Fig. 6A).—Small, bifid buds, apparently partially segmented.

Abdomen (Fig. 6A, I).—Somite 1 with paired dorsal setae; pleopods on somites 2–5 longer; uropod primordia on somite 6; lateral spinules and posterolateral spines noticeably longer.

Telson (Fig. 6A, I).—Similar to penultimate third stage, but bearing 5 additional setae on posterior margin as shown. All furcal paired spines still evident.

Color.—Carapace remaining essentially translucent with violet and gold highlights; dorsal spine clear, diffused with violet distally, faintly tipped with orange; lateral spine clear, becoming pale gold distally; rostral spine clear. Chromatophores appear as follows: stellate, black or brown posterior to dorsal spine base, at rostral spine insertion, around mandibulary mouthparts, dorsally at junction of abdominal somites 2–3, 3–4, and on proximal endopodal segments of maxillipeds 1 and 2; red dots at bases of lateral and rostral spines, and eyestalks; stellate, red on ventrolateral margin of carapace, dorsally along eyestalks, and laterad to bases of proximal lateral spines on telson; orange-red medially between eyestalks on frontal region, medially on antennule; orange along mesial margin of maxilliped 3. Eyestalk bases and maxillipeds 1 and 2 pale gold to golden orange. Antennule, antenna, mandibulary mouthparts, junctions of abdominal somites, and telson diffused with pale violet, color stronger at articulations, along margins, and especially outlining pleopods. Mandible coral or orange, bordered in violet. Pink highlights on abdominal somites and telsonal surface; corneas of eyes reddish in reflected light.

Megalopa

RCL by CW:0.76 × 0.68–1.72 × 1.20 (1.32 × 1.09) mm; 5 specimens examined.

Remarks.—Megalopae molting from stage III were little distinguished from those molting from the fourth zoeal stage, differing primarily in extra setation on some appendages, probably of little significance.

Carapace (Fig. 7A–D).—Subrectangular, setose, antero- and posterolateral mar-

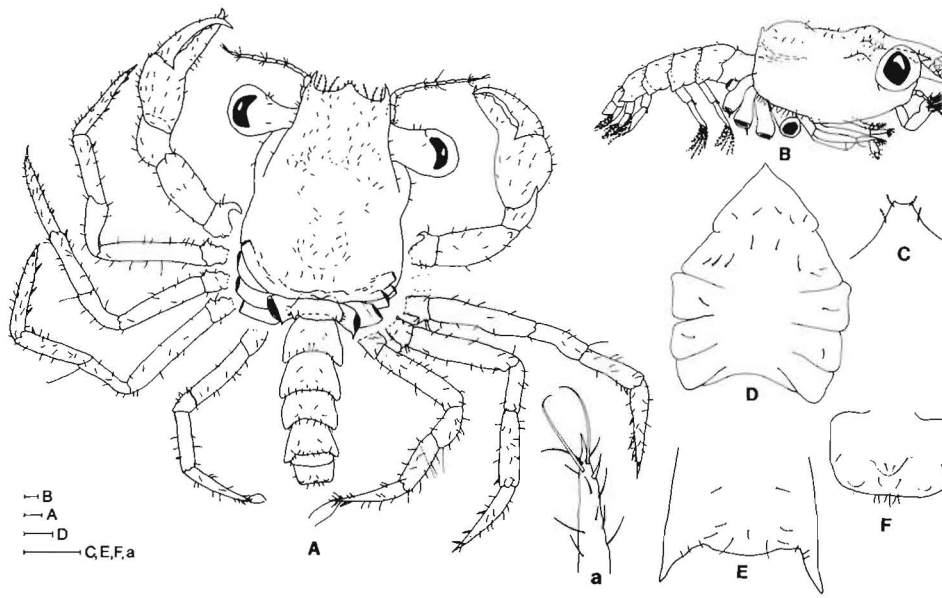

Fig. 7. *Micropanope barbadensis*, megalopa: A, dorsal view; a, Dactyl of 5th pereopod detail; B, Lateral view; C, Rostrum detail; D, Sternum; E, Abdominal somite detail; F, Telson detail, dorsal view. Scale lines in 0.1 mm.

gins rounded, smooth, without spines; frontal region well-developed, extending beyond eyes, anterolateral angle produced into sharp curved spine; orbits little excavated, appearing slightly concave along dorsal margin; rostral spine well-developed, deflexed, extending beyond anterolateral spines, bluntly bifid at tip. Dorsal surface of carapace with transverse row of 3 small, low, rounded protuberances on gastric region, larger inflated prominence on cardiac region, followed by a short, acute, tuberclelike swelling immediately posteriorly on intestinal region; posterolateral branchial regions distinctly rugose. Sternum oblately cordate, with setae as illustrated.

