

LARVAL DEVELOPMENT OF *PANOPEUS BERMUDENSIS*
 BENEDICT AND RATHBUN, 1891
 (BRACHYURA, XANTHIDAE) WITH NOTES ON
 ZOEAL CHARACTERS IN XANTHID CRABS

Joel W. Martin, Frank M. Truesdale, and Darryl L. Felder

A B S T R A C T

Four zoeal stages and one megalopal stage are described and illustrated for the xanthid crab *Panopeus bermudensis*. The zoeae are immediately distinguished from all other known xanthid zoeae by a combination of characters: the absence of lateral carapace spines, an unusually placed spine on the telsonal furca, and the absence of an antennal exopod. The derivation of these allegedly apomorphic characters from more plesiomorphic xanthid zoeal stock is discussed, and possible phylogenies for the Xanthidae are examined in the context of available larval characters.

Systematics of the genus *Panopeus* H. Milne Edwards have long been problematic. Traditional specific characters of adults in this genus, such as carapace and cheliped morphology, may reflect adaptation to environment rather than "true" phyletic distance (see Martin and Abele, in press). Students of xanthid taxonomy have therefore turned to other characters of the adults, such as male pleopod morphology (Guinot, 1967a, b, 1978; Williams, 1965; Martin and Abele, in press), or to larval characters (e.g., Rice, 1980; Martin, 1984), or characters of juveniles (Martin *et al.*, 1984) for elucidation of relationships in the *Panopeus* species complex. To what extent zoeal characters may themselves be modified convergently for a planktonic existence is unknown (see Martin *et al.*, 1984, and Felder *et al.*, in press), but it is generally accepted that larval characters are of some phylogenetic significance within the Brachyura, and that those cases of apparently convergent evolution among crab larvae (e.g., Williamson, 1982) are the exception rather than the rule.

Within the genus *Panopeus*, larvae are known only for *Panopeus herbstii* H. Milne Edwards, 1834, and *Panopeus turgidus* Rathbun, 1930 (see Martin, 1984). In addition, a late zoea attributed to *P. africanus* A. Milne Edwards, 1867, was described by Rice and Williamson (1977), and larvae described as *Panopeus* sp. were illustrated by Kurata (1970). The larvae attributed by Kurata (1970) to *Panopeus occidentalis* are probably those of *Hexapanopeus angustifrons* (Benedict and Rathbun, 1891) (see Martin *et al.*, 1984).

Panopeus bermudensis Benedict and Rathbun, 1891, is a small, cryptic xanthid known from the western Gulf of Mexico (Felder, 1973), both coasts of Florida, Bermuda, and the Bahamas south to Santa Catarina, Brazil, and along the west coast of America from Mexico to Peru (Camp *et al.*, 1977; Gore *et al.*, 1978; Rathbun, 1930). Lebour (1944a) described a first stage zoea from laboratory-hatched eggs of a crab she identified as *Panopeus bermudensis*. Rice (1980) noted that the larva of Lebour's *P. bermudensis* was exceptional amongst the majority of other Xanthinae larvae in having a well-developed antennal exopod typical of all known pilumnine larvae. The marked difference between the fourth zoeal stage of a *P. bermudensis* from south Texas (Martin *et al.*, 1984) and Lebour's (1944a) first zoea suggests that Lebour's identification of the parental female was incorrect. Unfortunately, neither adults nor larvae of Lebour's specimens are extant. The identifications of the parental *P. bermudensis* in our study are well established.

Table 1. Duration of larval stages of *Panopeus bermudensis* Benedict and Rathbun at 25°C.

Stage	Duration (days)				Died in molt	Number molting to next stage
	Minimum	Mean	Mode	Maximum		
Zoea I	4	5.3	5	7	—	8
Zoea II	3	3.3	3	4	—	6
Zoea III	3	3.2	3	4	—	6
Zoea IV	3 ¹	3.8	4	4	2	1 (to megalopa) 1 (to stage V)
Zoea V	6 ²	—	—	—	—	—
Megalopa	7 ²	—	—	—	—	—

¹ Molted to stage V.² Died in stage.

Additionally some of our larvae allowed to mature over a 2-year period exhibited established characters (notably gonopod and carapace morphology) of adult males of the species as described by Rathbun (1930), Monod (1956), and Felder (1973). The complete larval development of this species has never been described.

MATERIALS AND METHODS

Two ovigerous female *Panopeus bermudensis* were collected from rock jetties on South Padre Island, Cameron County, Texas, on 28 May 1979. In the laboratory, each crab was placed in a separate 10-cm diameter glass jar filled with artificial sea water of 30‰ salinity (Instant Ocean). The ovigerous females were kept under a 12 h photoperiod until hatching; temperature in the laboratory during this period ranged from 24–28°C. Eggs of one female hatched on 3 June 1979 and the larvae were cultured en masse. Eggs of the second female hatched on 7 June 1979; 12 of these larvae were reared in polystyrene trays, one zoea per compartment, and the remainder were reared en masse. Separate glass jars of 10-cm diameter were used for mass culture of larvae from each hatch. Mass cultures were kept under a 12 h photoperiod; temperature in the laboratory ranged from 26–28°C. The trays were placed in a constant temperature incubator at 25°C with a 12 h photoperiod. Artificial seawater (30‰) was changed daily in each tray compartment and in the mass-rearing jars. All larvae were fed freshly hatched brine shrimp nauplii (Brazilian source) daily. Exuviae, dead larvae, and a developmental series of larvae from the mass cultures were preserved in 70% ethanol. Larvae obtained from both ovigerous females were used in the descriptions. Drawings of the exuviae and of entire larvae were made with the aid of a compound microscope and camera lucida. Five individuals were examined at each stage and a minimum of two larvae per stage were dissected in glycerol. All setal counts are sequenced from proximal to distal. Measurement of the carapace length is from the orbit to the posterior carapace border.

Parental females and larval series are deposited in the Zoological Collection of the University of Southwestern Louisiana; duplicates from the larval series are deposited in the National Museum of Natural History, Washington, D.C., USNM No. 216756.

REARING RESULTS

No prezoae were observed. Four zoeal stages and a single megalopa were routinely obtained, although one tray-reared zoea IV molted to a fifth stage in which it died (Table 1). This aberrant fifth stage was larger than any zoea IV and had chelate first pereopods, setose pleopods, and a distorted carapace; we feel that this was an unsuccessful attempt to molt to the megalopal stage and that four zoeal stages followed by a megalopa is the normal sequence.

Survival amongst the tray-reared larvae was poor, but one individual reached megalopa after 14 days and two others died while molting from zoea IV to megalopa, 14 and 16 days, respectively, after hatching (Table 1). No first crabs were obtained. Some larvae reared en masse from the 3 June 1979 hatch reached megalopa in 12 days and first crab in 18 days; several of these first crabs subsequently reached maturity in the laboratory. Larvae reared en masse from the 7 June 1979 hatch reached only zoea III.

DESCRIPTION OF THE LARVAE

First Zoea

Size.—Carapace length (CL) 0.35 mm; tip of dorsal carapace spine (DS) to tip of rostral spine (RS) 1.30 mm.

Carapace (Fig. 1A).—Cephalothorax smooth, weakly calcified, slightly globose, with extremely long rostrum (twice length of carapace) and elongate posteriorly directed dorsal spine (longer than carapace). No lateral spines in this or subsequent stages. Minute setae occasionally present on posterolateral borders.

Abdomen (Fig. 1A, G).—Five somites, all with pair of minute dorsolateral setae; somites 2 and 3 with distinct lateral knobs.

Telson (Fig. 1A, B, G).—Trapezoidal, with long slender furcae recurved dorsally at distal tip; posterior margin with 3 pairs of stout serrate setae; furcae with single dorsal spine located about two-thirds distance from base to posterior tip.

Antennule (Fig. 1D).—Stout, conical, with 3 or 4 aesthetascs of different lengths.

Antenna (Fig. 1F).—Protopod subequal to rostrum in length, unarmed, tapering distally but terminating in slightly dilated distal tip; exopod and endopod absent.

Mandible.—Not examined.

