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A COMPARATIVE STUDY OF MORPHOLOGY AND ONTOGENY IN JUVENILE STAGES OF FOUR WESTERN ATLANTIC XANTHOID CRABS (CRUSTACEA: DECAPODA: BRACHYURA)

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Four species of xanthoid crabs of the family Panopeidae (*sensu* Guinot 1978) (*Panopeus bermudensis*, *P. herbstii* forma simpsoni, *P. turgidus*, and *Eurypanopeus depressus*) were reared in the laboratory from eggs to the fifth crab instar. The fourth (last) zoeal stage and megalopa are described for *P. bermudensis* and *P. turgidus*. The carapaces of the first, second, third and fifth crab stages are described for all four species; mouthparts and fifth pereopods are described for selected stages of all four species. The zoea of *P. bermudensis* is a modified member (lacking lateral carapacial spines) of Rice's group I xanthid zoeas (Rice, A. L., 1980 *Trans. Zool. Soc. Lond.* **35**, 271–424) and is markedly different from the zoeas of the other three species. The zoea of *P. turgidus* is very similar to the zoea of *P. herbstii*, although the megalopa of *P. turgidus* resembles that of *E. depressus*. Carapaces of early crab stages were similar in all four species. Differences in carapace morphology and mouthpart setation were more evident in the fifth crab stage than in the first and third crab stages. A discriminant analysis based upon setation of selected mouthparts and spination of the fifth pereopod dactyl was used to demonstrate quantitatively ontogenetic divergence in phena of the four species. Results of this analysis reflect the minimum expression of adult specializations in the early crab stages, a quality that may justify use of these conservative stages in the ellucidation of lineages of brachyuran groups.

1. Introduction

Most of the characters used in identification of brachyuran crabs are based upon descriptions of mature adults. It is therefore difficult and sometimes impossible to identify crabs at juvenile and immature stages. Yet in the field, the crab stages encountered are often not mature and are not always identifiable by adult characters. At given times in given biotopes, a greater part of the population biomass of these crustaceans will be in the postlarval stages rather than in either the planktonic zoeal stages or the mature stage. It is therefore desirable that the identification of early crab stages be facilitated.

An equally important justification for study of early crab stages is the possible application of such studies in deciphering phylogenies within the Brachyura. To date, phylogenetic studies of immature Brachyura have centred largely on the zoeal stages (Aikawa 1929, 1933, 1937; Gurney 1942; Lebour 1928; Rice 1980, 1981*a*; Wear 1970; Williamson 1976); such studies are based upon the hypothesis that zoeal stages should exhibit more conservative characters than adults and that phylogenetic schemes based upon zoeal stages would be less subject to difficulties inherent in those based upon adult morphology. More specifically, Williamson (1976) observed that relationships based upon adults are 'often confused by ecological adaptations' and that similar adult body forms may be the 'result of convergent evolution'. In contrast, he observed that zoeas 'are virtually all planktonic and nearly all planktotrophic', that 'zoea larvae show little sign of convergent evolution', and that planktonic life 'does not have the effect of moulding them [zoeas] into a particular shape'. Similarly, Rice (1980) argued that almost all zoeas are 'adapted for life in the relatively uniform midwater environment' and that 'adult specializations are not usually reflected in the developmental stages'. Thus, it is hypothesized that the phylogenist, without invoking recapitulationism, may more easily recognize ancestral features in zoeal stages than in adults where features may be masked by adaptive peculiarities.

In practice, zoeal studies have contributed little to the resolution of problems in brachyuran classification. Rice (1980) tentatively founded some phylogenetic lines on the basis of zoeal morphology but noted that this process could not be extended to more highly evolved groups. More recently, Rice (1981 *a*, *b*) has shown even greater caution in the interpretation of larval information and noted that groupings based on the larvae may be just as misleading as those based upon adults. In particular, he has noted that major divergences may not be reflected in larval stages because of parallel adaptation by zoeas to the same general life-style. In contradiction to Williamson (1976), this would imply that planktonic life may in fact mould zoeal morphologies.

The limited utility of zoeal stages in phylogenetic studies has stimulated interest in alternatives. For instance, Rice (1981 *b*) recently examined the phylogenetic significance of brachyuran megalopas and commented that this was the only phase of the brachyuran life cycle that had not been previously examined for classificatory evidence. However, to our knowledge, there has been no attempt to base phylogenetic interpretations on early crab stages of brachyurans. To date, early crab instars have been described for few species and their value as a phylogenetic tool has not been assessed. Could it be that these early instars, the first to exhibit fully the brachyurized body form, show more conservative and phylogenetically significant characters than do either larvae or adults? Within narrow limits, the present study begins to address this question.

The *Panopeus* complex of the family Panopeidae (*sensu* Guinot 1978) is a taxonomically problematical group of mud crabs. Four species of this complex were selected for this study because they are frequently encountered in shallow waters of the northwestern Gulf of Mexico. The species considered are *Panopeus bermudensis* Benedict & Rathbun, 1891, *Panopeus herbstii* H. Milne Edwards, 1834 (simpsoni form of Rathbun 1930), *Panopeus turgidus* Rathbun, 1930, and *Eurypanopeus depressus* (Smith, 1869). There has been recent controversy over the correct generic placement of *P. turgidus*. It was placed in the genus *Eurypanopeus* by Abele (1970), and Menzel (1971) used this name in a checklist for northwest Florida. The adults of *P. turgidus* and *E. depressus* are certainly very similar and one might assume that these two species are very closely related. The appropriate generic placement of *P. bermudensis* could also be questioned, particularly on the basis of Lebour's (1944) description of a first zoea that she assigned to this species. That description differs markedly from those of other panopeid zoeas and would suggest that *P. bermudensis* is not closely allied to the other members of the *Panopeus* complex. Finally, zoeas of *P. herbstii* (described by Costlow & Bookhout 1961 *a*) are as similar to zoeas of *E. depressus* (described by Costlow & Bookhout 1961 *b*) as they are to zoeas of other species within the genus *Panopeus* (Lebour 1944, Rice & Williamson 1977, Kurata 1970). Adult males of both *P. herbstii* and *E. depressus* also share many characters; for example, mature males of both species usually have a diagnostic red spot on the inner surface of the third maxilliped, as do females of *E. depressus*.

The purpose of the present study is the description of the early crab stages of the above named species and the analysis of the phylogenetic significance of early crab stages. In addition to descriptions of the early crab stages, the fourth (last) zoeal and megalopal stages are illustrated for *P. bermudensis* and *P. turgidus*, as these stages have not been previously described for those species. Descriptions of these zoeas and megalopas were necessary to enable comparison of phyletic schemes based upon crab stages with existing schemes based upon larval stages.

(*a*) *Present knowledge of larval and juvenile xanthids*

Compared to xanthid larvae and adults, juvenile xanthid crabs are virtually unknown. Illustrations of the carapace of the first crab stage sometimes accompany a larval description, but such studies of early crabs are invariably lacking in detailed descriptions. Although some include a description of a xanthid early crab stage (table 1), few treat stages beyond the first crab stage, and even fewer include detailed descriptions of the appendages of the early crab stages. However, larvae of xanthid crabs have been the subject of more studies than have larvae of any other brachyuran family. Rice (1980) published an excellent summary of brachyuran zoeal morphology and included remarks on phyletic interpretation of xanthoid larval morphology. Not mentioned by Rice (1980) are the descriptions of *Pilumnoides perlatus* (Poeppig, 1836) larvae by Fagetti & Campodonico (1973) and *Neopanope texana* Stimpson, 1858 larvae by McMahn (1967); these and other references are included in a recent review of xanthid larvae by Martin (1984).

Members of the xanthoid family Panopeidae (*sensu* Guinot 1978) all have zoeal stages that are classifiable as group I xanthid zoeas of Rice (1980) and Martin (1984), with the exception of *Panopeus bermudensis* Benedict & Rathbun, as described by Lebour (1944). Within the family Panopeidae, Guinot included (from the Xanthinae of Balss 1957) the genera *Eurypanopeus*, *Hexapanopeus*, *Lophopanopeus*, *Lophoxanthus*, *Metopocarcinus*, *Neopanope*, *Panopeus*, *Rhithropanopeus*, and some species previously assigned to the genus *Micropanope*; Guinot also included the genus *Eurytium* (from the Pilumninae of Balss) and several genera showing 'goneplacid facies' (from the Goneplacidae of Balss). In reference to subdivisions of the Xanthidae (*sensu largo*) by Guinot (1978), Rice (1980) stated that 'insufficient xanthid larvae have been described to allow a detailed examination of the zoeal evidence for or against Guinot's scheme'. However, for the panopeid genera listed above, zoeal stages are now known from every genus except *Lophoxanthus* and *Metopocarcinus* (table 2). Ultimate generic placement of species previously assigned to *Micropanope* will depend upon acceptance and application of Guinot's (1967) generic revisions. Recently, larvae of the type species, *M. sculptipes* Stimpson, 1871 have been described by Andryszak & Gore (1981) and larvae of *M. barbadensis*, which apparently does not belong to any established genus, have been described by Gore *et al.* (1981).

TABLE 1. DESCRIPTIONS OF EARLY CRAB STAGES IN THE XANTHOIDEA

species	crab stages described	author
Eurypanopeus depressus	1, 2, 3, 5	present study
Eurytium limosum	1	Kurata *et al.* 1981
Lophopanopeus bellus bellus	1	Hart 1935
Menippe mercenaria	'juvenile'	Manning 1961
Menippe mercenaria	1–2	Kurata 1970
Neopanope sayi	1	Birge 1883†
Neopanope sayi	1	Chamberlain 1961
Neopanope sayi	1	Kurata 1970
Panopeus bermudensis	1, 2, 3, 5	present study
Panopeus herbstii	1, 2, 3, 5	present study
Panopeus herbstii	1	Kurata 1970
Panopeus occidentalis‡	1	Kurata 1970
Panopeus turgidus	1, 2, 3, 5	present study
Pilumnus hirtellus	1	Lebour 1928
Pilumnus novaezealandiae	1–5	Wear 1967
Pilumnus sayi	1	Kurata 1970
Pilumnus vestitus	1–6	Hale 1931
Pilumnus sp.	1	Cano 1891†
Rhithropanopeus harrisii	1–2	Kurata 1970
Xantho incisus	1	Lebour 1928
Xantho sp.	1 + 'older crab'	Cano 1891†

† descriptions repeated in Hyman (1925).
‡ questionable identification, possibly *Hexapanopeus angustifrons.*

TABLE 2. DESCRIPTIONS OF LARVAE WITHIN THE FAMILY PANOPEIDAE OF GUINOT (1978)

species	described stages	author
Eurypanopeus depressus	zoea 1–4, megalopa	Costlow & Bookhout 1961 *b*
Eurytium limosum	zoea 1–4, megalopa	Kurata *et al.* 1981
Hexapanopeus angustifrons	zoea 1–4, megalopa	Costlow & Bookhout 1966
Lophopanopeus bellus bellus	zoea 1–4, megalopa	Hart 1935
Lophopanopeus bellus diegensis	zoea 1–4, megalopa	Knudsen 1959
Lophopanopeus leucomanus leucomanus	zoea 1–4, megalopa	Knudsen 1958
Micropanope barbadensis†	zoea 1–4, megalopa	Gore *et al.* 1981
Micropanope sculptipes	zoea 1–4, megalopa	Andryszak & Gore 1981
Neopanope packardi	zoea 1–4, megalopa	Costlow & Bookhout 1967
Neopanope sayi	zoea 1–4, megalopa	Birge 1883; Chamberlain 1961
Neopanope texana	zoea 1–4, megalopa	McMahan 1967
Panopeus ?africanus (ASM 27)	zoea 2	Rice & Williamson 1977
Panopeus bermudensis	zoea 1	Lebour 1944
Panopeus bermudensis	zoea 4, megalopa	present study
Panopeus herbstii	zoea 1–4, megalopa	Costlow & Bookhout 1961 *a*
Panopeus occidentalis‡	zoea 1–4, megalopa	Kurata 1970
Panopeus turgidus	zoea 4, megalopa	present study
Panopeus sp.	zoea 1–4, megalopa	Kurata 1970
Rhithropanopeus harrisii	zoea 1–4, megalopa	Connolly 1925; Hood 1962

† currently without an assigned genus;
‡ questionable identification, possibly *Hexapanopeus angustifrons.*

In at least two cases, identification of a panopeid parental female is questionable. The larvae of *Panopeus occidentalis* Saussure, 1857 were described by Kurata (1970); the collector of the parental female identified the adult as *Hexapanopeus angustifrons* (R. W. Heard, Gulf Coast Research Lab, Ocean Springs, Mississippi, personal communication). Comparison of Kurata's (1970) illustration to larvae of *H. augustifrons* Benedict & Rathbun, 1891 (described by Costlow

& Bookhout 1966) suggests that Kurata (1970) did in fact rear *H. angustifrons* and not *P. occidentalis*. The larvae of *Panopeus* sp. (Kurata 1970) resemble the zoea of *P. herbstii* H. Milne Edwards, 1834 (described by Costlow & Bookhout 1961 *a*) except for having dorsolateral knobs on segments 2–5 in *Panopeus* sp.; these larvae cannot at present be assigned to any known species. Lebour's (1944) description of the first zoea of *Panopeus bermudensis* strongly resembles the pilumnid zoeas in Rice's (1980) group II xanthid zoeas; the identification of Lebour's parental female must also be questioned.