Abdomen (Fig. 7A, B, E).—Somites 2–4 with posteroventral margins developed into blunt toothlike lobes, those of somite 5 more acute; setation typically as illustrated.

Telson (Fig. 7F).—Length 0.68–0.72 × width, subquadrate, posterior angles rounded, 3 low rounded prominences dorsally; setation variable but similar to that shown.

Pereopods (Fig. 7A, a).—Chelipeds large, inflated, subequal, right slightly larger than left, slightly more robust; chelae with irregular low, blunt teeth in gape; ventral margin of palms distinctly sinuous; carpus and merus unarmed, ischium produced into short, sharp, recurved spine ventrally. Walking legs long, thin, setose, dorsal margins lacking spinules diagnostic for the genus, all movable segments smooth except for ischia of first 3 pairs each bearing small, distinct fixed, plus blunt movable, spine; bases of all walking legs each with fixed spine; dactyls of pereopods 2–4 with 3 ventral, and a smaller supernumerary lateral tooth; dactyl of pereopod 5 with 1 lateroventral tooth, plus 2 long thin curved setae distally (''brachyuran feelers'').

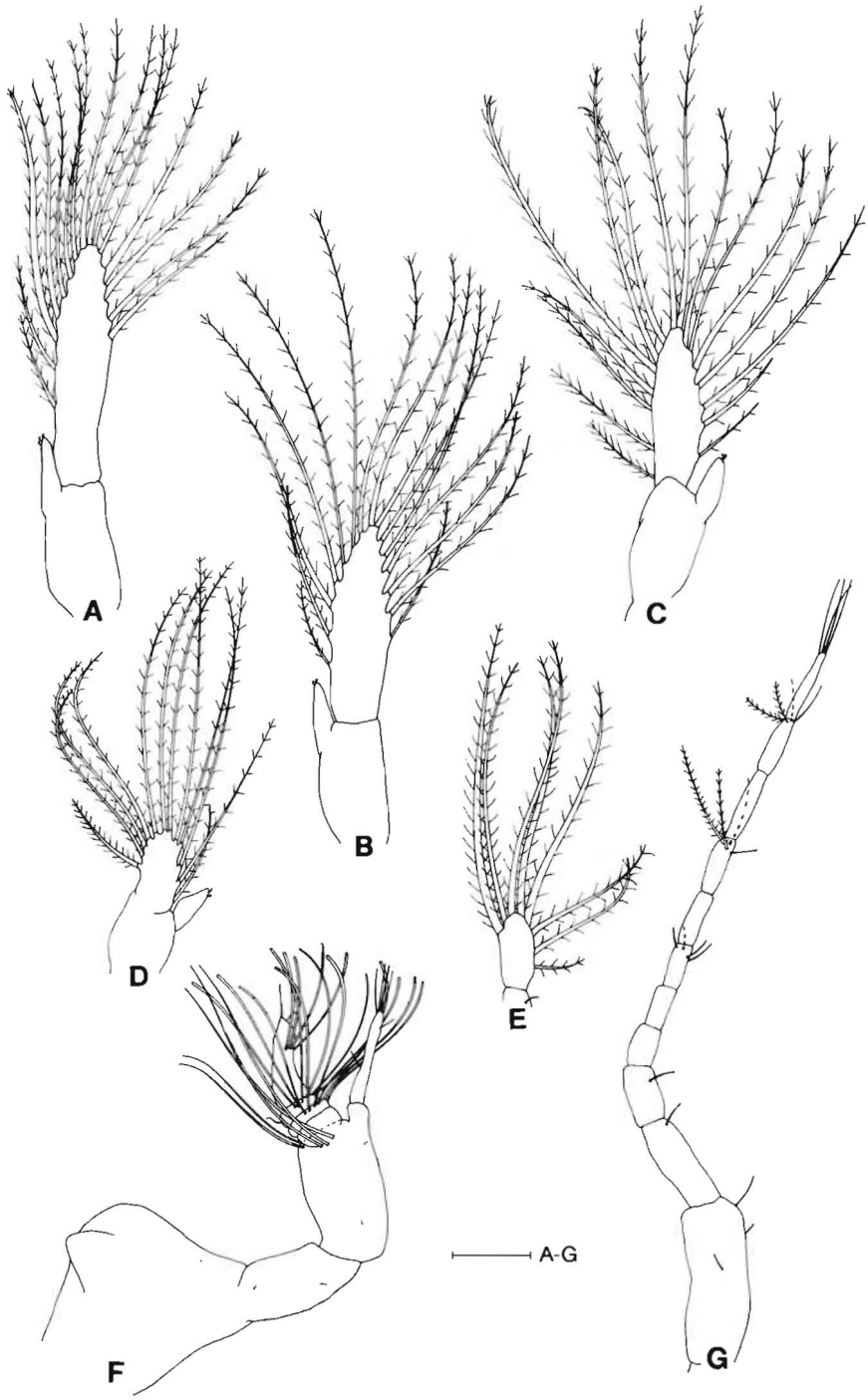

Fig. 8. *Micropanope barbadensis,* megalopal swimming and sensory appendages: A, Pleopod 1; B, Pleopod 2; C, Pleopod 3; D, Pleopod 4; E, Uropod; F, Antennule; G, Antenna. Scale line is 0.1 mm.

Pleopods (Fig. 8A–E).—Decreasing in size on somites 2–6, those on somites 2–5 each with small endopod, latter bearing minute hooks functioning as *appendices internae*; that of somite 6 [=uropod] lacking endopod; setation on exopods typically as illustrated.

Antennule (Fig. 8F).—Biramous; peduncle three-segmented, bulbous basal segment with lobelike protuberance dorsally, third peduncular segment with 5 long setae proximal to junction of upper ramus, other setae variable; upper ramus four- (occasionally indistinctly five-) segmented, aesthetascs progressing distally in tiers as follows: (0), 0, 6, 6, 4 + 2 setae terminally; lower ramus slender, one-segmented, 6 setae.