Maxillule (Fig. 1C).—Endopod 2-segmented, short proximal article with 1 long plumose seta, elongate distal article with 2 subterminal and 4 terminal plumose setae; basal endite with 4 or 5 serrate spines and 1–3 plumose setae; coxal endites with 6–8 stout plumose setae.

Maxilla (Fig. 1E).—Endopod bilobed, with 3 + 5 setae; scaphognathite with 4 plumose setae and setose terminal process; basal endite bilobed with 3 + 3 plumose setae; coxal endite bilobed with 4 + 3 setae as illustrated.

Maxilliped 1 (Fig. 1H).—Basis with 9 or 10 plumose ventral setae arranged in groups of 2 or 3; endopod 5-segmented, setation 3, 2, 1, 2, 4; exopod with 4 natatory setae.

Maxilliped 2 (Fig. 1I).—Basis with 3 plumose setae; endopod 3-segmented, setation 1, 1, 3; exopod with 4 natatory setae.

Second Zoea

Size.—CL 0.42 mm, tip of DS to tip of RS 1.60 mm.

Carapace (Fig. 2A).—As in first stage but with posterolateral border less pronounced; DS more erect.

Abdomen (Fig. 2A, F).—As in first stage but posterolateral knobs more pronounced; knob on somite 2 distinctly larger than that on somite 3.

Telson (Fig. 2A, B, F).—As in first stage but median sinus slightly deeper and narrower.

Antennule (Fig. 2D).—More ovate basally than in first stage and with 5 aesthetascs of unequal lengths.

Antenna (Fig. 2E).—As in first stage; endopod now present as small basal protuberance; exopod absent.

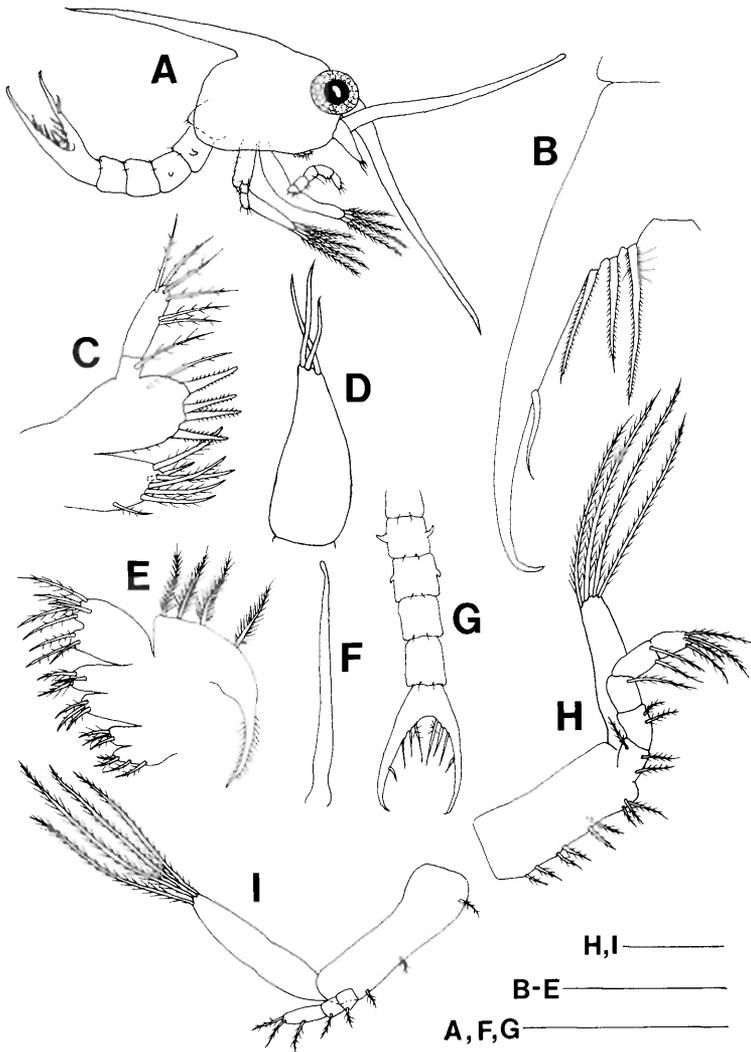


Fig. 1. *Panopeus bermudensis*, first zoea. A, lateral view; B, telsonal furca; C, maxillule; D, antennule; E, maxilla; F, antenna; G, abdomen; H, first maxilliped; I, second maxilliped. Scale = 0.1 mm for B, C and H, I; 0.5 mm for A, F, G.

Mandible.—Not examined.

Maxillule (Fig. 2C).—Endopod as in first stage; basal endite with 5 serrate spines and 5 or 6 plumose setae plus 1 long basal plumose seta; coxal endite with 7–9 plumose setae.

Maxilla (Fig. 2G).—Endopod as in first stage, scaphognathite with 9 plumose setae and pubescent terminal process; basal endite proximal and distal lobes with 4 and 3 setae, respectively; coxal endite proximal and distal lobes with 5 and 4 setae, respectively.

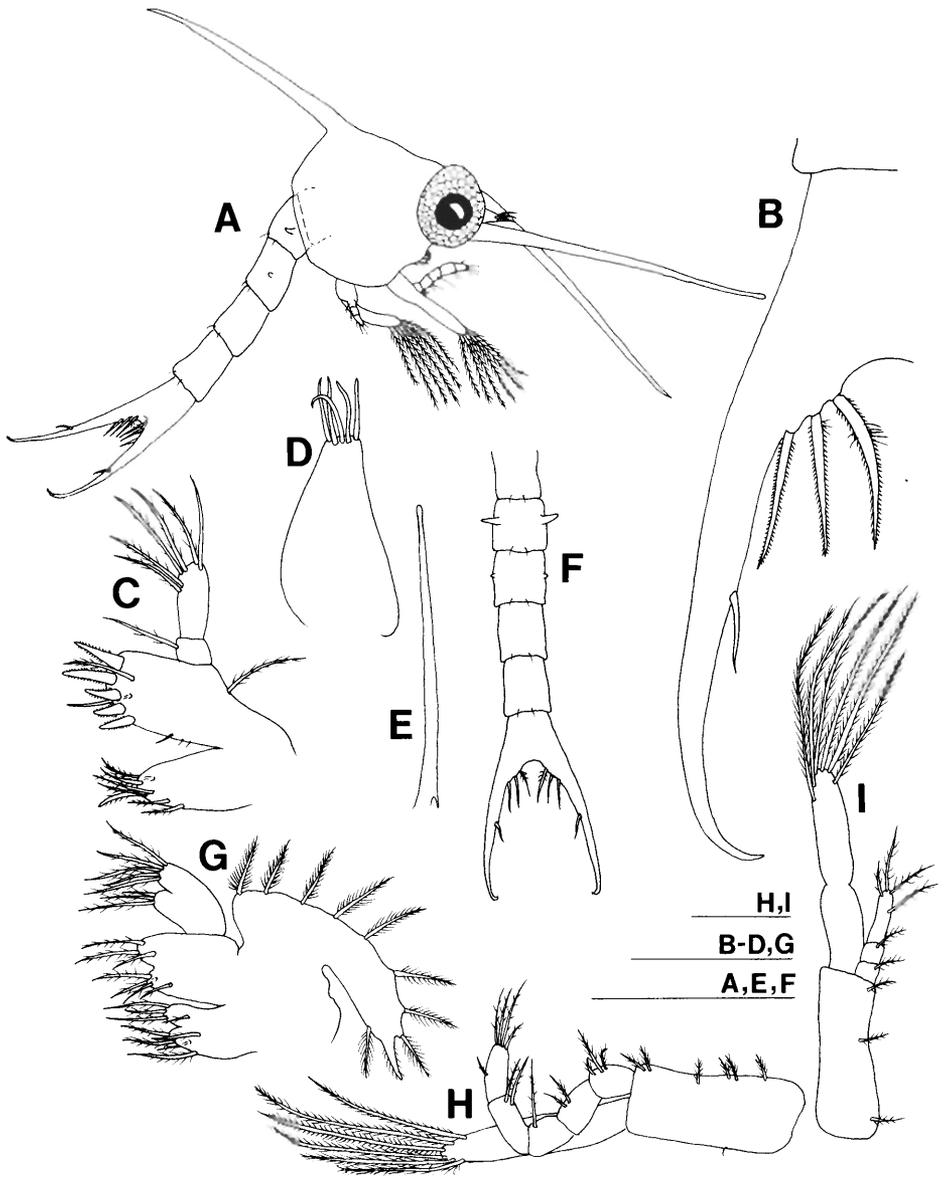


Fig. 2. *Panopeus bermudensis*, second zoea. A, lateral view; B, telsonal furca; C, maxillule; D, antennule; E, antenna; F, abdomen; G, maxilla; H, first maxilliped; I, second maxilliped. Scale = 0.1 mm for B-D and G-I; 0.5 mm for A, E, F.