In addition, one non-panopeid xanthid has been assumed incorrectly to be a panopeid. Fielder *et al.* (1979) cite Monod (1956) as having assigned *Leptodius parvulus* to the genus *Panopeus*. However, if it is assumed that Lebour (1944) was dealing with western Atlantic material from Bermuda under *L. parvulus* (*sensu* Rathbun 1930), that species has now been assigned to *Xanthodius parvulus* by Manning & Holthuis (1981).

Megalopas of western Atlantic xanthids have recently been reviewed by Andryszak & Gore (1981). Within the Panopeidae, two groups of megalopas can be seen, one group with and one group without prominent anterolateral horns. However these groupings do not seem to correspond with currently accepted groupings of adults, and at present no attempts have been made to phyletically reorder the xanthids according to megalopal characters. Likwise, there has been no previous attempt to use early crab stages in reassessment of xanthid relationships. No doubt this is in part because of a lack of detailed descriptions of these stages.

The few studies that do include detailed descriptions of juvenile xanthids are of little comparative value. Hale (1931) described the first crab of *Pilumnus vestitus*, but because of the abbreviated larval development of this species (the eggs hatch as megalopas) the first crabs take up a natatory existence and are therefore not comparable to the first crab stages of other xanthids. Wear (1967) described the first five crab stages of *Pilumnus novaezealandiae*, but did not include descriptions of the appendages. The great majority of the descriptions of juvenile xanthid crabs are limited to non-detailed line drawings of the first crab stage (for example Hart 1935; Chamberlain 1961; Kurata *et al.* 1981). Phylogenetic relationships based upon juvenile xanthids were briefly alluded to by Martin & Felder (1980).

2. Materials and methods

Ovigerous females of *Panopeus bermudensis*, *Panopeus turgidus*, *Panopeus herbstii* simpsoni form of Rathbun (1930), and *Eurypanopeus depressus* were collected during the spring and summer of 1979 from the following localities: South Padre Island, Cameron County, Texas, from rock jetties (*P. bermudensis*); Port Isabel, Cameron County, Texas, from grass beds adjacent to Tarpon Hole (*P. turgidus*); Dauphin Island, Alabama, from shallow-water rubble on north side of the causeway (*P. herbstii*); Grande Isle, Louisiana, from shallow-water rubble on north side of the island (*E. depressus*). The ovigerous females were isolated in large finger bowls filled with 30‰ salinity Instant Ocean, and maintained at 22–24 °C until the eggs hatched. The single ovigerous female *P. herbstii* was an exception; her eggs hatched in a large plastic bucket en route to the laboratory.

When the eggs hatched, most of the stage 1 zoeas were transferred to a 10 l aquarium half-filled with 30‰ salinity Instant Ocean and maintained at a temperature of approximately 25–27 °C. Some stage 1 zoeas were removed and placed in polystyrene trays, one zoea per compartment (after Roberts 1975). Zoeas were fed daily on newly hatched *Artemia* (Brazilian strain) nauplii.

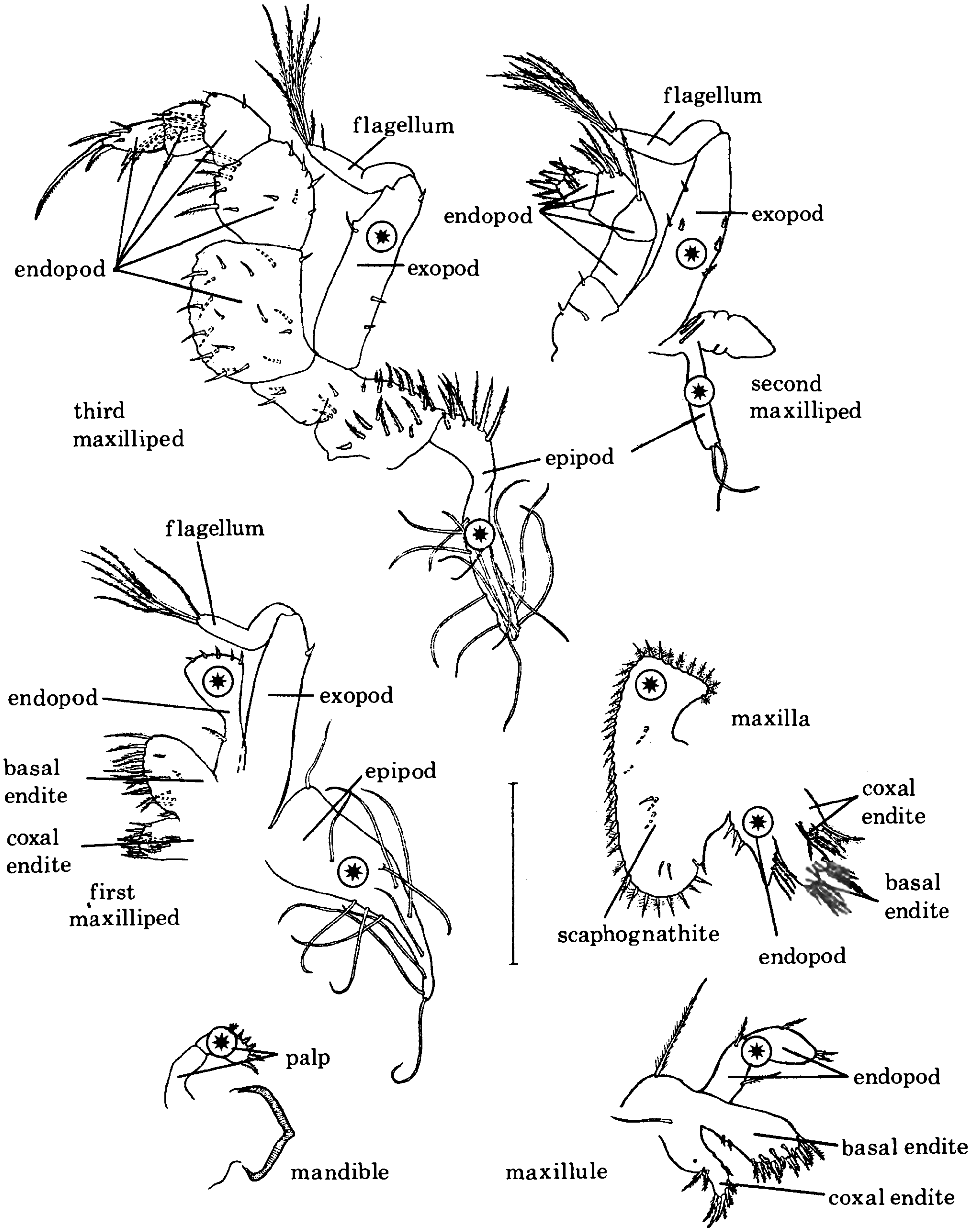


FIGURE 1. Brachyuran mouthparts. Encircled star shows segments where setation and spination were used for statistical analysis.

Water in the polystyrene trays was changed daily. When zoeas in the mass cultures moulted into megalopas, a megalopa was placed in each compartment of a polystyrene tray and given newly hatched *Artemia* and fresh seawater daily. Exuviae (moults) of the megalopas and of the first several crab stages (and any dead crabs) were preserved in 70% (by volume) ethanol. Crabs were monitored through at least five instars. When the rearing was discontinued, the remaining live crabs were transferred to 20 l aquaria where they were allowed to reach adult size. In these larger aquaria the crabs were fed a ready-made food developed for feeding larval frogs (Culley *et al.* 1977).

Drawings of the carapaces of the crab stages were made with the aid of a Wild M-5 stereoscope with drawing tube. Appendages of the crab stages and the zoeas and megalopas of *P. bermudensis* and *P. turgidus* were drawn with the aid of a Zeiss compound stereoscope and camera lucida. Drawings were made from exuviae which were soaked in glycerine at least 1 h before drawing or dissecting, or both, and returned to 70% (by volume) ethanol afterwards. Unless otherwise stated, ten individuals per species per stage were examined, and a minimum of three individuals per species per stage were dissected. Only two fourth stage zoeas and two megalopas were examined for *P. bermudensis* and *P. turgidus*. Because there was considerable variation in size for any given stage for each species, but much less variation in stage-specific characters, size of the crab stages is indicated only by the bar accompanying each illustration. Larvae were measured with an ocular micrometer.

Terminology used in this study follows that of McLaughlin (1980) for the mouthparts, Factor (1978) for the mouthparts and types of setae thereon, and Felder (1973) and McLaughlin (1980) for the areas of the crab carapace. The six brachyuran mouthparts are shown (figure 1) for convenient reference. Spelling of the plural for zoea (zoeas) and megalopa (megalopas) follows the recommendations of Rice (1981 *b*).

For statistical comparisons of the four species, setal counts from ten areas of the mouthparts (figure 1) were used in a discriminant analysis. These areas are (1) proximal segment of exopod of maxilliped 3; (2) epipod of maxilliped 3; (3) proximal segment of exopod of maxilliped 2; (4) epipod of maxilliped 2 (long setae only); (5) endopod of maxilliped 1; (6) epipod of maxilliped 1; (7) scaphognathite of maxilla (fringing setae only); (8) endopod of maxilla (long setae only); (9) endopod of maxillule (both segments); (10) mandibular palp (distal segment only). An additional character was (11) the number of subterminal spines on the dactyl of the fifth pereopod (walking leg).

The discriminant analysis employed was the WILKS method of the stepwise SPSS DISCRIMINANT subprogram of Klecka (1975), in which the significance criterion used is the overall multivariate *F* ratio for differences among the group centroids. Because some mouthparts were damaged during dissection an SPSS option was used that substituted group means for missing values.

No attempt was made to compare conspecific crabs from different parents. Several ovigerous females were obtained for each species, except for *P. herbstii*, and crabs were picked at random from the resulting broods. Only one ovigerous female of *P. herbstii* was obtained, and so all juvenile crabs of *P. herbstii* are from a single parent.

In an effort to avoid ambiguous or repetitive descriptions, the advice of Rice (1979) has been followed throughout this study; many characters clearly visible in the illustrations are not described again in the text. All setal formulae are in a proximal-to-distal arrangement. Abbreviations used in the text are c.l. (carapace length), c.w. (carapace width), and t.l. (total length). Specimens were placed in the archives of the University of Southwestern Louisiana Invertebrate Collection under catalogue numbers designated here by the prefix USL ARcMd.

3. Results

(*a*) *Larvae*

All four species had four zoeal stages followed by a megalopal stage. Complete larval development in the polystyrene trays required 13–19 d (table 3). The complete larval development of *P. herbstii* and *E. depressus* has been described by Costlow & Bookhout (1961 *a*, *b*).

TABLE 3. HATCHING DATES AND TIME REQUIRED FOR COMPLETE LARVAL DEVELOPMENT OF *PANOPEUS HERBSTII*, *PANOPEUS TURGIDUS*, *EURYPANOPEUS DEPRESSUS*, AND *PANOPEUS BERMUDENSIS* IN POLYSTYRENE TRAYS

	hatching dates	stage	days after hatching
P. herbstii	3 July 1979	1	0
		2	5–6
		3	9–13
		4	13–18
		megalopa	16–19
P. turgidus	2 June 1979	1	0
	6 June 1979	2	4–5
	5 May 1979	3	7–8
	30 May 1979	4	9–11
	4 April 1979	megalopa	13–15
E. depressus	14 August 1979	1	0
	15 August 1979	2	4–5
	17 August 1979	3	7–9
	19 August 1979	4	10–13
		megalopa	13–17
P. bermudensis	3 June 1979	(not monitored)	
	7 June 1979		

(i) Panopeus bermudensis, *Benedict & Rathbun*, 1891, *fourth zoeal stage*

Size. c.l. 0.72 mm, c.w. 0.5 mm. Tip of dorsal to tip of rostral spine 2.85 mm.

Carapace. (Figures 2*a*, *b*.) c.l. less than dorsal spine which is less than rostral spine. No lateral spines present.

Abdomen. (Figure 2*c*.) Somites 2 and 3 with dorsolateral knobs, those of somite 3 very small; telson forks (figure 3*a*) each with one dorsal spine about midway along length of caudal furca, 3+1 pairs of internal spines.

Antennule. (Figure 2*e*.) Three tiers of aesthetascs, arranged 1, 4, 4.

Antenna. (Figure 2*d*.) Spinous process shorter than rostrum, smooth, slightly dilated at tip. Exopod absent. Endopod present as a small bud.

Maxillule. (Figure 3*b*.) Endopod 2-segmented, with 1+6 setae. Basal endite with about 10 serrate and cuspidate spines; coxal endite with about 9 plumose-serrate spines.

Maxilla. (Figure 3*c*.) Endopod 2-lobed, with 3+5 setae; scaphognathite with 21–23 plumose setae. Basal endite bilobed, with 5+7 setae; coxal endite also bilobed and with 4–5+4–5 setae.

Maxilliped 1. (Figure 3*d*.) Exopod with 8 natatory setae; basis with 7 setae. Endopod 5-segmented, with 3, 2, 1, 2, 4+1+1 setae.

Maxilliped 2. (Figure 3*e*.) Exopod with 10–11 natatory setae, basis with 3 setae; endopod 3-segmented with 1, 1, 5 setation.

Maxilliped 3. not developed.