Antenna (Fig. 8G).—Peduncle three-segmented, sparsely setose; flagellum usually of 8 articles, setose as shown.

Mandible (Fig. 9A).—Truncately spade-shaped, small fine hairs dorsally; palp three-segmented with 0, 0, 10 spinose setae.

Maxillule (Fig. 9B).—Protopod with 3 basal setae; endopod one-segmented, 3 lateral, 2 terminal setae; basal endite bearing 6 stout spines, 14 strong setae terminally, plus 2 thinner axillary setae; coxal endite with 6 terminal, 10–11 lateral processes.

Maxilla (Fig. 9C).—Endopod unsegmented, 3 proximal, 2 distal setae; basal endite processes 10–11 on distal, 8 on proximal, lobes; coxal endite bearing 7, 8 processes on respective lobes; scaphognathite with 45–46 marginal setae plus several smaller setae dispersed on blade.

Maxilliped 1 (Fig. 9D).—Exopod two-segmented, 1–2 lateral, 5 terminal plumose setae; endopod poorly calcified, naked except for 3 setae on dorsal lobe; protopod bilobed, basal endite with about 25, coxal endite about 10, setae; epipod well-developed, 7 processes along margin.

Maxilliped 2 (Fig. 9E).—Exopod two-segmented, 2 short setae, 5–6 terminal plumose setae; endopod five-segmented, numbers and position of processes as shown, those on dactyl noticeably spinelike; protopod naked or sparsely setose; epipod bilobed, 2 terminal setae on one lobe.

Maxilliped 3 (Fig. 9F).—Exopod two-segmented, lateral and distal plumose setae as illustrated; endopod five-segmented, ischium laterally expanded, margins dentate, about 15 processes in megalopae from third zoeae, about 21 in those from fourth zoeae, armature on remaining segments variable, consisting of numerous spines and fewer setae, in positions illustrated; dactyl with 2 long, strong dentate spines apically; protopod heavily setose; epipod with 4–5 proximal setae, 8–10 thin distal processes; fragil podobranch present.