Maxilliped 1 (Fig. 2H).—Basis with 6 or 7 setae; endopod 5-segmented, setation 3, 2, 1, 2, 4 + 1; exopod with 6 natatory setae.

Maxilliped 2 (Fig. 2I).—Basis with 3 plumose setae; endopod 3-segmented, setation 1, 1, 3 + 1; exopod with 6 natatory setae.

Third Zoea

Size.—CL 0.50 mm; tip of DS to tip of RS 2.40 mm.

Carapace (Fig. 3B).—As in previous stages but with 5 or 6 short setae bordering posterolateral margin.

Abdomen (Fig. 3B, I).—Six somites; somites 2-6 with pair of minute dorsolateral setae; lateral knobs on somites 2 and 3; somite 6 approximately one-half length of somites 4 and 5; pleopod buds on somites 2-6.

Telson (Fig. 3B, D, I).—As in previous stages but with fourth pair of short setae on posterior margin within medial sinus.

Antennule (Fig. 3E).—As in previous stages but with 4 long and 2 short aesthetascs.

Antenna (Fig. 3H).—As in previous stage; endopod slightly larger.

Mandible.—Not examined.

Maxillule (Fig. 3A).—Endopod as in previous stages; basal endite with 4 or 5 serrate spines and 3-5 plumose setae; coxal endite with 6 or 7 stout plumose setae.

Maxilla (Fig. 3F).—Endopod as in previous stages; scaphognathite with 15 or 16 plumose setae; basal endite proximal and distal lobes with 3 + 1 and 4 + 1 setae, respectively; coxal endite with 4 + 4 setae.

Maxilliped 1 (Fig. 3C).—Basis with 9 or 10 setae; endopod unchanged; exopod with 8 natatory setae.

Maxilliped 2 (Fig. 3G).—Basis with 3 setae; endopod unchanged; exopod with 8-10 natatory setae.

Fourth Zoea

Size.—CL 0.72 mm; carapace width (CW) 0.5 mm; tip of DS to tip of RS 2.85 mm.

Carapace (Fig. 4B, C).—CL less than DS which is less than RS; 8-10 short setae on posterolateral border.

Abdomen (Fig. 4B, H).—Somites 2 and 3 with dorsolateral knobs, those of somite 3 very small; paired dorsolateral setae on somites 2-6, scattered dorsal setae now on somites 2 and 3; pleopod buds slightly larger than in previous stage.

Telson (Fig. 4G, H).—Unchanged from previous stage.

Antennule (Fig. 4F).—Aesthetascs arranged in tiers: 1 or 2, 4, 3 long plus 1 short; endopod bud present.

Antenna (Fig. 4D).—As in previous stages but with endopod larger, nearly one-eighth length of protopod.

Mandible.—Not examined.

Maxillule (Fig. 4A).—Endopod unchanged; basal endite with 4 or 5 strong serrate spines and 6 or 7 plumose setae; coxal endite with 9 or 10 spines and setae.

Maxilla (Fig. 4E).—Endopod bilobed with 3 + 5 setae, those on distal lobe in

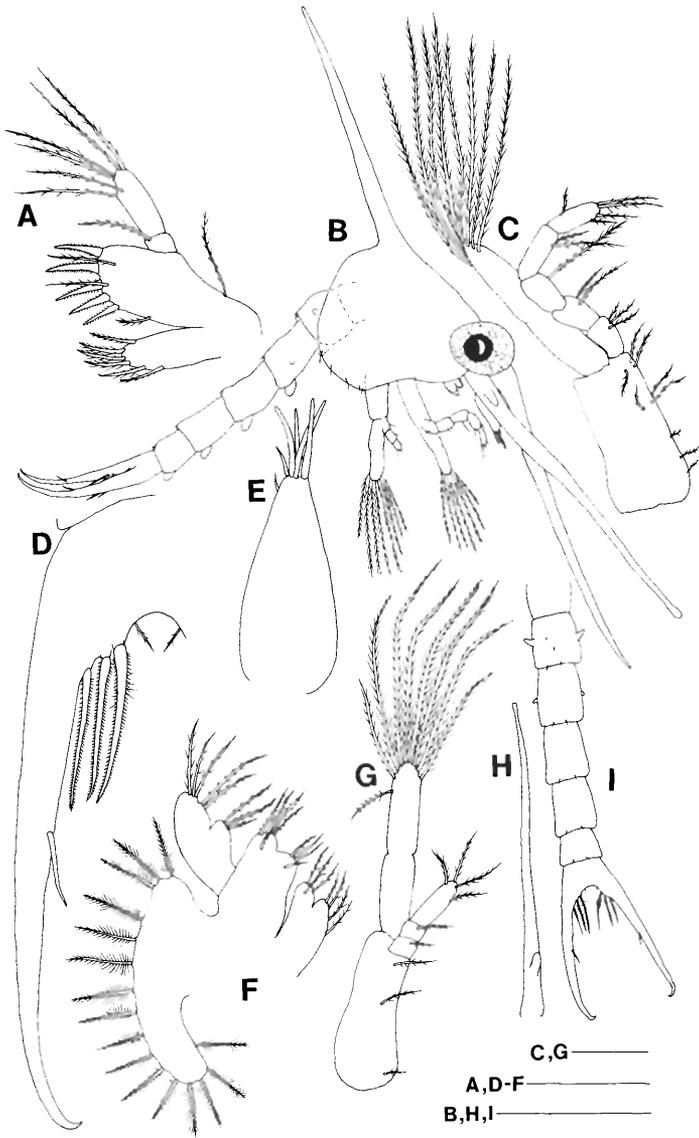


Fig. 3. *Panopeus bermudensis*, third zoea. A, maxillule; B, lateral view; C, first maxilliped; D, telsonal furca; E, antennule; F, maxilla; G, second maxilliped; H, antenna; I, abdomen. Scale = 0.1 mm for A and C-F; 0.5 mm for B, H, I.

groups of 2 and 3; scaphognathite with 21–23 plumose setae; basal endite proximal and distal lobes with 4 + 1 and 6 + 1 setae, respectively; coxal endite proximal and distal lobes both with 4 or 5 setae.

Maxilliped 1 (Fig. 4I).—Basis with 7 or 8 setae; endopod setation 3, 2, 1, 2, 4 + 1 + 1; exopod with 8 natatory setae.

Maxilliped 2 (Fig. 4J).—Basis with 2 or 3 setae; endopod setation 1, 1, 4 + 1; exopod with 10 or 11 natatory setae.