(ii) Panopeus bermudensis, *megalopa*

Size. c.l. 0.88 mm, t.l. 1.66 mm, c.w. 0.70 mm.

Carapace. (Figure 4*a*.) Subquadrate, slight medial depression of front. Sharp anterolateral horns. Rostrum blunt, bifid.

Abdomen. (Figure 4*a*.) Somites sparsely covered with minute hairs.

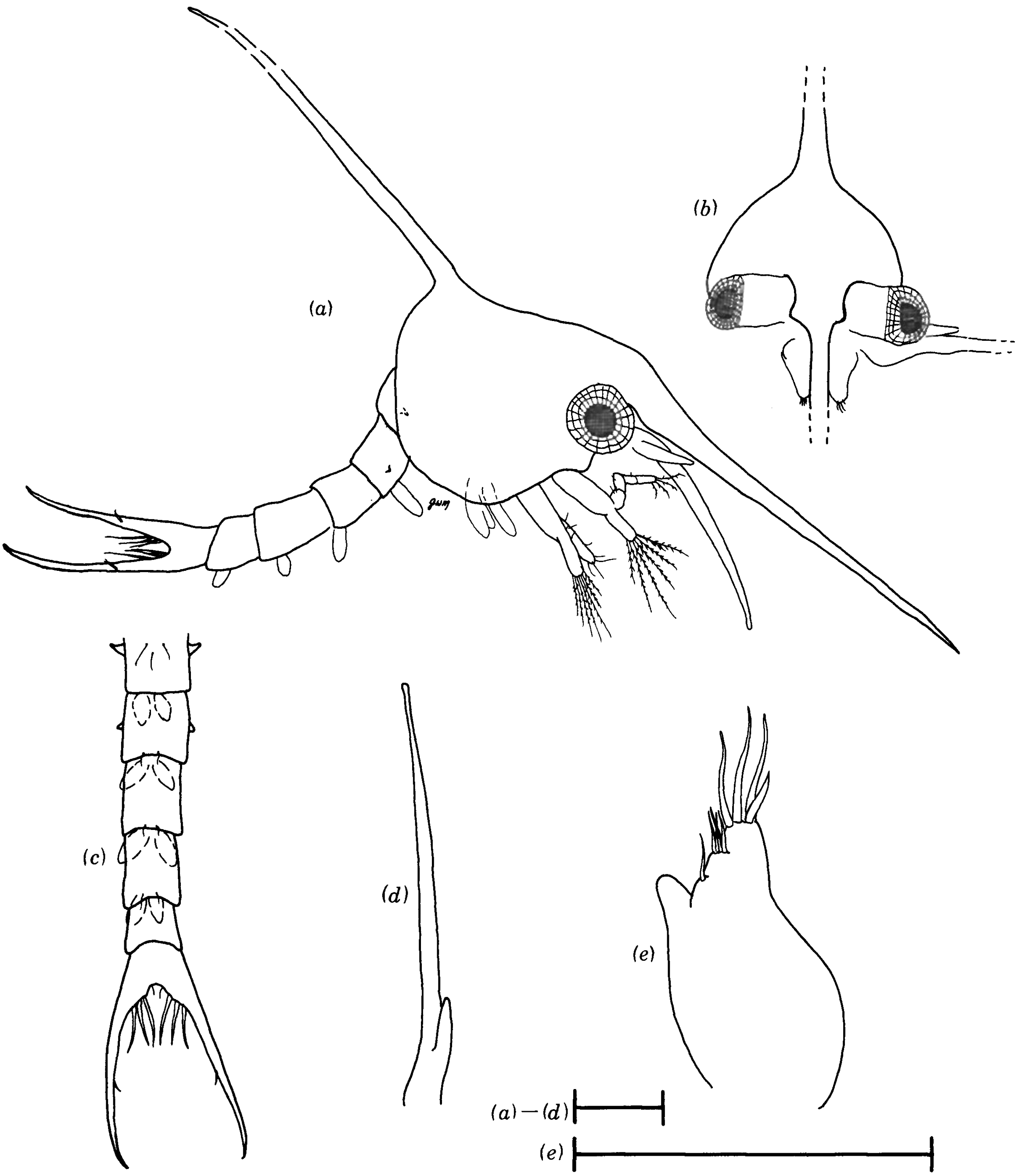


FIGURE 2. *Panopeus bermudensis*, fourth zoea. (*a*) Lateral view; (*b*) frontal view; (*c*) dorsal view of abdomen; (*d*) antenna; (*e*) antennule. Scale = 0.25 mm.

Telson. (Figure 4*b*.) Subquadrate, posterior angles rounded, 4 dorsal setae.

Antennule. Not examined.

Antenna. (Figure 4*c*.) Flagellum 11-segmented, setation 2, 1, 1–0, 0, 0, 2–3, 0, 4, 0, 4, 4.

Mandible. (Figure 5*f*.) Asymmetrical, with spade-shaped cutting edge; palp 2-segmented, setation 0, 7–8.

FIGURE 3. *Panopeus bermudensis*, fourth zoea. (*a*) Telson; (*b*) maxillule; (*c*) ma (*d*) maxilliped 1; (*e*) maxilliped 2. Scale = 0.50 mm.

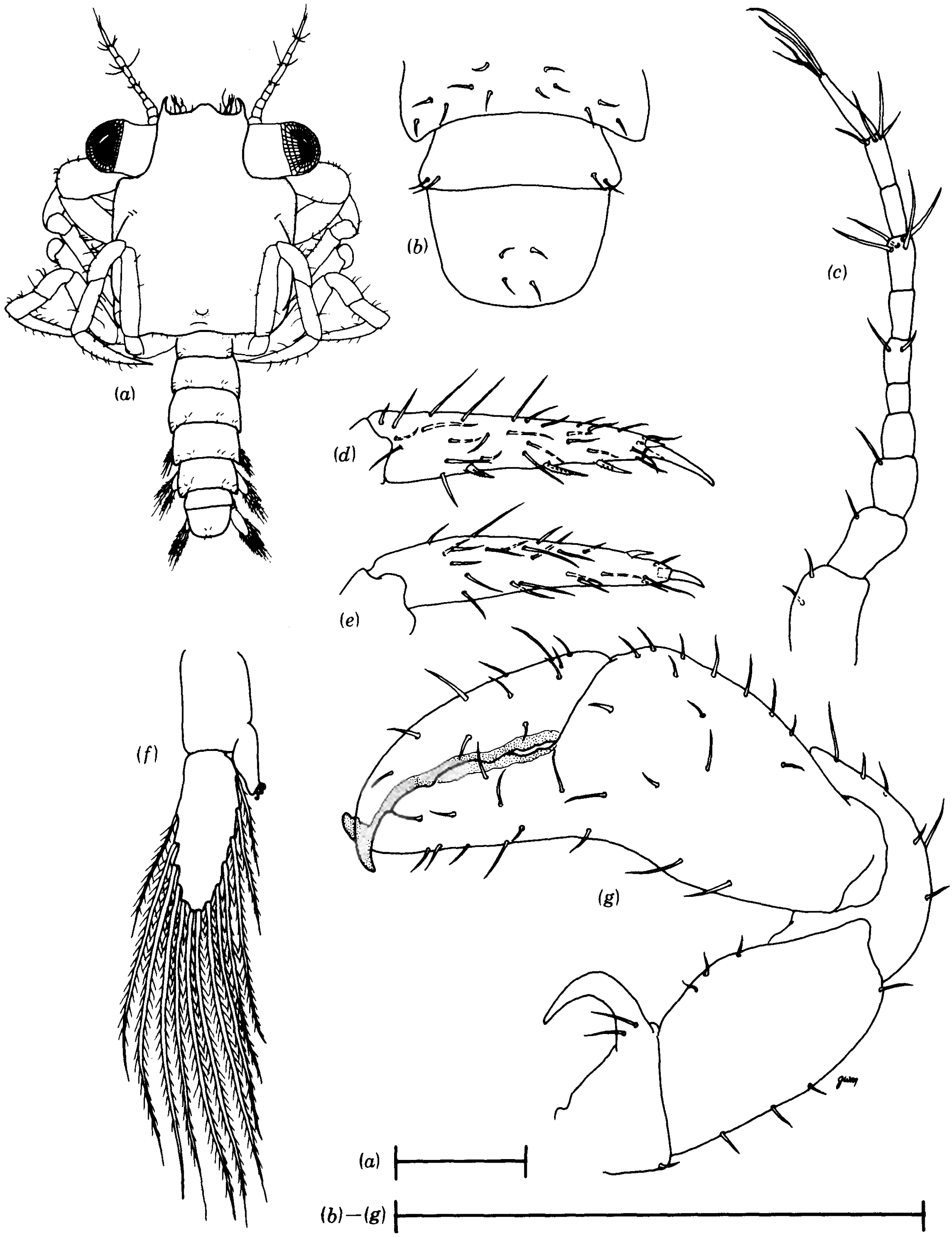


FIGURE 4. *Panopeus bermudensis*, megalopa. (*a*) Dorsal view; (*b*) telson and abdominal somites 5 and 6; (*c*) antenna; (*d*) dactyl of pereopod 3; (*e*) dactyl of pereopod 5; (*f*) pleopod 3; (*g*) cheliped. Scale = 0.50 mm.

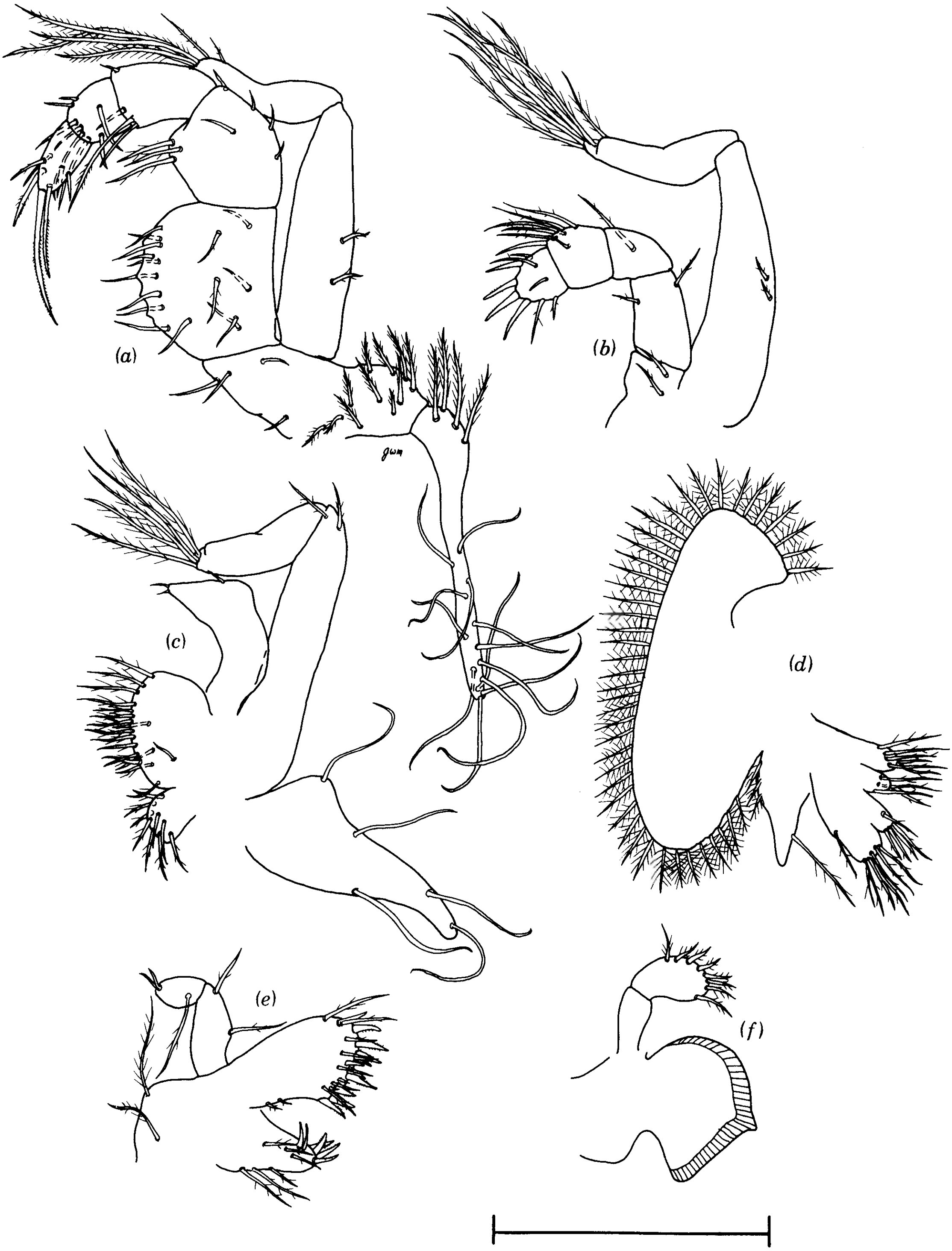


FIGURE 5. *Panopeus bermudensis*, megalopa mouthparts. (*a*) Maxilliped 3; (*b*) maxilliped 2; (*c*) maxilliped 1; (*d*) maxilla; (*e*) maxillule; (*f*) mandible. Scale = 0.25 mm.