Color.—Carapace clear orange, blending to gold posteriorly, margins outlined in dark orange; posterolateral margin with radiating dark strings of tiny brown or black chromatophores; orbital margins orange dorsally, gold ventrally; eyestalks, antennulae, antennae, and labial mouthparts generally clear, mandibles orange with burnt sienna or brown border. Chelae clear, cutting edges of movable fingers orange, lateral surfaces of immovable fingers mostly orange, ventral margins of palms darker, but becoming golden yellow dorsad and blending into orange; coxae rose orange; remaining segments mostly clear with scattered orange spots. Walking legs clear, basal and coxal segments outlined in orange, distal articulations lavender, dactyli horn colored. Abdominal somites with faint orange color on margins, diffusing into gold laterally on pleura. Corneas of eyes reflect brown.

Fig. 9. *Micropanope barbadensis*, megalopal feeding appendages: A, Mandible; B, Maxillule; C, Maxilla; D, Maxilliped 1; E, Maxilliped 2; F, Maxilliped 3. Scale line is 0.1 mm.

Discussion

The larvae of *Micropanope barbadensis* show a disconcerting similarity to zoeal stages of many other xanthid crabs, and except perhaps for general coloration and chromatophore positioning, recognition of the species among other xanthid larvae in the plankton may prove difficult. Easily observed features such as maxillipedal setal formulae, abdominal and carapacial spine numbers, positions, and lengths, are not overtly distinguishable from those seen in other xanthid zoeae. The larvae of *M. barbadensis* do share some of the features of xanthid larvae enumerated by Wear (1970) at the familial level, including a carapace with dorsal, rostral, and a pair of smaller lateral spines; an abdomen with lateral knobs or tubercles on somites 2 and 3, plus posterolateral spines on somites 3–5; and telsonal furcae with three smaller lateral spines on each fork, these spines not disappearing in later stages. The number of larval stages (previously listed as four within the family) is no longer a valid distinguishing familial character, as several previously noted studies have shown, and in *M. barbadensis* can vary between 3 and 4 zoeal stages. Another category, that of the antenna having either a vestigial exopod or one from ½ to ¾, to nearly as long as the protopod, although remaining of some value, needs emendation as shown by the present study. In *M. barbadensis* the protopodal spines range from 4.5 to 10.3 times longer than the exopod, depending on the zoeal stage, with a mean length of 6.1–7.8 times longer than the exopod within any given stage. Thus, the relatively well developed exopod is intermediate in relation to the protopodal spine length in this species, being about $^1/_4$ to $^1/_7$ its length, and differing substantially from that noted in other xanthid larvae. This is the most notable morphological feature exhibited by *M. barbadensis,* and with the exception of zoeae of *Paramedaeus noelensis* (Suzuki, 1979) and perhaps *Heterozius rotundifrons** (Wear, 1968), both western Pacific species, is not seen in the larvae of other xanthid genera. Moreover, data obtained in our laboratory from the larvae of *Micropanope sculptipes* show the zoeal stages of that species to be extremely close to *M. barbadensis* in general morphological features, and to exhibit similar antennal exopod:protopod ratio (Andryszak and Gore, in prep.). This value, approximately $^1/_4$–$^1/_7$, while being of some aid insofar as species identification is concerned (provided it is used with a careful comparison of morphological features in dissected appendages), appears to have more value in the larvae at the generic level of *Micropanope sensu lato.* It will be recalled, however, that the genus *Micropanope* was emended by Guinot (1967) to include only *M. sculptipes* and one other species, and that *M. barbadensis* was considered perhaps closer to Guinot's *Coralliope,* a genus established to accommodate a West African and an eastern Pacific species, both previously placed in *Micropanope.* The latter two species have affinities with *Domecia* and *Maldivia,* among others, and not with *Micropanope* (emend.) or any of the Panopeinae *sensu* Guinot. Without knowing the larvae of *Domecia* or *Maldivia,* little more can be said regarding Guinot's placement, or just how *M. barbadensis* larvae will fit in this scheme. The antennal exopod features in the larvae of *M. barbadensis* and *M. sculptipes* would nevertheless seem to indicate close relationships between these two taxa, even though the adults will eventually be in separate genera.