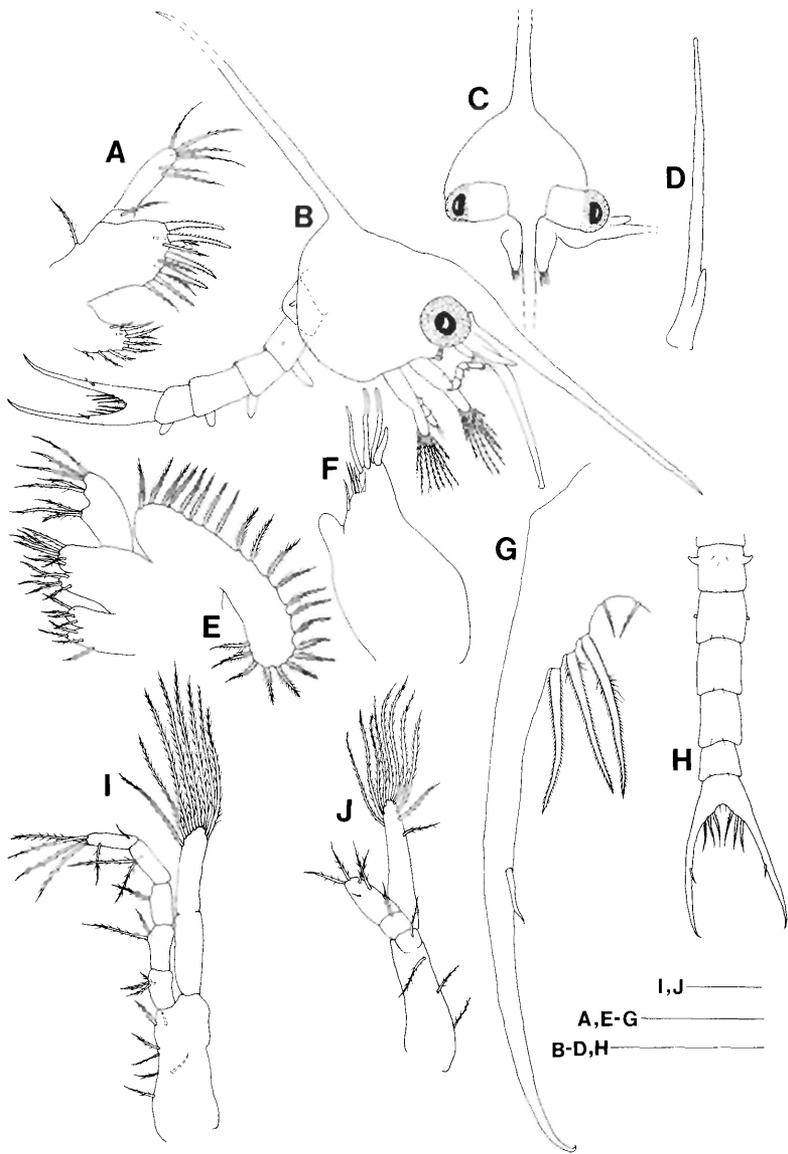


Fig. 4. *Panopeus bermudensis*, fourth zoea. A, maxillule; B, lateral view; C, frontal view; D, antenna; E, maxilla; F, antennule; G, telsonal furca; H, abdomen; I, first maxilliped; J, second maxilliped. Scale = 0.1 mm for A, E-G, and I, J; 0.5 mm for B-D, H.

Megalopa

Size.—CL 0.88 mm, CW 0.70 mm, total length (TL) 1.66 mm.

Carapace (Fig. 5A).—Subquadrate, frontal region with slight medial depression anteriorly, sharp anterolateral horns, rostrum blunt; short setae over broad posterolateral evaginations.

Abdomen (Fig. 5A).—Six somites plus telson, all covered sparsely with minute setae.

Telson (Fig. 5B).—Subquadrate with posterior angles rounded; 4 dorsal setae.

Antennule.—Not examined.

Antenna (Fig. 5C).—Antennae 11-segmented, setation 2, 1, 1 or 0, 0, 0, 2 or 3, 0, 4, 0, 4, 4; demarcation between flagellum and peduncle unclear.

Mandible (Fig. 6F).—Asymmetrical with asymmetrically lunate cutting edge with mucronate tip; palp 2-segmented, setation 0, 7 or 8.

Maxillule (Fig. 6E).—Protopod area with 1 or 2 long plumose setae; endopod 2-segmented, setation 2, 3; basal endite with 21 or 22 cuspidate spines and serrate setae; coxal endite with 12 or 13 spines and setae.

Maxilla (Fig. 6D).—Endopod with 1 or 2 plumose subterminal setae; scaphognathite with 40–44 fringing setae; basal endite setation 5 or 6 + 8 or 9; coxal endite setation 6 or 7 + 4 or 5.

Maxilliped 1 (Fig. 6C).—Exopod 2-segmented, setation 2, 5; endopod unsegmented, with 2 or 3 setae; basal endite with 17–19 setae; coxal endite with 9 or 10 setae; epipod with 5 or 6 long naked setae.

Maxilliped 2 (Fig. 6B).—Exopod 2-segmented, setation 2, 5 or 6; endopod 4-segmented, setation 1 or 2, 1, 6, 8 or 9; epipod not seen.

Maxilliped 3 (Fig. 6A).—Exopod 2-segmented, setation 2, 5 or 6; endopod 4-segmented, setation 16–18, 4–6, 8, 7 or 8; epipod with 4 setae plus 12 or 13 long naked setae.

Pereiopods.—Chelipeds (Fig. 5G) with large ischial recurved hook and 4 or 5 irregular teeth on fingers, borders of fingers slightly corneous; dactyl of pereiopod 3 (Fig. 5D) with 3 strong serrate ventral spines and 1 subterminal dorsal spine; dactyl of pereiopod 5 (Fig. 5E) with 1 dorsal spine and 1 short terminal seta.

Pleopod 3 (Fig. 5F).—Thirteen natatory setae, endopod with 3 hooked setae.

DISCUSSION

Zoal Characters of the Genus *Panopeus* and its Allies

Although larvae are known for only three species of the genus *Panopeus* H. Milne Edwards, larval descriptions are available for some members of other closely related genera. The genera *Eurytium* Stimpson, *Eurypanopeus* A. Milne Edwards, *Hexapanopeus* Rathbun, *Rhithropanopeus* Rathbun, *Neopanope* A. Milne Edwards, and *Micropanope* Stimpson (sensu lato) have at various times been placed together in one complex, section, or subfamily of the Xanthidae. All of these genera are morphologically similar as adults, and distinction of species within them has proved difficult. Larvae are known for only 14 species in this complex (Table 2), so that any conclusions drawn from the available data must be viewed with some caution, at least until larval descriptions of more genera and species become available. However, some generalizations apply to most of these larvae.

The antennal exopod in all species is reduced (less than one-fourth the length of the spinous process) or absent, and armed with 2 or fewer short terminal setae (except in *Micropanope* sensu lato). Rostral, dorsal, and lateral carapace spines