Maxillule. (Figure 5*e*.) Protopodite area with 1–2 long plumose setae. Endopod 2-segmented, setation 2, 3. Basal endite with 21–22 cuspidate spines and serrate setae; coxal endite with 12–13 spines and setae.

Maxilla. (Figure 5*d*.) Endopod with 1–2 plumose setae, scaphognathite with 40–44 fringing setae. Basal endite setation 5–6 + 8–9, coxal endite setation 6–7 + 4–5.

Maxilliped 1. (Figure 5*c*.) Exopod 2-segmented, setation 2, 5. Endopods unsegmented, with 2–3 setae. Basal endite with 17–19 setae, coxal endite with 9–10 setae. Epipod with 5–6 long naked setae.

Maxilliped 2. (Figure 5*b*.) Exopod 2-segmented, setation 2, 5–6. Endopod 4-segmented, setation 1–2, 1, 6, 8–9. Epipod not seen.

Maxilliped 3. (Figure 5*a*.) Exopod 2-segmented, setation 2, 5–6. Endopod 5-segmented, setation 16–18, 6–8, 4, 8, 7–8. Epipod with 4 setae plus 12–13 long naked setae.

Pereopods. Chelipeds (figure 4*g*) with large basi-ischial recurved hook and 4–5 irregular teeth on fingers; finger borders slightly corneous. Pereopod 3 with 3 strong ventral serrate spines and 1 subterminal dorsal spine on dactyl (figure 4*d*). Pereopod 5 with 1 dorsal spine and 1 short terminal seta on dactyl (figure 4*e*).

Pleopod 3. (Figure 4*f*.) Thirteen natatory setae, endopod with 3 hooked setae.

(iii) Panopeus turgidus *Rathbun*, 1930, *fourth zoeal stage*

Size. c.l. 0.78 mm. Tip of dorsal to tip of rostral spine 1.54 mm. Width of carapace not measured.

Carapace. (Figure 6*a*.) Dorsal spine longer than c.l. which is longer than rostral spine. Obvious lateral spines present. Numerous setae on posterior border.

Abdomen. (Figure 7*a*.) Somites 2 and 3 with dorsolateral knobs; those of somite 3 smaller. Telson forks (figure 6*c*) each with 1 dorsal and 2 lateral spines, plus 3 pairs of internal spines between furcae.

Antennule. (Figure 6*e*.) Three tiers of aesthetascs, arranged 2, 4, 5.

Antenna. (Figure 6*b*.) Spinous process equal to or longer than rostral spine and with several distal spinules. Exopod reduced, with 1 terminal seta. Endopod with 3 terminal setae.

Maxillule. (Figure 7*c*.) Endopod 2-segmented, setation 1, 4. Basal endite with 11–13 cuspidate-serrate spines and setae, coxal endite with 9–10 serrate-plumose setae.

Maxilla. (Figure 7*b*.) Endopod 2-lobed, setation 3, 3 + 2. Scaphognathite with 22–24 fringing plumose setae.

Maxilliped 1. (Figure 6*d*.) Exopod with 8–9 natatory setae; basis with 9–10 setae. Endopod 5-segmented, setation 2–3, 2, 1, 2, 5 + 1.

Maxilliped 2. (Figure 6*f*.) Exopod with 9–10 natatory setae; basis with 4 setae. Endopod 3-segmented, setation 1, 1, 5.

Maxilliped 3. Not developed.

(iv) Panopeus turgidus, *megalopa*

Size. c.l. 0.76 mm, t.l. 1.62 mm, c.w. 0.68 mm.

Carapace. (Figure 8*a*.) Subquadrate, front medially depressed. No anterolateral horns. Rostrum broadly triangular, deflected ventrally. Two groups of 4 setae on either side of midline.

Abdomen. (Figure 8*a*.) Posterolateral borders of somites 3–5 produced posteriorly, sparsely setose on posterior borders of somites.

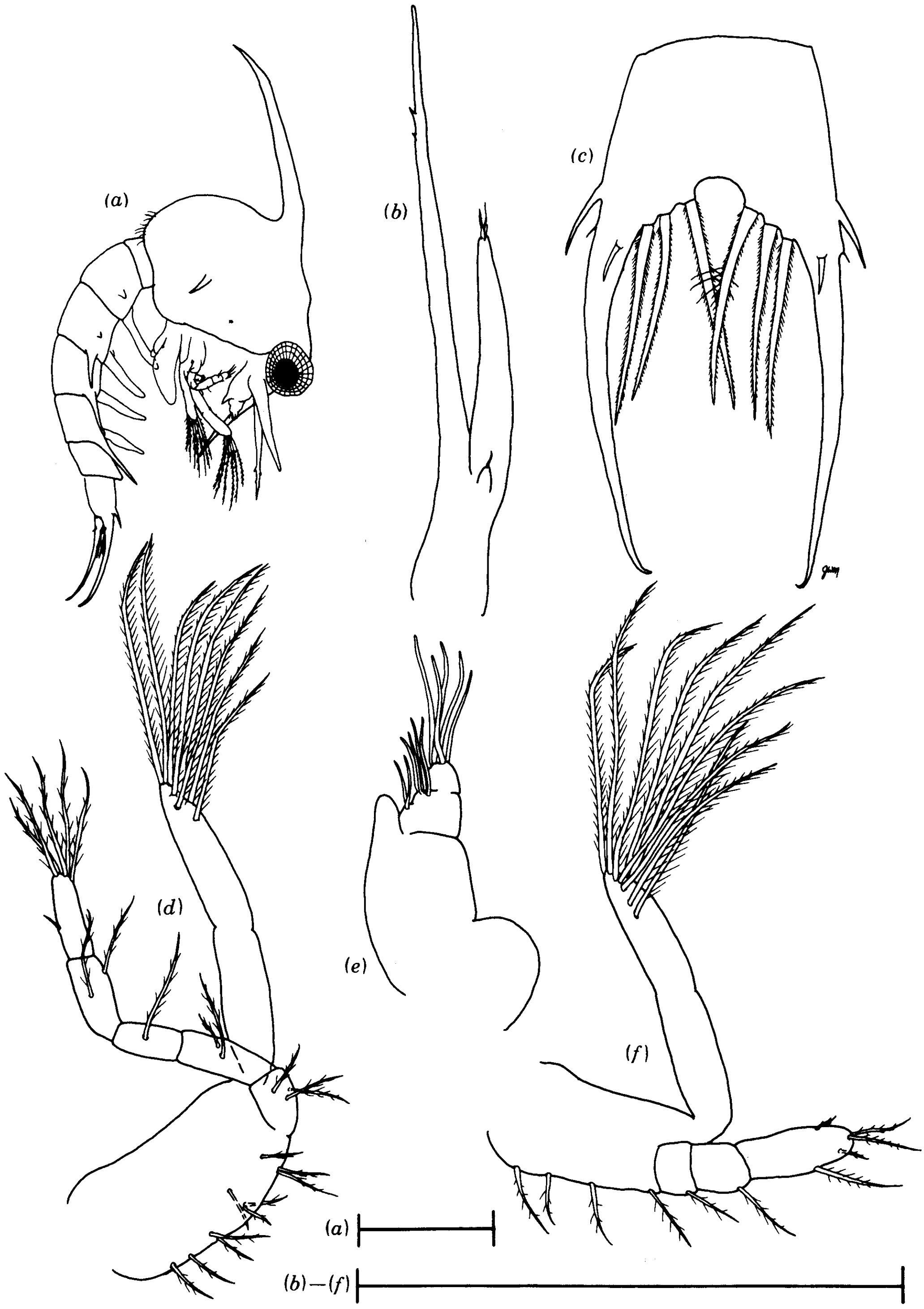


FIGURE 6. *Panopeus turgidus*, fourth zoea. (*a*) Lateral view; (*b*) antenna; (*c*) telson; (*d*) maxilliped 1; (*e*) antennule; (*f*) maxilliped 2. Scale = 0.50 mm.

Telson. (Figure 8*b*.) Subquadrate, posterolateral corners with small, blunt spines. Three pairs of serrate spines on posterior border.

Antennule. Not examined.

Antenna. (Figure 8*c*.) Flagellum 10-segmented, setation 2–4, 2, 1, 0, 0, 0, 4, 0, 3, 3–4.

Mandible. (Figure 9*f*.) Asymmetrical, with spade-shaped cutting edge. Palp 2-segmented, setation 0, 7–8.

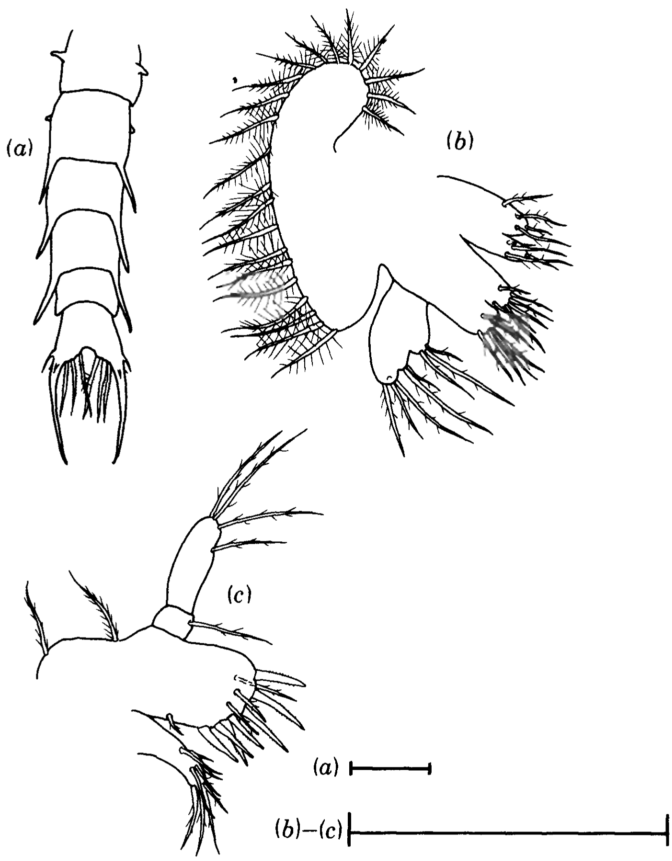


FIGURE 7. *Panopeus turgidus*, fourth zoea. (*a*) Dorsal view of abdomen; (*b*) maxilla; (*c*) maxillule. Scale = 0.25 mm.

Maxillule. (Figure 9*e*.) Protopodite area with 2–3 plumose setae. Endopod 2-segmented, setation 1, 6. Basal endite with 18–20 cuspidate-serrate spines and setae, coxal endite with 10–11 spines and setae.

Maxilla. (Figure 9*d*.) Endopod trilobed, with 8 plumose setae arranged 3 + 2 + 3. Scaphognathite with 36 fringing plumose setae. Basal endite with 7 + 9 setae, coxal endite with 5 + 5 setae.

Maxilliped 1. (Figure 9*c*.) Exopod 2-segmented, setation 1, 8. Endopod indistinctly segmented, with about 14 setae. Basal endite with 19 setae, coxal endite with 9–10 setae. Epipod with 5–6 long naked setae.

Maxilliped 2. (Figure 9*b*.) Exopod 2-segmented, setation 0, 8. Endopod 4-segmented, setation 4, 1, 6, 10. Epipod not seen.

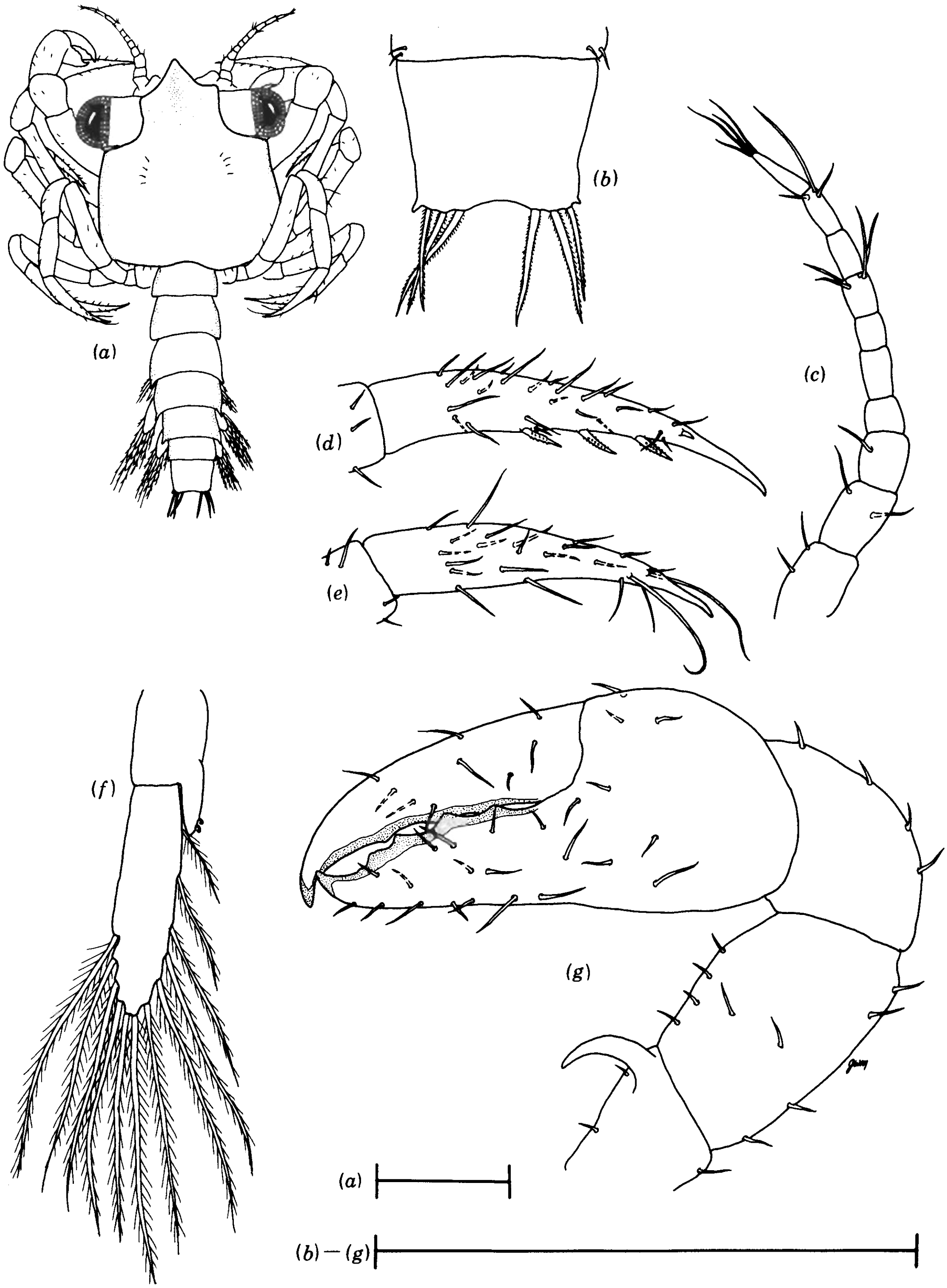


FIGURE 8. *Panopeus turgidus*, megalopa. (*a*) Dorsal view; (*b*) telson; (*c*) antenna; (*d*) dactyl of pereopod 3; (*e*) dactyl of pereopod 5; (*f*) pleopod 3; (*g*) cheliped. Scale = 0.50 mm.