In regard to the larvae of *Paramedaeus noelensis* and *Heterozius rotundifrons,* mentioned earlier, the relative length of the antennal exopod to the protopod

* Wear (1968, 1970) has presented evidence which suggests that *H. rotundifrons* may not belong to the Xanthidae, but is a primitive form with obscure relationships.

ranges from about $^1/_3$ to $^2/_5$ in the former, and about $^1/_6$ in the latter species. These values are close to those seen in the 2 *Micropanope* species. While not excluding other larval characters which may assume eventual importance, we concur with Wear (1970) who held that the most important single character in separating species, and distinguishing major groups of genera, is the length of the antennal exopod to the protopodal spine. If we assume Aikawa's (1929) original categorization of antennal types A–D to remain valid, then an additional category must be established to contain those larvae in which the exopod is intermediate in length ($^1/_7$–$^2/_5$) to the protopod. Antennal exopods in the new group are considerably shorter than those of Group A ("nearly equal"), Group B ($^1/_2$–$^3/_4$), and considerably longer than "minute" or "rudimentary" (Group C) in length relative to the protopodal spine. Group D antennae are considered deviations and need not concern us here. To the intermediate group, which we here establish as Group E, we assign *Micropanope barbadensis, M. sculptipes* (Andryszak and Gore, in prep.), *Paramedaeus noelensis* (Suzuki, 1979), and *Heterozius rotundifrons* (Wear, 1968). It will be interesting to see whether larvae of *Maldivia* or *Domecia* fit the new Group E as established herein, or if other species presently assigned to *Micropanope sensu lato* will have larvae which can be similarly categorized.

It is difficult to suggest other morphological features which may enable *M. barbadensis* larvae to be identified in the plankton. Not only do xanthid larvae exhibit a bewildering array of characters, but many of these characters assume varying degrees of importance to students, so that emphasis placed by some authors is ignored by others. The following features, however, may prove of some value and include the presence of small, tuberclelike bumps along the dorsal, lateral, and rostral spines; small setules along the dorsal spine; a distinct dorsomedial knob or protuberance anterior to the dorsal spine; several small hairs along the ventrolateral carapace margins in stages III and IV; the very strong distal spination on the antennal protopodal spine; the paired setae on the coxa of maxilliped 1; the general shape of the mandibles; and the length of the antennal protopodal spine relative to the rostral spine. All these features are clearly illustrated in the section describing the larvae.

The megalopal stage of *M. barbadensis* shows little resemblance to the adult, lacking the anterolateral dentition common to many xanthid species and quite noticeable in the adults of the genus *Micropanope*. A rostral protuberance is well-developed in the megalopa but is lacking in the adult. A transverse series of prominences on the gastrohepatic region become much more flattened in the adult, and the distinct spinelike teeth on the inner orbital angle, so prominent in the megalopa, become bluntly rounded with maturity. The cheliped carpus in the megalopa lacks the strong bifid spine on the anterodistal angle, and the granulation on the chelipeds and carapace, which characterizes the adults, is poorly developed, if at all, in the megalopal stage. The telson is rectangular, as in several other xanthid megalopae, but bears 3 rounded prominences which are either not present or are not mentioned in descriptions of other megalopae. Most notably, however, the megalopa of *M. barbadensis* exhibits recurved ischial spines on the anterior 4 pairs of pereopods, a feature presently unique to the species.

As noted by Wear (1970), Saba *et al.* (1979a, b), and others, the classification scheme erected by Lebour (1928) to categorize xanthid megalopae is now of little value, because the characters enumerated (rostral, ischial, and dactylar) show so much variation among the known postlarvae. Investigations presently being conducted on the postlarvae of *Micropanope sculptipes* suggest that frontal region configuration, in conjunction with telsonal and pereopodal ischial features may provide some uniformity, at least within known postlarvae of western Atlantic

genera (Andryzak and Gore, in prep.), and these data will be presented in due course.

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