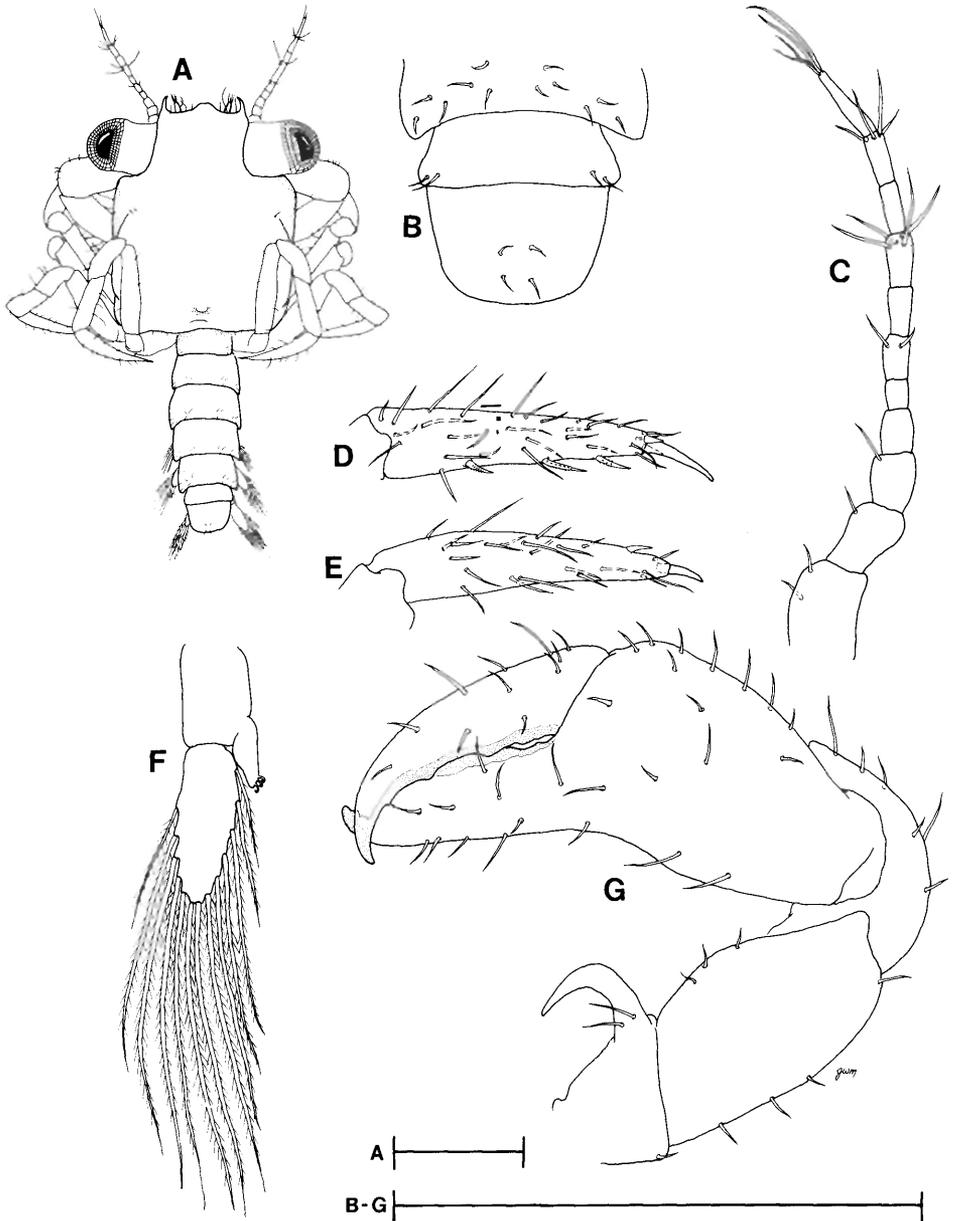


Fig. 5. *Panopeus bermudensis*, megalopa. A, dorsal view; B, telson and abdominal somites 5 and 6; C, antenna; D, dactylus of pereopod 3; E, dactylus of pereopod 5; F, pleopod 3; G, cheliped. Scale = 0.5 mm.

are all well developed, and the rostral spine is subequal to the antennal spinous process. Dorsolateral knobs are found on the second and third abdominal somites, but not on the more posterior somites, with two exceptions: zoeae of *Rhithropanopeus harrisi* have a dorsolateral knob on the second abdominal somite only

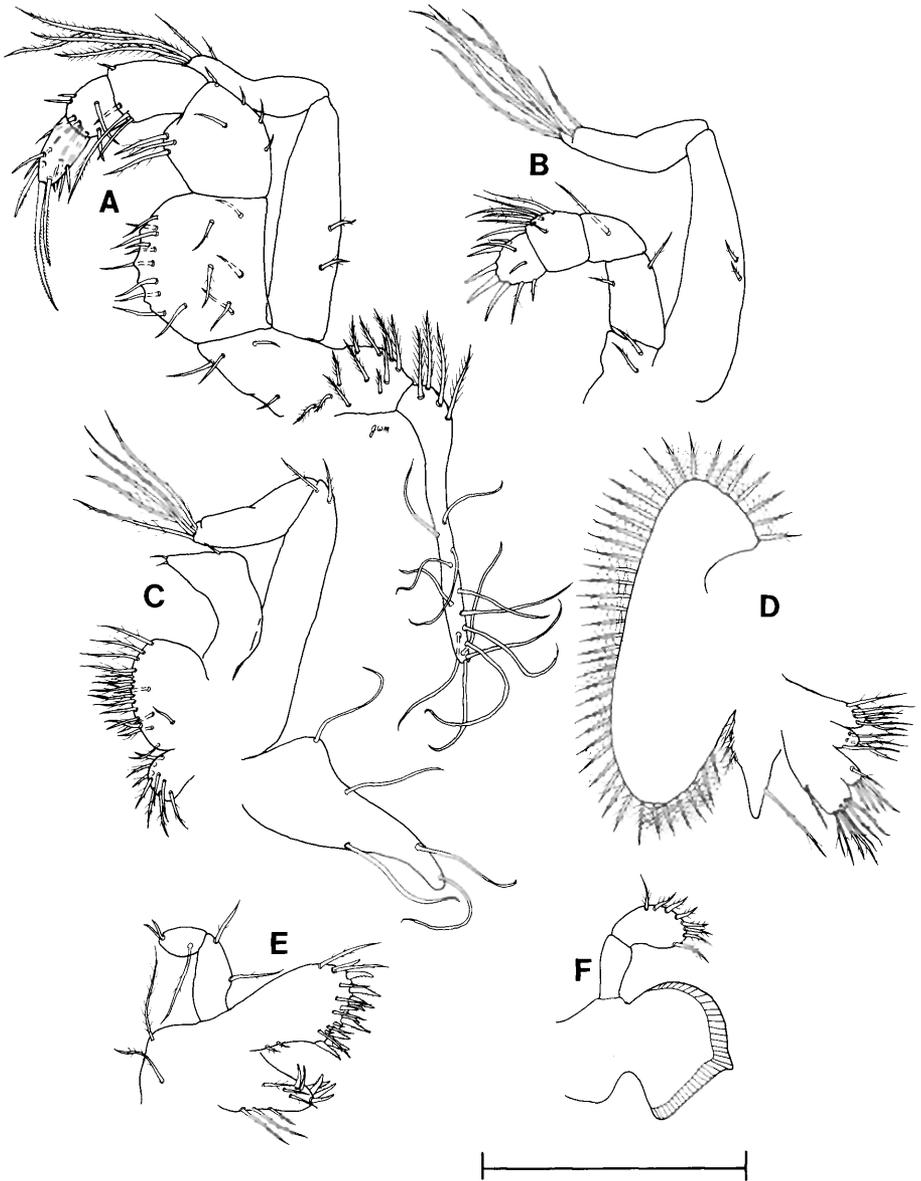


Fig. 6. *Panopeus bermudensis*, megalopa mouthparts. A, maxilliped 3; B, maxilliped 2; C, maxilliped 1; D, maxilla; E, maxillule; F, mandible. Scale = 0.25 mm.

(see Fig. 7C), and the larvae of an unidentified species of *Panopeus* (see Kurata, 1970) have knobs on abdominal somites 2–5. The distal segment of the endopod of the maxillule in all species bears 6 setae of which 2 are subterminal, and the endopod of the maxilla always has 8 setae in groups of 3 and 5. The proximal, or first segment of the endopod of the first maxilliped bears 3 setae (2 in *Micropanope* sensu lato), and that of the endopod of the second maxilliped bears a single seta.

Rice (1980) used these characters to define a distinct group of xanthid larvae, which included the genus *Panopeus* and its allies, as well as all other species in the subfamily Xanthinae of Balss (1957). There are three exceptions. One was the zoea designated as *Panopeus bermudensis* by Lebour (1944a) (see Fig. 7G). That zoea differs from the Group I xanthid zoeae of Rice (1980) and Martin (1984) in having an antennal exopod (1) equal to or longer than the spinous process and (2) with a prominent outer seta about halfway along its length. It now seems that Lebour's specimen was misidentified. The antennal exopod, rostrum, and median telsonal indentation are all typical of a separate group of xanthid zoeae which contains the genus *Pilumnus* Leach and its allies (e.g., Fig. 7K); Martin (1984) lists Lebour's zoeal description with other known descriptions of *Pilumnus* larvae.