FIGURE 9. *Panopeus turgidus*, megalopa mouthparts. (*a*) Maxilliped 3; (*b*) maxilliped 2; (*c*) maxilliped 1; (*d*) maxilla; (*e*) maxillule; (*f*) mandible. Scale = 0.25 mm.

Maxilliped 3. (Figure 9*a*.) Exopod 2-segmented, setation 1–2, 8. Endopod 5-segmented, setation 13–14, 13–14, 4–6, 8, 8. Epipod with 4–5 plumose setae plus 11 long naked setae.

Pereopods. Chelipeds (figure 8*g*) with large recurved basi-ischial hook. Fingers with 4–5 irregular teeth, borders slightly corneous. Pereopod 3 with 3 strong serrate ventral spines and 1 subterminal dorsal spine on dactyl (figure 8*d*), pereopod 5 with 2 long setae on dactyl (figure 8*e*).

Pleopod 3. (Figure 8*f*.) Twelve natatory setae, endopod with 2 hooked setae.

TABLE 4. DEVELOPMENTAL TIME REQUIRED TO REACH THE FIRST FIVE CRAB STAGES OF *PANOPEUS BERMUDENSIS*, *PANOPEUS HERBSTII*, *PANOPEUS TURGIDUS* AND *EURYPANOPEUS DEPRESSUS* IN POLYSTYRENE TRAYS

species	crab stages	days after hatching
Panopeus bermudensis	1	17–18
	2	23–24
	3	28–31
	4	35–37
	5	43–46
Panopeus herbstii	1	23–28
	2	26–34
	3	32–42
	4	40–59
	5	50–88
Panopeus turgidus	1	15–18
	2	21–29
	3	25–34
	4	29–39
	5	33–43
Eurypanopeus depressus	1	14–18
	2	21–25
	3	27–43
	4	31–48
	5	37–71

(*b*) *Crab stages*

The first crab stage was reached about 15 d after hatching in all species except *P. herbstii*. Megalopas of *P. herbstii* did not reach the first crab stage until 23–28 d after hatching of the eggs. The fifth crab stage was reached as early as 33 d after hatching in some individuals of *P. turgidus*, and as late as 88 d after hatching in some individuals of *P. herbstii* (table 4). Development was monitored only in the polystyrene trays, and is therefore not indicative of developmental time in the mass culture aquaria.

(i) *General description of the panopeid first crab*

Carapace. Subquadrate, nearly as long as wide, with three to four anterolateral teeth; fourth often poorly developed or absent. Front slightly bilobed with medial depression. Frontal margin minutely crenulate. Medial portion of orbital groove apparent. Many setae in the hepatic and epigastric regions, lightly setose in other regions. Areolations not clearly defined. Deep, robust in frontal view. Sternum broadly triangular and sparsely setose.

Eyes. Large, often extending beyond outermost carapace spines.

Abdomen. Loosely flexed beneath thorax, segments clearly defined (not fused).

Telson. Subtriangular, rounded posteriorly, with several setae.

Mandibles. Asymmetrical, with spade-shaped cutting edges. Palp 2-segmented, distal segment with 6–9 setae.

Maxillule. Endopod 2-segmented, setation variable. Basal and coxal endites with cuspidate, serrate, and plumose spines and setae. Protopodite area with 1–2 long plumose setae.

Maxilla. Endopod unsegmented, setation variable. Basal and coxal endites bilobed, with plumose setae. Scaphognathite with 35–50 fringing plumose setae, usually 40–45.

Maxilliped 1. Exopod 2-segmented with 1–2 setae on proximal segment. Several long plumose setae on flagellum. Endopod unsegmented with 6–14 setae, several of which are short naked terminal spines. Distal end of endopod occasionally produced into a blunt tip with additional setae. Epipod with 11–17 long naked setae. Basal and coxal endites with many plumose setae.

Maxilliped 2. Exopod 2-segmented, proximal segment with 2–12 setae, usually with 2 stout serrate spines on lateral border and 1 stout spine on medial border. Flagellum with several long plumose setae. Endopod 4-segmented, terminal and subterminal segments with heavy cuspidate spines. Second segment (carpus) usually with 1 long serrulate seta extending beyond the propodus. Epipod with 2–5 long naked setae.

Maxilliped 3. Exopod 2-segmented, proximal segment with small protrusion along distal fourth of medial edge and with 3–8 setae. Flagellum with several long plumose setae. Endopod 5-segmented, proximal segment slightly scalloped along medial edge. Distal segment of endopod with several long, serrate setae. Epipod with several basal plumose setae and 12–19 long naked setae.

Pereopods. Chelipeds approximately symmetrical, with many distinct tubercles on manus and carpus. Fingers with some light pigmentation, inner borders of fingers with a thin transparent cutting edge; teeth irregular and indistinct. Basis with several ventrolateral spines or tubercles, never with a large recurved hook. Merus with several granules in a line along the ventral border. Pereopod 5 with 0–2 (rarely 4) subterminal spines on dactyl, and with serrulate setae on all segments.

(ii) Panopeus bermudensis, *Benedict & Rathbun*, 1891, *first crab stage*

Carapace. (Figures 10*a*, 11*a*.) As described for general panopeid first crab. No granulated ridges present.

Eyes, telson and abdomen. (Eyes, figure 10*a*.) As described for general panopeid first crab.

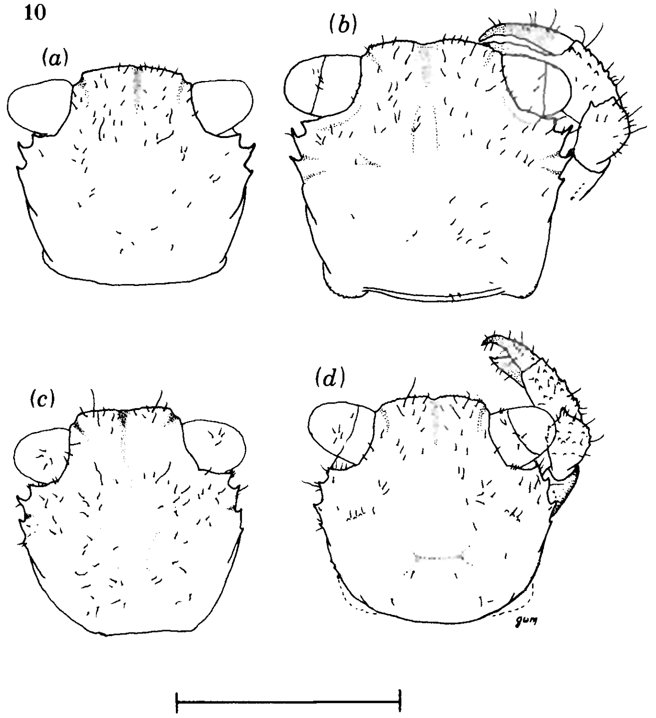
Mandible. (Figure 12*f*.) Palp setation 0, 6–8 (usually 8).

Maxillule. (Figure 12*e*.) Endopod with 4–5 setae, arranged 2–3, 2. Basal endite with 23–24 cuspidate and serrate spines and setae, coxal endite with 14–15 spines and setae.

Maxilla. (Figure 12*d*.) Endopod with 1–2 (usually 1) plumose setae. Basal and coxal endites bilobed with setation 9+7 and 5+3, respectively. Scaphognathite with 43–47 fringing setae and 6–8 setae on blade.

Maxilliped 1. (Figure 12*c*.) Exopod setation 2, 5–6. Endopod with 8–11 setae, 4–5 of which are short terminal spines. Basal and coxal endites with 23–24 and 13–14 setae, respectively. Epipod with 15–18 long naked setae.

Maxilliped 2. (Figure 12*b*.) Exopod setation 7–11 on proximal segment and 5–6 on flagellum. Endopod setation 3, 1, 7, 11. Epipod with 3–4 plumose setae and 2–4 long naked setae.



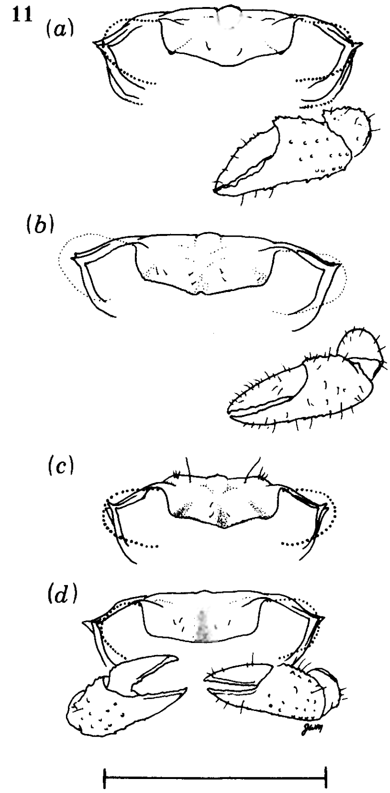


FIGURE 10. Dorsal view of the carapace of the first crab stage. (*a*) *Panopeus bermudensis*; (*b*) *Panopeus herbstii*; (*c*) *Panopeus turgidus*; (*d*) *Eurypanopeus depressus*. Scale = 1.0 mm.

FIGURE 11. Frontal view of the carapace of the first crab stage. (*a*) *Panopeus bermudensis*; (*b*) *Panopeus herbstii*; (*c*) *Panopeus turgidus*; (*d*) *Eurypanopeus depressus*. Scale = 1.0 mm.

Maxilliped 3. (Figure 12*a*.) Exopod setation 4–6, with 5–6 long setae on flagellum. Endopod setation 21, 14, 10, 9, 7. Epipod with 7–8 plumose setae and 12–15 long naked setae.

Pereopods. Chelipeds (figure 11*a*) as described for general panopeid first crab, with many obvious tubercles on manus and carpus. Fingers lacking pigmentation. Pereopod 5 (figure 13*a*i) with 0–1 subterminal dorsal spine on dactyl.

(iii) Panopeus herbstii, *H. Milne Edwards*, 1834, *first crab stage*

Carapace. (Figures 10*b*, 11*b*.) As described for general panopeid first crab. Frontal margin often with medial notch in frontal view. No granulated ridges present.

Eyes, telson and abdomen. (Eyes, figure 10*b*.) As described for general panopeid first crab.

Mandible. (Figure 14*f*.) Palp setation 0, 8–9.

Maxillule. (Figure 14*e*.) Endopod with 3–6 setae, usually arranged 0–2, 2–3. Basal and coxal endites with 18–19 and 14–15 cuspidate and serrate spines, respectively.

Maxilla. (Figure 14*d*.) Endopod with 1–7 (usually 1) plumose setae. Basal and coxal endites with setation 10 + 5, 7 + 5, respectively. Scaphognathite with 35–50 fringing setae, and 7–9 setae on blade.