By removing Lebour's description of "*P. bermudensis*" from the Group I xanthid larvae of Rice (1980) a seemingly contradictory example is eliminated. However, our description of the larvae of *P. bermudensis* introduces a new problem. All previously known larvae of the genus *Panopeus* and its allies, and even less closely related members of the Xanthinae, have well-developed lateral carapace spines (compare Figs. 7C and I with 7D). These are absent in all zoeal stages of *P. bermudensis*. Furthermore, no other known xanthid zoea has a telsonal furca that bears spines so far posterior as in *P. bermudensis*. These characters led Martin (1984) to postulate a separate xanthid zoeal group, Group VI, to accommodate this species. However, other characters of larvae of *P. bermudensis* are quite similar to those of other species in the *Panopeus* complex, and it is probable that the lack of lateral carapace spines as well as the loss of an antennal exopod are derived character states. Rice (1980) noted that the lack of lateral carapace spines does not always seem to be significant, since they are absent in *Heteropanope glabra* (see Aikawa, 1929) but are present in *H. serratifrons* (see Wear, 1968). Thus, larval characters of *P. bermudensis* may not be as atypical of the genus *Panopeus* as would be the characters of Lebour's "*P. bermudensis*."

Among the remaining larval descriptions of *Panopeus* and its allies (Table 2), systematic relationships are little clarified by zoeal morphology. For example, larvae of the genera *Panopeus* and *Eurytium* are indistinguishable at the first zoeal stage (Martin, 1984), and variation of telsonal armature within the genus *Lophopanopeus* encompasses the range of characters seen in telsons of *Panopeus*, *Eurytium*, *Eurypanopeus*, and *Neopanope*. However, zoeal evidence does not appear to support Guinot's (1967a) restriction of the genus *Micropanope*, as discussed by Martin (1984).

Zoeal Characters and Adult Classification in the Family Xanthidae MacLeay, 1838

Despite the large size of the family Xanthidae, there have been surprisingly few attempts to subdivide it into sections or subfamilies. Schemes for subdivision of the Xanthidae have been proposed by Dana (1852), Alcock (1898), A. Milne Edwards (1862), Ortmann (1893), Balss (1957), and most recently by Guinot (1978).

Few of the workers mentioned above had access to data from xanthid larvae for their proposed classifications. Despite larval descriptions of about 80 xanthid species (Martin, 1984), the gap between knowledge of adult and larval morphology is extensive. However, the lack of adequate numbers of detailed xanthid larval descriptions has not precluded various workers from commenting on the phylogenetic implications of xanthid larvae.

The contributions of earlier workers such as Hyman (1925), Aikawa (1929,

Table 2. Distinguishing characters of zoea larvae in the *Panopeus* species complex.

Species (source of description)	Rostrum	Antennal protopod	Antennal exopod	Carapace spination	Telson furca spination	Abdominal somite armature	Basal segment of endopod, Mxp 1
<i>Panopeus bermudensis</i> (present study)	smooth, ~2 × carapace length	smooth, slightly dilated at tip	absent	lateral spines absent	furca smooth; 1 dorsal spine posteriorly	lateral knobs on somites 2 and 3; no sharp posterolateral processes	3 setae
<i>Panopeus herbstii</i> (Costlow and Bookhout, 1961a)	smooth, ≅ carapace length	spinous distally	minute, with apical seta	well-developed rostral, dorsal, and lateral spines	furca smooth; 1 dorsal, 2 lateral spines	lateral knobs on somites 2 and 3; sharp posterolateral processes on somites 3-5	3 setae
<i>Panopeus turgidus</i> (Martin <i>et al.</i> , 1984)	smooth, ≅ carapace length	spinous distally	minute, with apical seta	well-developed rostral, dorsal, and lateral spines	furca smooth; 1 dorsal, 2 lateral spines	lateral knobs on somites 2 and 3; sharp posterolateral processes on somites 3-5	3 setae
<i>Panopeus ?africanus</i> (ASM 27) (Rice and Williamson, 1977)	smooth, ≅ carapace length	spinous distally	minute, with apical seta	well-developed rostral, dorsal, and lateral spines	furca minutely spinulose; 1 dorsal, 2 lateral spines	lateral knobs on somites 2 and 3; sharp posterolateral processes on somites 3-5	3 setae
<i>Panopeus</i> sp. (Kurata, 1970)	smooth, ≅ carapace length	spinous distally	minute, with apical seta	well-developed rostral, dorsal, and lateral spines	furca smooth; 1 dorsal, 2 lateral spines	lateral knobs on somites 2-5; sharp posterolateral processes on somites 3-5	3 setae
<i>Eurypanopeus depressus</i> (Costlow and Bookhout, 1961b)	smooth, ~1.5 × carapace length	spinous distally	minute, with apical seta	well-developed rostral, dorsal, and lateral spines	furca smooth; 1 dorsal spine	lateral knobs on somites 2 and 3; sharp posterolateral processes on somites 3-5	3 setae

Table 2. Continued.

Species (source of description)	Rostrum	Antennal protopod	Antennal exopod	Carapace spination	Telson furca spination	Abdominal somite armature	Basal segment of endopod, Mxp 1
<i>Hexapanopeus angustifrons</i> (Costlow and Bookhout, 1966)	smooth, ~1.5 × carapace length	smooth	minute process	well-developed rostral, dorsal, and lateral spines	furca smooth; unarmed	lateral knobs on somites 2 and 3; sharp posterolateral processes on somites 3–5	3 setae
<i>Rhithropanopeus harrisi</i> (Chamberlain, 1962)	smooth, ~2 × carapace length	smooth	minute process	well-developed rostral, dorsal, and lateral spines	furca smooth; 1 dorsal spine	lateral knobs on somite 2; sharp posterolateral processes on somites 4 and 5, pronounced	2 or 3 setae
<i>Dyspanopeus texana</i> * (McMahan, 1967)	smooth, ≈ carapace length	smooth	minute, with apical seta	well-developed rostral, dorsal, and lateral spines	furca smooth; 1 dorsal spine	lateral knobs on somites 2 and 3; sharp posterolateral processes on somites 3–5	3 setae
<i>Dyspanopeus sayi</i> * (Chamberlain, 1961)	smooth, ~2 × carapace length	smooth	minute, with apical seta	well-developed rostral, dorsal, and lateral spines	furca smooth; 1 dorsal spine	no lateral knobs; blunt posterolateral processes on somites 3–5	3 setae
<i>Neopanope packardii</i> (Costlow and Bookhout, 1967)	smooth, ≈ carapace length	spinous distally	minute process	well-developed rostral, dorsal, and lateral spines	furca smooth; 1 dorsal spine	lateral knobs on somites 2 and 3; sharp posterolateral processes on somites 3–5	3 setae
<i>Eurytium limosum</i> (Kurata <i>et al.</i> , 1981)	smooth, ≈ carapace length	spinous distally in first zoea only	minute, with apical seta	well-developed rostral, dorsal, and lateral spines	furca smooth; 1 dorsal, 2 lateral spines (only 1 lateral in zoea 2–4)	lateral knobs on somites 2 and 3; sharp posterolateral processes on somites 3–5	not figured

Table 2. Continued.

Species (source of description)	Rostrum	Antennal protopod	Antennal exopod	Carapace spination	Telson furca spination	Abdominal somite armature	Basal segment of endopod, Mxp 1
<i>Micropanope sculpipes</i> (Andryszak and Gore, 1981)	smooth, \cong carapace length	spinous	reduced ($< \frac{1}{6}$ protopod), 1 apical spine, 3 apical setae	well-developed rostral, dorsal, and lateral spines	furca smooth; 1 dorsal, 1 lateral spine	lateral knobs on somites 2 and 3; sharp posterolateral processes on somites 3-5	2 setae
<i>Micropanope barbadosis</i> † (Gore et al., 1981)	smooth, \cong carapace length	spinous	reduced ($< \frac{1}{4}$ protopod), 2 or 3 apical setae plus 1 spinule	well-developed rostral, dorsal, and lateral spines	furca smooth; 2 dorsal, 1 lateral spines	lateral knobs on somites 2 and 3; sharp posterolateral processes on somites 3-5	2 setae

* Transferred from the genus *Neopanope* by Martin and Abele (in press).

† Removed from the genus *Micropanope* by Guinot (1967a); currently without an assigned genus.

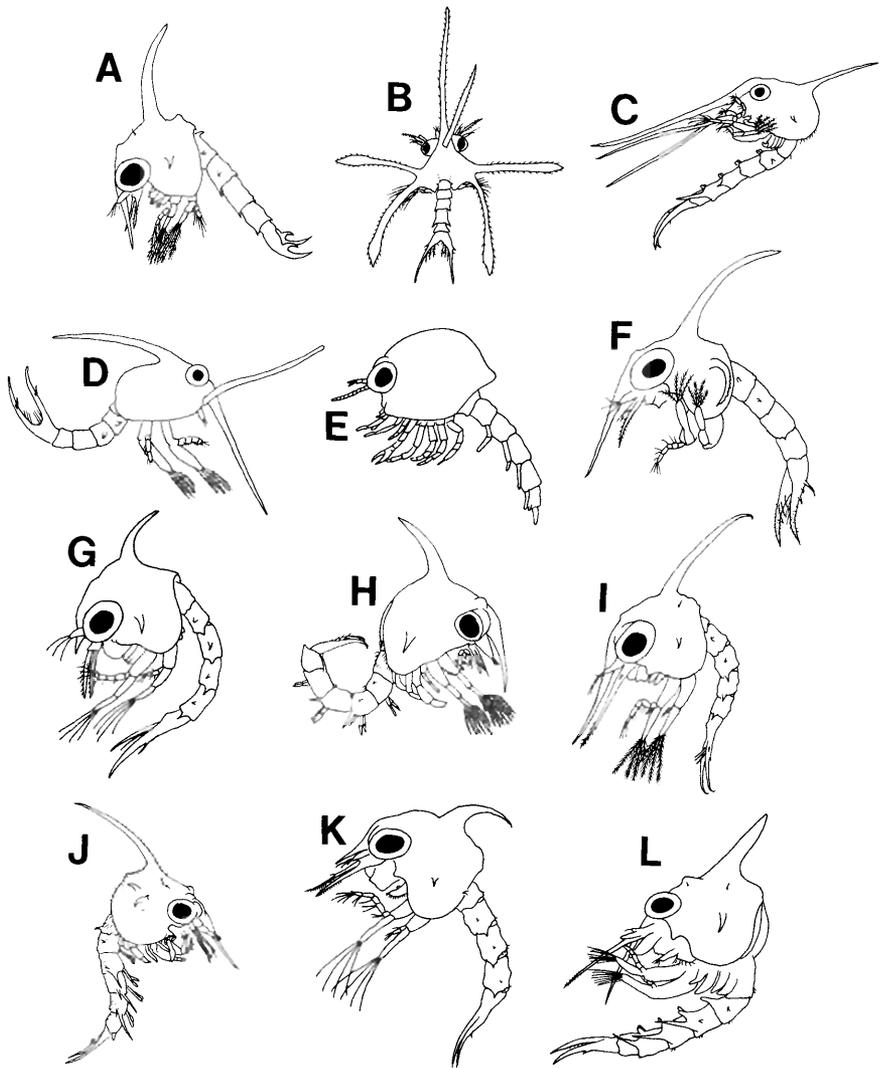


Fig. 7. Some examples of the diversity of carapace and abdomen morphology among xanthid zoeae. A, *Ozius truncatus* A. Milne Edwards (after Wear, 1968); B, *Tetralia* sp. (after George and John, 1975); C, *Rhithropanopeus harrisi* (Gould) (after Connolly, 1925); D, *Panopeus bermudensis* Benedict and Rathbun (present study); E, *Pilumnus lumpinus* Bennett (after Wear, 1967); F, *Pilumnoides perlatus* (Poeppig) (after Fagetti and Campodonico, 1973); G, *?Pilumnus* sp. (after Lebour, 1944a [as *Panopeus bermudensis*]); H, *Menippe nodifrons* Stimpson (after Scotto, 1979); I, *Eurytium limosum* (Say) (after Kurata *et al.*, 1981); J, ASM 26 (probably Trapeziinae) (after Rice and Williamson, 1977); K, *Pilumnus holosericus* Rathbun (after Kurata, 1970 [as *Pilumnus* sp.]); L, *Leptodius exaratus* (H. Milne Edwards) (after Fielder *et al.*, 1979). Not drawn to scale.

1933, 1937), Lebour (1928, 1944b), Wear (1970), and Hashmi (1970) are briefly discussed by Rice (1980) and Martin (1984). Several of these workers (and also Gurney, 1938) noted that zoeal groupings based on morphology of the antennal exopod and on telsonal and carapacial spines did not closely correspond to classifications based on adult characters. One reason for these discrepancies is the

fact that telsonal, and especially carapacial, morphology and spination vary greatly among xanthids (see Fig. 7); larvae of even congeneric species often differ markedly in characters of the carapace. But morphology of the antennal exopod varies much less than does carapacial morphology; consequently many workers have employed this character in separating xanthid larvae.

Rice (1980) established four xanthid zoal groups on the basis of traditional characters, such as morphology of the antennal exopod, and on previously unused characters, such as the setation of the mouthparts. Martin (1984) added two more xanthid zoal groupings to accommodate larvae of *Micropanope* (sensu lato) and *Panopeus bermudensis*, although the latter will herein be reassigned. Thus, there are six groups of xanthid larvae currently recognized. Group I contains larvae of the genera *Atergatis*, *Cataleptodius*, *Chlorodiella*, *Cycloxanthops*, *Cymo*, *Dyspanopeus*, *Etisus*, *Eurypanopeus*, *Eurytium*, *Heteractaea*, *Heterozius*, *Hexapanopeus*, *Leptodius* [but not the apparent pilumnine zoea assigned to *L. parvulus* by Lebour (1944a)], *Lophopanopeus*, *Medaeus*, *Neopanope*, *Panopeus* [but, prior to the present paper, not *P. bermudensis* as assigned by Martin (1984)], *Pilodius*, *Paraxanthias*, *Pseudomadaeus*, *Rhithropanopeus*, *Xantho*, and *Xanthodius*; the most obvious character of this group is the greatly reduced antennal exopod. Group II contains the genera *Actumnus*, *Eurycarcinus*, *Heteropanope*, *Heteropilumnus*, *Lobopilumnus*, *Pilumnopoeus*, and *Pilumnus*, zoeae of which possess a well-developed spinulose antennal exopod about equal to or slightly longer than the spinous process and with a prominent outer seta about halfway along its length. Group III contains the genera *Baptozius*, *Carpilius*, *Epixanthus*, *Eriphia*, *Homalaspis*, *Ozius*, *Pilumnoides*, *Platyxanthus*, *Tetralia*, and *Trapezia*, all of which have a robust antennal exopod about half the length of the spinous process and armed with three unequal terminal setae. Group IV consists of the genera *Menippe* and *Sphaerozius*, and differs from the other groups in that the antennal exopod is about half the length of the spinous process and tipped with two unequal setae; in addition the setation of the mouthparts is reduced. Group V contains only the genus *Micropanope* (sensu lato, not sensu Guinot, 1967a), zoeae of which possess a reduced antennal exopod that bears three terminal setae, and which bear only two setae on the basal segment of the first maxilliped. Group VI was established by Martin (1984) to accommodate larvae of *P. bermudensis*, which lack lateral carapace spines and an antennal exopod; however, we herein propose to abandon recognition of Group VI as a distinct group, and to assign *P. bermudensis* to Group I. Additional characters which define or distinguish these larval groupings are given by Martin (1984).

Rice (1980: 328) and Martin (1984) lamented the fact that these larval groupings do not closely correspond to Balss's (1957) division of the Xanthidae into four subfamilies. Rice suggested that this discrepancy might lend some support to Guinot's (1978) more complex division of the family. However, larval evidence for Balss's subfamilies is not entirely lacking, especially in context of our present findings. It now appears that all larvae known for species in Balss's subfamily Xanthinae belong to Group I. This conclusion requires that we account for three exceptions previously mentioned by Rice: *Panopeus bermudensis* and *Leptodius parvulus* as described by Lebour (1944a) and *Homalaspis plana* as described by Fagetti Guiata (1960, 1970).