Maxilliped 1. (Figure 14*c*.) Exopod setation 1, 5–6. Endopod with 8–14 setae, 5–6 of which

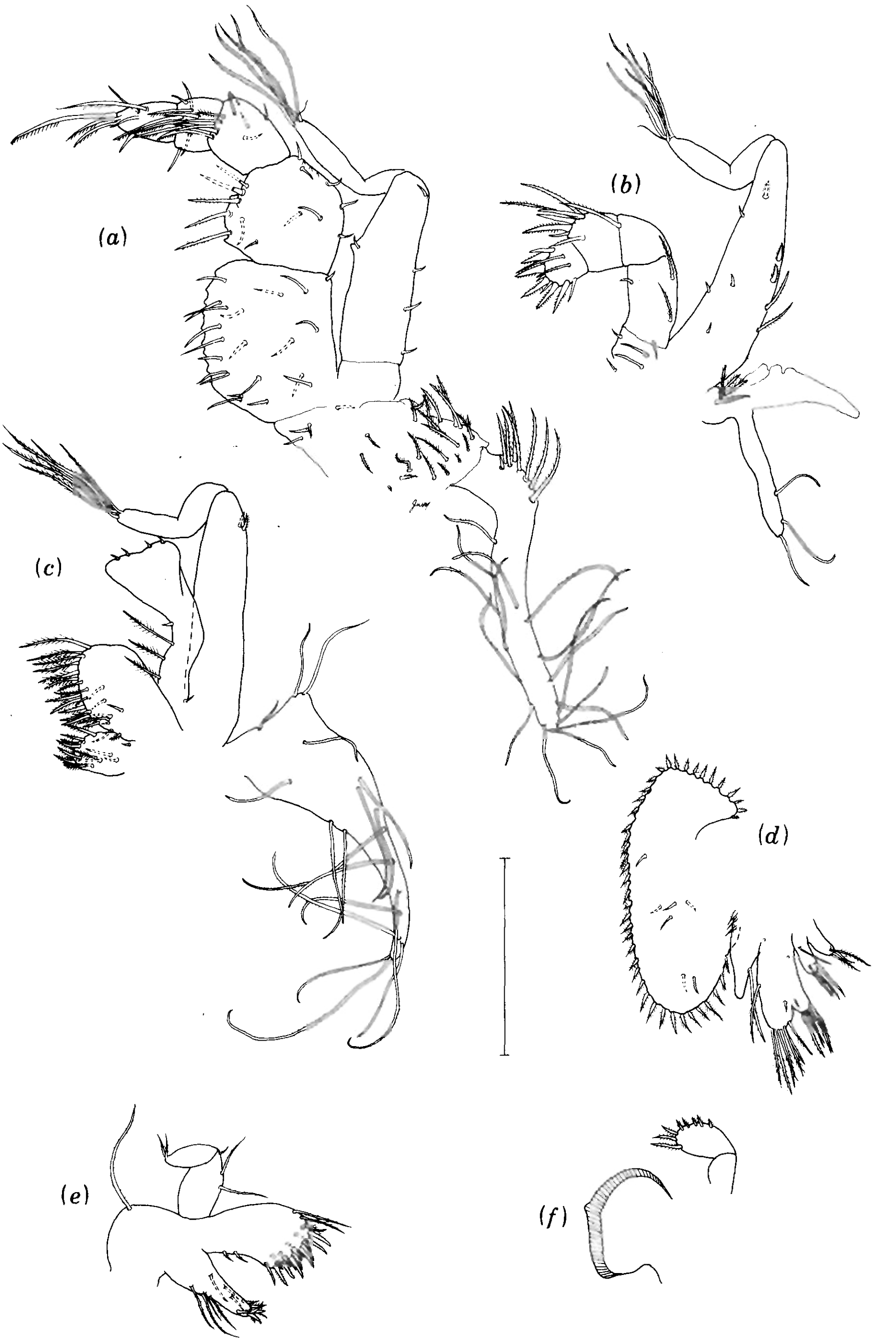


FIGURE 12. *Panopeus bermudensis*, first crab stage mouthparts. (*a*) Maxilliped 3; (*b*) maxilliped 2; (*c*) maxilliped 1; (*d*) maxilla; (*e*) maxillule (*f*) mandible. Scale = 0.25 mm.

are short terminal spines. Basal endite setation 24–28, coxal endite setation 15–17. Epipod with 11–15 long naked setae.

Maxilliped 2. (Figure 14*a*.) Exopod setation 2–9, 3–6. Endopod setation 2–3, 1, 7, 11. Epipod with 2–3 plumose setae and 4–5 long naked setae.

Maxilliped 3. (Figure 14*b*.) Exopod setation 5–7, with 5–6 setae on flagellum. Endopod setation 26–27, 14–15, 9–11, 9–11, 9. Dorsal edge of merus with several cornified teeth, ventral edge of merus with 1–2 cornified teeth. Epipod with 9–10 plumose setae and 16–17 long naked setae.

Pereopods. Chelipeds (figure 10*b*, 11*b*) as described for general panopeid first crab. Fingers with light brown pigmentation. Dactyl of cheliped lacking basal tooth. Pereopod 5 (figure 13*b*ii) with 0–1 (usually 0) subterminal dorsal spine on dactyl.

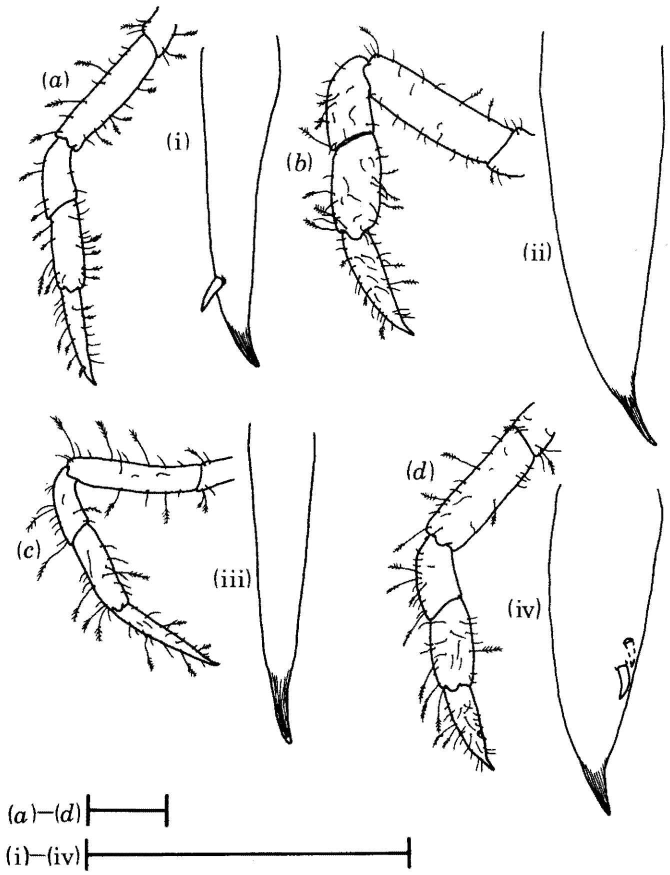


FIGURE 13. Pereopod 5 of the first crab stages. (*a*)–(*d*) Entire pereopod; (i)–(iv), dactyl with setae removed. (*a*i) *Panopeus bermudensis*; (*b*ii), *Panopeus herbstii*; (*c*iii), *Panopeus turgidus*; (*d*iv), *Eurypanopeus depressus*. Scale = 0.25 mm.

(iv) Panopeus turgidus, *Rathbun*, 1930, *first crab stage*

Carapace. (Figures 10*c*, 11*c*.) As described for general panopeid first crab. Usually without medial notch in frontal margin in frontal view. No granulated ridges present. Carapace almost as long as wide, but variable.

Eyes, telson and abdomen. (Eyes, figure 10*c*.) As described for general panopeid first crab.

Mandible. (Figure 15*e*.) Palp setation 0–1, 7–8.

Maxillule. (Figure 15*f*.) Endopod with 3–5 setae, arranged 1–2, 3–4. Basal endite with 18–21 cuspidate and serrate spines and setae, coxal endite with 13–14 spines and setae.

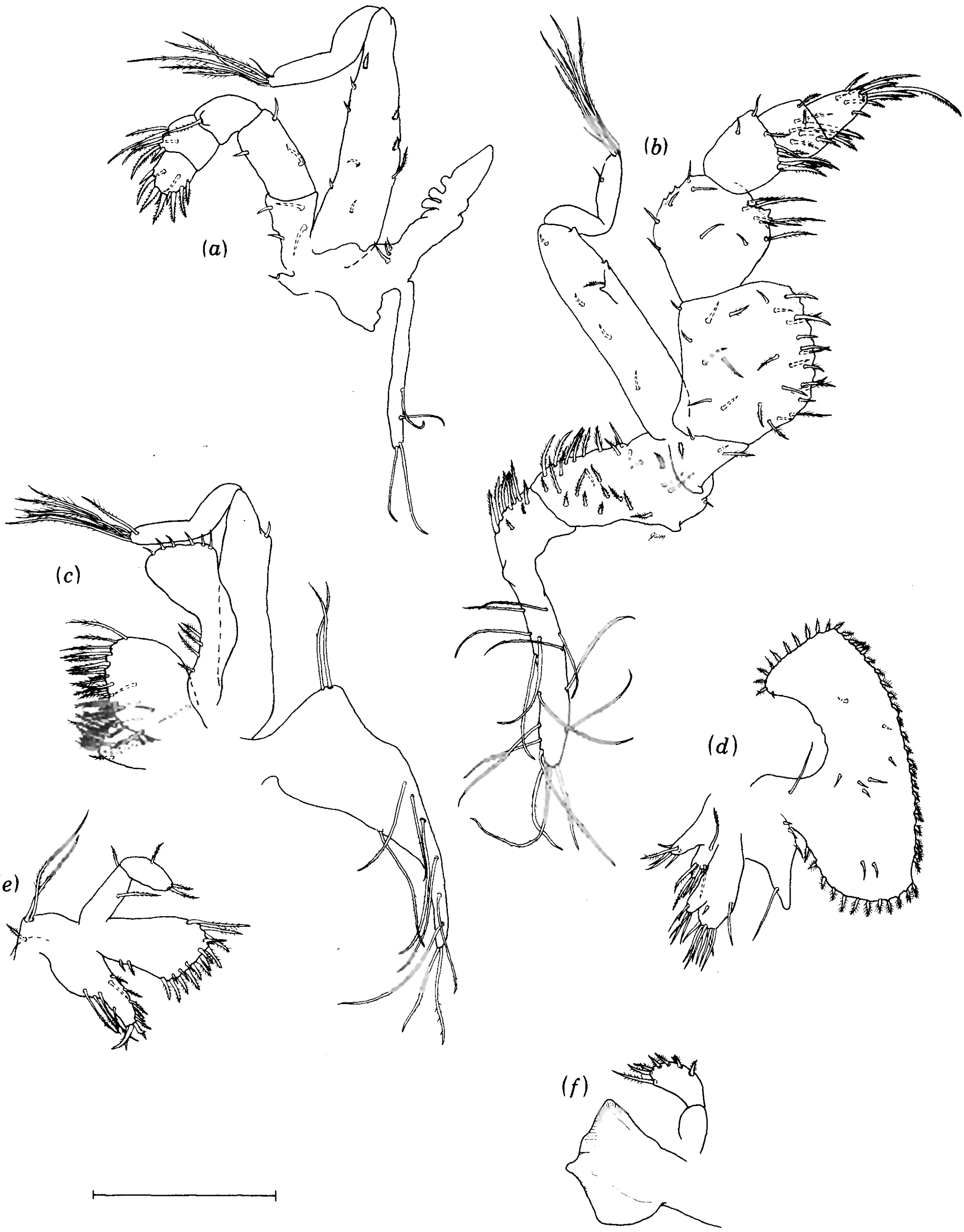


FIGURE 14. *Panopeus herbstii*, first crab stage mouthparts. (*a*) Maxilliped 2; (*b*) maxilliped 3; (*c*) maxilliped 1; (*d*) maxilla; (*e*) maxillule; (*f*) mandible. Scale = 0.25 mm.

Maxilla. (Figure 15*d*.) Endopod with 1–7 plumose setae. Basal and coxal endites with setation 8+5–8 and 5+3–4, respectively. Scaphognathite with 40–45 fringing setae and 6–7 setae on blade.