We have shown that Lebour's "*P. bermudensis*" zoea is most probably a misidentified pilumnine larva; this also appears to be the case for larvae she assigned to "*Leptodius parvulus*" [now *Xanthodius parvulus* (Fabricius)]. The larvae of *Xanthodius denticulatus* (White) were described by Lebour (1944a) and have as expected Group I xanthid form, but the larvae described by Lebour as "*Leptodius*

parvulus" are clearly of the Group II xanthid form; the latter have an elongate antennal exopod and reduced rostrum, and therefore are most probably allied to the genus *Pilumnus* Leach. In our opinion, the parental female designated as "*Leptodius parvulus*" was probably misidentified.

The genus *Homalaspis* was included by Guinot (1977) in the family Platyxanthidae. Although the more extensive subdivisions of the Xanthidae (sensu lato) by Guinot (1978) have not been accepted by most modern workers, it is generally accepted that the genera *Homalaspis*, *Platyxanthus*, and *Pelaeus* are indeed deserving of distinct familial status (Manning and Holthuis, 1981; Abele and Felgenhauer, 1982).

Thus, all three exceptions to the Group I xanthid larvae (*Panopeus bermudensis*, *Leptodius parvulus*, and *Homalaspis plana*) can be explained as probable misidentifications of parental adults (*P. bermudensis* and *L. parvulus*) or incorrect subfamilial assignment on the basis of adult characters (*H. plana*). This being so, the definition of the subfamily Xanthinae of Balss (1957) on the basis of adult characters is now largely in accord with a grouping based upon larval characters. Agreement between larval groupings and the remaining three subfamilies of Balss is not so clear. Among the Pilumninae of Balss is the genus *Eurytium*, the larvae of which conform to the Group I xanthids (Kurata et al., 1981). However, *Eurytium* was removed from the Pilumninae by Guinot (1978) and included in her Panopeidae; the remaining pilumnine genera (the Pilumnidae of Guinot) have larvae of the Group II form. The subfamilies Menippinae and Trapeziinae of Balss (1957) do not closely agree with any larval groupings, since the Menippinae of Balss contains genera with Group III larvae (*Baptozius*, *Eriphia*, and *Ozius*) as well as the two genera known to have Group IV larvae (*Menippe* and *Sphaerozius*).

Although Rice (1980) noted that insufficient larvae have been described to allow an examination of the zoeal evidence for the more complex subdivisions of the Xanthidae (sensu lato) by Guinot (1978), he also noted that some of Guinot's groupings were definitely not supported by larval evidence. Specifically, Rice noted that larvae of the *Panopeus* complex (Guinot's Panopeidae) do not sufficiently differ from larvae of the remaining Xanthinae (Guinot's restricted Xanthidae) to warrant separate familial status for these groups. But Rice also noted that there is larval evidence to separate *Homalaspis* from the remainder of Balss's Xanthinae, so that Guinot's removal of that genus to her newly created Platyxanthidae (see Guinot, 1977) appears justified.

Finally, we feel that the larval characters of *Panopeus bermudensis* as described herein do not warrant separate generic placement or recognition of a separate larval group as was suggested by Martin (1984). Rather, we feel that because the characters of the mouthparts and antennal exopod are so similar to other Group I xanthid zoeae this species is merely a modified member of the Group I xanthids that superficially differs from others in that group. A similar case involving majid larvae was discussed by Williamson (1982).

Plesiomorphic Xanthid Zoeal Characters and Possible Xanthid Phylogenies

Rice (1980: 353) considered well-developed spines and highly setose and highly segmented appendages to be plesiomorphous features; he considered reduced spination, setation, and segmentation to be derived or apomorphous among brachyuran larvae. Using this assumption and relying on Dollo's principle of irreversibility of evolution, Rice (1980, 1983) deduced that the Xanthidae is the

only brachyuran family that contains members whose larvae could possibly have given rise to the advanced conditions of other brachyuran families. However, he noted that many xanthids possess derived features, such as the reduced antennal exopod of the Xanthinae (the Group I zoeae) and the reduced appendage setation of *Menippe* and *Sphaerozius* (Group IV zoeae). Therefore, the only group of xanthid larvae that could have given rise to the more advanced xanthids and other brachyuran families is the Group III zoeae. Rice (1980) refers to this assemblage as the "third group" (page 327), but as the "fourth xanthid zoal group" (page 354); Martin (1984) refers to it as "Group III," as in the present paper.

Probable primitive characters among xanthid larvae are: (1) a well-developed spinulose antennal exopod, (2) 6 setae on the endopod of the maxillule, (3) 8 setae on the endopod of the maxilla, (4) 3 setae on the proximal segment of the endopod of the first maxilliped, (5) 3 spines on each furca of the telson, and (6) posterodorsal or posterolateral knobs on abdominal somites 2-5. No known xanthid zoea possesses this complete complement of characters, although combinations of most of these characters are found in some Group II and Group III larvae.

Rice (1980, fig. 47) placed the genera *Homalaspis*, *Ozius*, and *Eriphia* at the stem of his "suggested principal evolutionary lines amongst the primitive Brachyrhyncha." In this scheme, the larval features of Group III are seen as giving rise to Groups I (Xanthinae), II (Pilumninae), and IV (Menippinae), and by a separate evolutionary pathway to the genera *Heterozius* and *Corystoides*, both of which were placed by Balss (1957) in the Atelecyclidae, subfamily Acanthocyclinae. The zoeae of *Heterozoius* and *Corystoides* share the character of dorsolateral knobs on only the second abdominal somite, but differ from each other in almost all other features, including spination of the carapace and setation and segmentation of the mouthparts. Rice (1980: 334) recognized that both genera differed from the remaining atelecyclids and suggested that they be separated from other members of the family. However, he considered the two genera closely related (1980, fig. 47). Martin (1984) included *Heterozius* as a questionable member of the Group I xanthid zoeae, although he failed to mention that it differs from other Group I larvae in lacking a dorsolateral knob on the second abdominal somite and in having 4 rather than 3 segments in the endopod of the second maxilliped.

If we assume that the characters listed previously are indeed plesiomorphic (Rice, 1980), then species with Group III larvae could represent the most primitive xanthid group. More advanced xanthid zoeae might then be those with reduced mouthpart setation (Group IV) or with a reduced antennal exopod (Group I). It is less clear to us how species having Group II larvae (*Pilumnus* and its allies) could be a derived assemblage, since the antennal exopod, which is considered a conservative character by most students of zoal morphology, is more or less equal in length to or slightly longer than the spinous process in Group II larvae, but only about half as long as the spinous process in larvae of Group III. Thus, the shorter exopod of Group III would become further reduced in one lineage (leading to Group I) yet lengthen in another (leading to Group II).

An equally plausible xanthid phylogeny is one in which the plesiomorphous stem group is represented by a member of Group II. Larvae of Group II have an elongate antennal exopod and the full complement of setae on all appendages, but are extremely variable in other characters. At least three species, *Lobopilumnus agassizii* A. Milne Edwards (see Lebour, 1950), *Pilumnus holosericus* Rathbun (see Kurata, 1970, and Sandifer, 1974), and the zoea mistakenly attributed to *Panopeus bermudensis* by Lebour (1944a), have dorsolateral knobs on abdominal somites 2-5. Xanthid species which have larvae with a reduced antennal exopod (Groups I and III) and those which have larvae with reduced appendage setation

(Group IV) would then be considered more advanced. Species with Group V larvae could have arisen from either lineage, since the antennal exopod is reduced in Group V larvae but appendage setation is not so reduced as in Group IV. The most serious drawback to this phylogeny is that the rostrum in Group II is almost always greatly reduced, so that all evolutionary lineages are assumed to have convergently derived an elongate rostrum.

It is apparent that a more natural xanthid phylogeny must await further descriptions of xanthid zoeae, megalopae, juveniles, and additional characters of the adults.

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Addresses: (JWM) Department of Biological Science, Florida State University, Tallahassee, Florida 32306; (FMT) School of Forestry and Wildlife Management, Louisiana State University, Baton Rouge, Louisiana 70803; (DLF) Department of Biology, University of Southwestern Louisiana, Lafayette, Louisiana 70504.