Maxilliped 1. (Figure 15*c*.) Exopod setation 0–2, 5–6. Endopod with 7–11 setae, 4–5 of which are short terminal spines. Medial distal tip of endopod often produced into a blunt setose

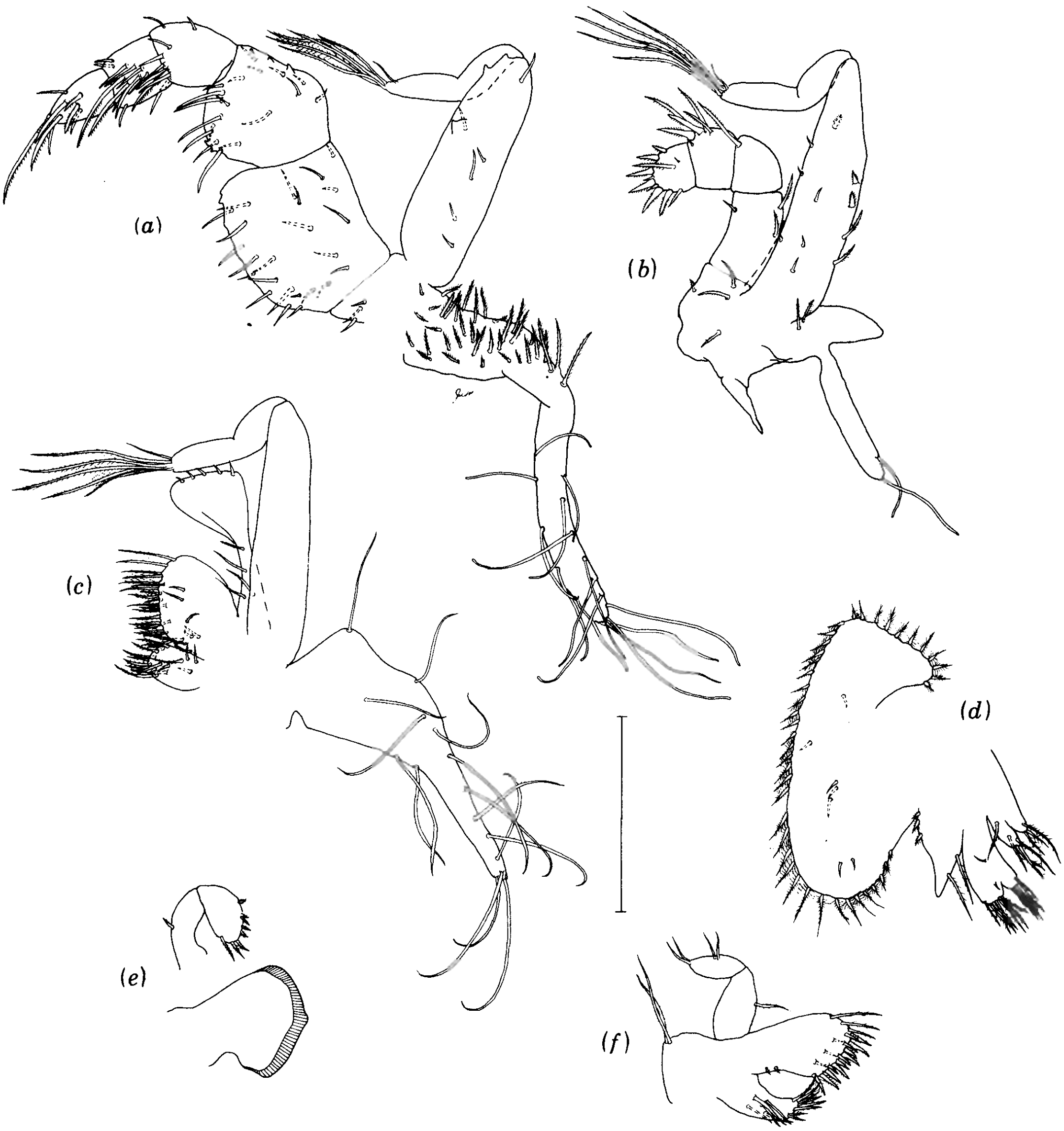


FIGURE 15. *Panopeus turgidus*, first crab stage mouthparts. (*a*) Maxilliped 3; (*b*) maxilliped 2; (*c*) maxilliped 1; (*d*) maxilla; (*e*) mandible; (*f*) maxillule. Scale = 0.25 mm.

process. Basal endite with 25–27 setae, coxal endite with 14–16 setae. Epipod with 14–17 long naked setae.

Maxilliped 2. (Figure 15*b*.) Expopod setation 7–12, 5–6. Endopod setation 3, 1, 6, 10–13. Epipod with 2–3 plumose setae and 2–5 long naked setae.

Maxilliped 3. (Figure 15*a*.) Exopod setation 3–7, 5–7. Endopod setation 19–26, 14–18, 9–10, 8–11, 8–9. Epipod with 5–7 plumose setae and 15–18 long naked setae.

Pereopods. Chelipeds as described for general panopeid first crab. Pereopod 5 (figure 13*c*iii) with 0–1 dorsal subterminal spine on dactyl.

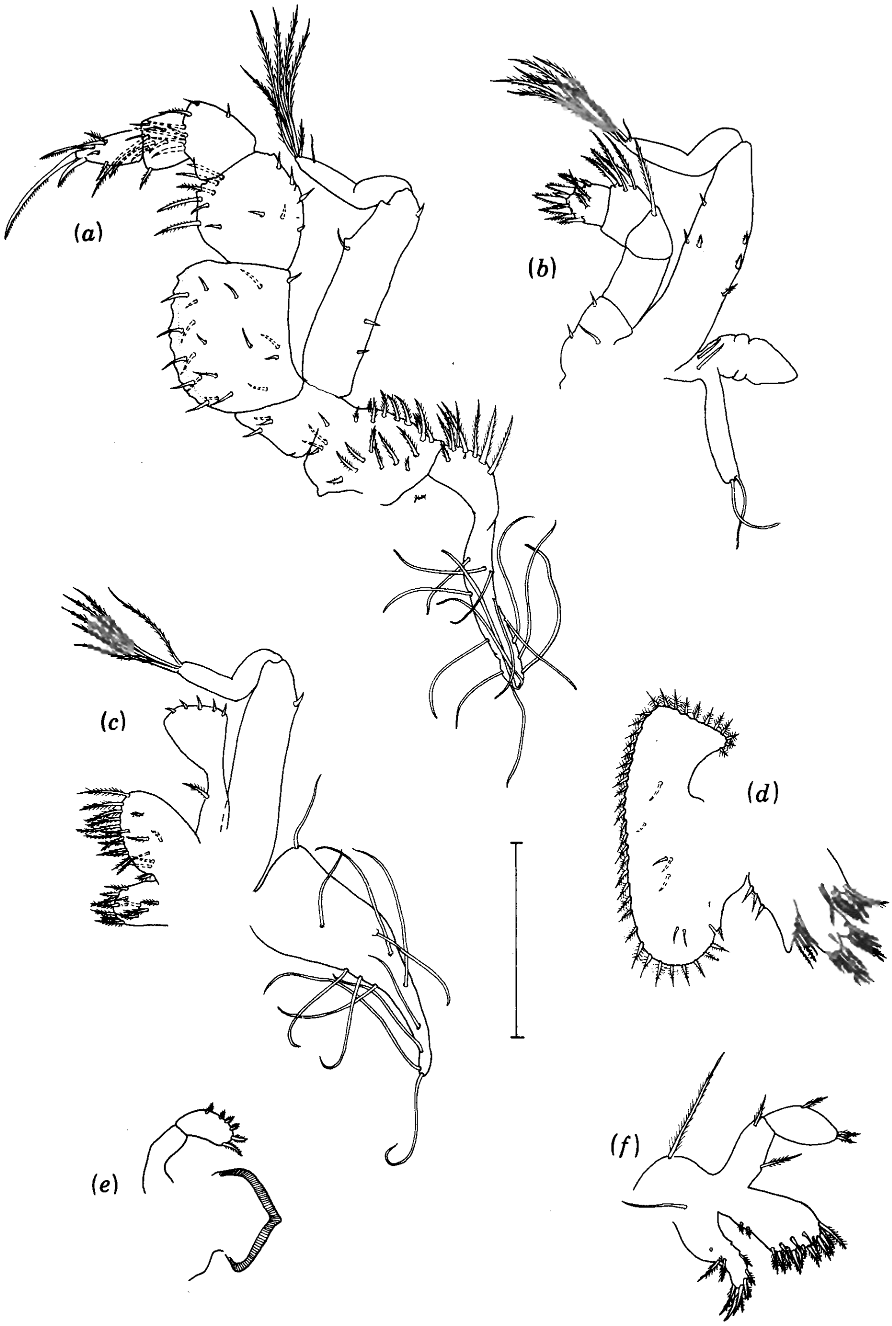


FIGURE 16. *Eurypanopeus depressus*, first crab stage mouthparts. (*a*) Maxilliped 3; (*b*) maxilliped 2; (*c*) maxilliped 1; (*d*) maxilla; (*e*) mandible; (*f*) maxillule. Scale = 0.25 mm.

(v) Eurypanopeus depressus (*Smith* 1869), *first crab stage*

Carapace. (Figures 10*d*, 11*d*.) As described for general panopeid first crab. Almost always with 2–3 granules in an oblique line on the branchial region. Frontal margin without distinct medial notch in frontal view.

Eyes, telson and abdomen. (Eyes, figure 10*d*.) As described for general panopeid first crab.

Mandible. (Figure 16*e*.) Palp setation 0, 6–7 (usually 6).

Maxillule. (Figure 16*f*.) Endopod with 3–5 setae, 1–2, 2–3. Basal endite with 18–20 cuspidate and serrate spines and setae, coxal endite with 13–15 spines and setae.

Maxilla. (Figure 16*d*.) Endopod with 3–4 plumose setae. Basal and coxal endites with setation 6–7 + 5–6 and 4–5 + 3–4, respectively. Scaphognathite with 40–45 fringing setae and 6–7 setae on blade.

Maxilliped 1. (Figure 16*c*.) Exopod setation 1, 6. Endopod with 2–10 setae, usually with 4–5 short terminal spines. Basal endite with 20–25 setae, coxal endite with 15–19 setae. Epipod with 12–17 long naked setae.

Maxilliped 2. (Figure 16*b*.) Exopod setation 6–12, 5–6. Endopod setation 0–1, 1, 5, 11. Epipod with 1–2 plumose setae and 2–4 long naked setae.

Maxilliped 3. (Figure 16*a*.) Exopod setation 5–8, 6–7. Endopod setation 19–21, 13–14, 8–9, 7–9, 7–8. Epipod with 9–10 plumose setae and 14–19 long naked setae.

Pereopods. Chelipeds (figure 10*d*, 11*d*) with obvious tubercles on manus and carpus; fingers light brown. Pereopod 5 (figure 13*d*iv) with 1–4 terminal spines dorsally and ventrally on dactyl.

(vi) *General description of the panopeid second crab*

Carapace. Ovate to hexagonal, usually wider than long. Four anterolateral teeth, often with lateral spinules. (These four teeth are actually teeth 1, 3, 4 and 5 in the adult; anterolateral tooth 2 is not yet developed.) Frontal margin bilobed and minutely crenulate, with medial depression. Medial portion of orbital groove apparent. Depression between anterolateral teeth distinct, other areolations variable in development. Border of orbit minutely crenulate, usually fringed with several short setae. Not as deep in frontal view as first crab stages. Posterolateral borders granulate on ventral surface. Mesogastric region somewhat more clearly defined than in first crab stage. Setae mostly in gastric and hepatic regions. Sternum broadly triangular and sparsely setose.

Eyes. Large, occasionally extending beyond widest point of carapace. Indistinct separation of cornea from eyestalk.

Abdomen. Tightly flexed beneath thorax. Segments not fused.

Telson. Broadly triangular, posterolateral borders rounded. Sparsely setose.

Mouthparts. Not examined.

Pereopods. Chelipeds more or less symmetrical, with thin transparent cutting edge on both fingers. Pigmentation of fingers more apparent than in first crab stage. Carpus and manus tuberculate, less so on merus and basi-ischium. Basi-ischium with 2–3 anteriorly directed spines on ventrolateral border. Merus with several tubercles in a proximal-distal line on the ventral surface. Dorsum of dactyl with several small tubercles. Pereopod 5 not examined.

(vii) Panopeus bermudensis, *second crab stage*

Carapace. (Figures 17*a*, *b*.) Approximately hexagonal. Anterolateral teeth large and widely tapering, the last two directed more or less outward. First and second (first and third of adult) anterolateral teeth always with several spinules on outer border; other anterolateral teeth occasionally with spinules. Usually with 2–3 granules in an oblique line on the branchical region. Areolations distinct in frontal view. Frontal margin usually with wide shallow medial notch in frontal view.

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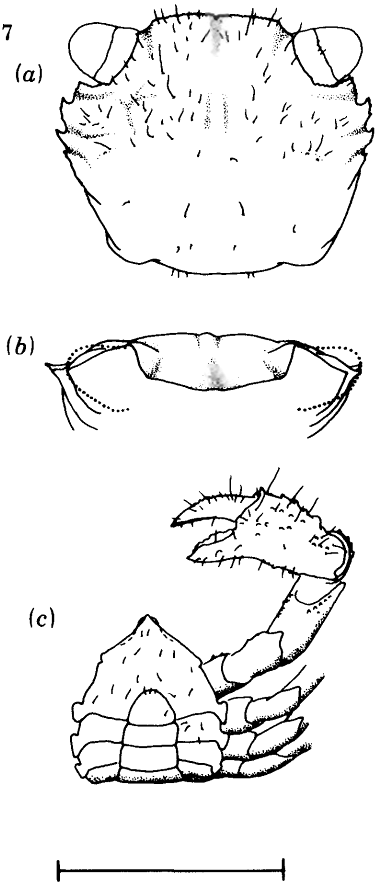

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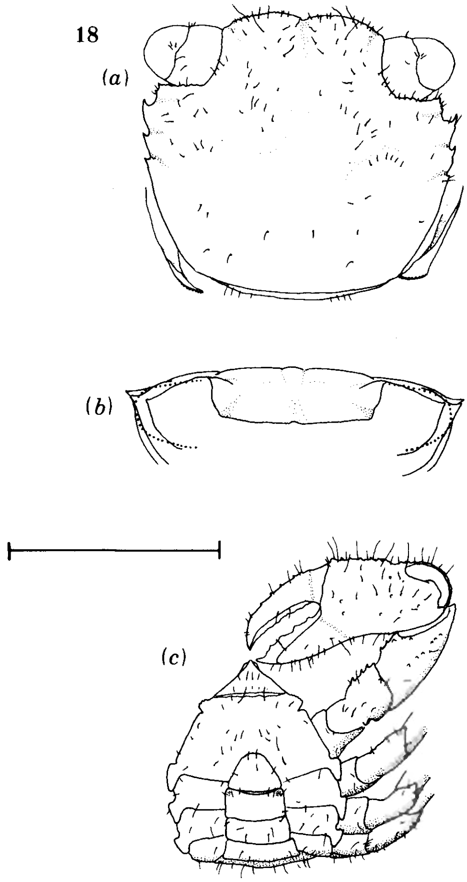


FIGURE 17. *Panopeus bermudensis*, second crab stage. (*a*) Carapace and eyes, dorsal view; (*b*) carapace, frontal view; (*c*) sternum and left pereopods, ventral view. Scale = 1.0 mm.

FIGURE 18. *Panopeus herbstii*, second crab stage. (*a*) Carapace and eyes, dorsal view; (*b*) carapace, frontal view; (*c*) sternum and left pereopods, ventral view. Scale = 1.0 mm.

Cheliped. (Figure 17*c*.) Large, distinct, numerous spines and tubercles on carpus and manus. Fingers without pigmentation.

(viii) Panopeus herbstii, *second crab stage*

Carapace. (Figures 18*a*, *b*.) Ovate to subquadrate. Anterolateral teeth directed forward, with lateral spinules, tapering broadly at first but terminating in a sharp, clear spine. Frontal margin usually with shallow medial notch in frontal view. No granules on branchial region.

Cheliped. (Figure 18*c*.) Distinct spines and tubercles on carpus and manus. Fingers light brown with large transparent cutting edges.

(ix) Panopeus turgidus, *second crab stage*

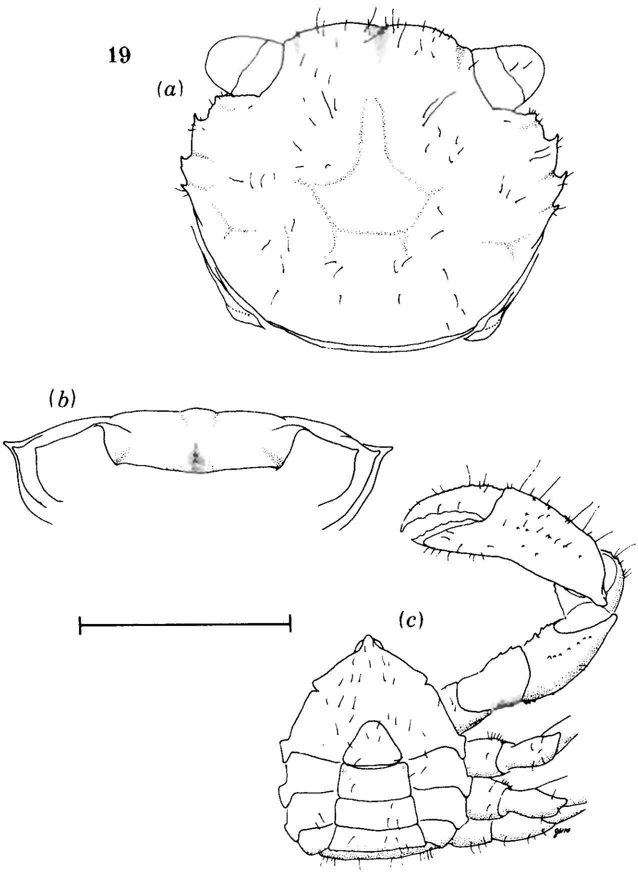
Carapace. (Figures 19*a*, *b*.) Ovate to subquadrate, with rounded and slightly produced frontal margin, without medial notch in frontal view. Anterolateral teeth ending in a sharp spine; third and fourth teeth usually directed outward. Occasionally with granules on branchial region.

Cheliped. (Figure 19*c*.) As described for general panopeid second crab. Fingers light brown.

(x) Eurypanopeus depressus, *second crab stage*

Carapace. (Figures 20*a*, *b*.) Broadly ovate, always with 3–5 granules in an oblique line across branchial region, usually with 2–3 granules on either side of the anterior projection of the mesogastric region. Frontal margin occasionally with shallow medial notch in frontal view. Anterolateral teeth often with lateral spinules; posterior-most two teeth usually directed outward.

Cheliped. (Figures 20*c*). Fingers light brown. No obvious 'spooning' of the immovable finger.



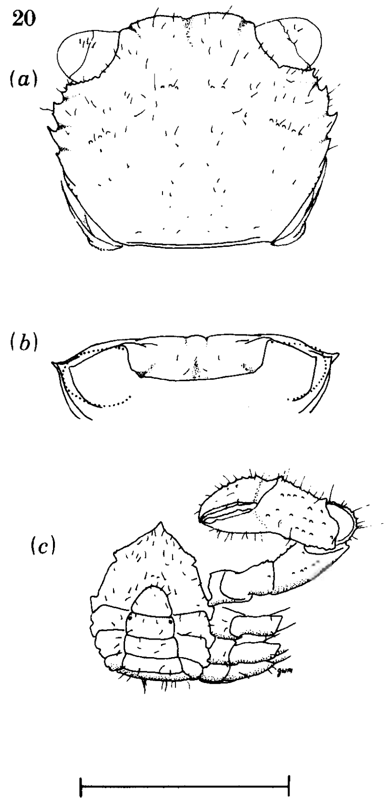


FIGURE 19. *Panopeus turgidus* second crab stage. (*a*) Carapace and eyes, dorsal view; (*b*) carapace, frontal view; (*c*) sternum and left pereopods, ventral view. Scale = 1.0 mm.

FIGURE 20. *Eurypanopeus depressus*, second crab stage. (*a*) Carapace and eyes, dorsal view; (*b*) carapace, frontal view; (*c*) sternum and left pereopods, ventral view. Scale = 1.0 mm.

(xi) *General description of the panopeid third crab*

Carapace. Ovate to hexagonal, always wider than long. Anterolateral teeth four, tooth 5 (the eventual tooth 2) can now be seen as a slight bulge on the posterolateral border of tooth 1. Frontal margin slightly bilobed and minutely crenulate, with central medial depression. Orbital groove distinct medially. Areolations now relatively distinct, especially the mesogastric region. Anterolateral borders appear as a clear, thin edge to the carapace. Posterior border of orbit minutely crenulate. Anterolateral teeth often with lateral spinules. Granulated ridges always present on branchial region, variable on other regions. Frontal view variable. Plumose setae scattered over carapace with smaller setae interspersed among them. Posterolateral borders granulate ventrally. Sternum broadly triangular and sparsely setose, occasionally with small tubercles just anterior to the telson.

Eyes. Large, never extending beyond widest point of carapace. Eyestalk slightly grooved just proximal to cornea.

Abdomen. As in second crab stage; segments not fused.

Telson. As in second crab stage.

Mandibles. Asymmetrical, with large spade-shaped cutting edge. Palp 2-segmented, with setation 1–5 and 6–10.

Maxillule. Endopod 2-segmented with 4–7 setae. Basal and coxal endites with many cuspidate spines and serrate setae. Protopodite area with 1–4 long plumose setae.

Maxilla. Endopod with 1–6 setae. Basal and coxal endites bilobed, each with numerous plumose setae. Scaphognathite with 50–73 short, plumose fringing setae and 10–21 setae on blade.

Maxilliped 1. Exopod 2-segmented, with several setae on proximal segment and 5–7 long plumose setae on flagellum. Endopod unsegmented, with 13–24 setae, several of which are short naked terminal spines; distal medial tip occasionally produced into a blunt process bearing additional setae. Epipod with 23–53 long setae, that now appear to be minutely serrulate.

Maxilliped 2. Exopod 2-segmented; proximal segment with 9–25 setae, flagellum with 5–6 long plumose setae. Proximal segment setation can be divided into lateral setae, lateral spines, medial spines, and a centrally located row of short spines. Endopod 4-segmented; distal two segments with several heavy cuspidate spines; carpus with 1–2 setae, one of which is long and extends beyond distal edge of propodus. Epipod with several plumose setae basally, and 5–13 long minutely serrulate setae.

Maxilliped 3. Exopod 2-segmented; proximal segment with 8–15 setae, flagellum with 6–7 long plumose setae in 2–3 tiers. Proximal segment of exopod with obvious setose protrusion about three quarters of the way distally along medial border. Medial border of exopod usually with several small tubercles; distal lateral edge with 1–2 plumose setae. Endopod 5-segmented with variable setation; distal two segments with long, heavy spines which are serrate along their distal half. Medial border of proximal segment scalloped. Medial and dorsal borders of merus with several blunt teeth.

Pereopods. Chelipeds more or less symmetrical; fingers still with a thin transparent cutting edge. Pigmentation on fingers more distinct. Carpus, manus and dactyl all tuberculate. Ventral margin of merus with row of granules; ventrolateral border of basi-ischium with several sharp anteriorly projecting spinules. Carpus of cheliped with prominent anteromedial tooth. Pereopod 5 with 0–4 subterminal spines on dactyl, variable with species.

(xii) Panopeus bermudensis, *third crab stage*

Carapace. (Figures 21 *a*, *b*.) Distinct areolations defined by relatively deep grooves. Mesogastric region well defined; branchial region subdivided by faint grooves. Always with 6–10 granules in an oblique line on the branchial region, often with granules on protogastric region extending from last anterolateral tooth into mesobranchial region. Frontal margin usually with shallow medial notch in frontal view. Deep, robust in frontal view. Anterolateral teeth wide, spatulate, and with many small spinules on borders; last two teeth directed more or less outward. Posterolateral borders relatively straight, usually granulate.

Abdomen and telson. (Figure 21*c*.) As described for general panopeid third crab.

Mandible. (Figure 22*f*.) Palp setation 3–4, 9–10 (usually 9).

Maxillule. (Figure 22*e*.) Endopod with 4–6 setae, usually arranged 2–4, 2. Protopodite area with 1–2 setae. Basal endite with 22–25 spines and setae, coxal endite with 15–17 spines and setae.

Maxilla. (Figure 22*d*.) Endopod with 1–2 long plumose setae and 2–4 short setae. Basal and coxal endites with setation 11–12 + 7–9 and 5–6 + 4–5, respectively. Scaphognathite with 61–73 fringing setae and 20–22 setae on blade.

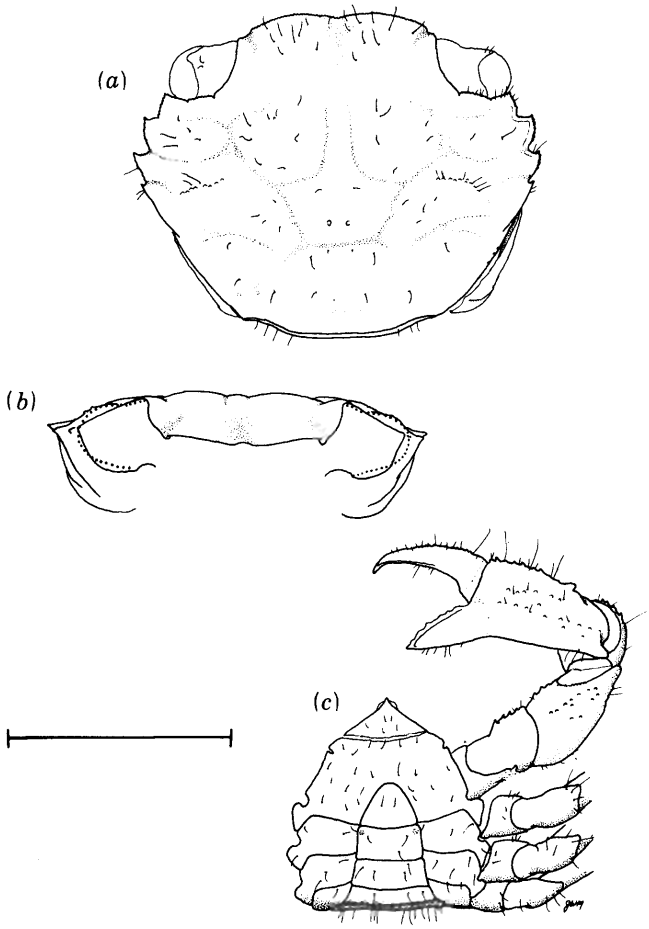


FIGURE 21. *Panopeus bermudensis*, third crab stage. (*a*) Carapace and eyes, dorsal view; (*b*) carapace, frontal view; (*c*) sternum and left pereopods, ventral view. Scale = 1.0 mm.

Maxilliped 1. (Figure 22*c*.) Exopod setation 5–6, 6–7. Endopod with 14–19 setae, 6–8 of which are short terminal spines. Basal and coxal endites with 41–43 and 20–23 setae, respectively. Epipod with 38–53 long setae.

Maxilliped 2. (Figure 22*b*.) Exopod setation 17–25, 5–6. Endopod setation 6–7, 1, 10–11, 11–12. Epipod with 6–7 plumose setae and 9–12 long setae.

Maxilliped 3. (Figure 22*a*.) Exopod setation 8–12, 6–8. Endopod setation 29–34, 20–22, 15–17, 12, 9. Epipod with about 20 plumose setae and 22–27 long setae.

FIGURE 22. *Panopeus bermudensis*, third crab stage mouthparts. (*a*) Maxilliped 3; (*b*) maxilliped 2; (*c*) maxilliped 1; (*d*) maxilla; (*e*) maxillule; (*f*) mandible. Scale = 0.25 mm.

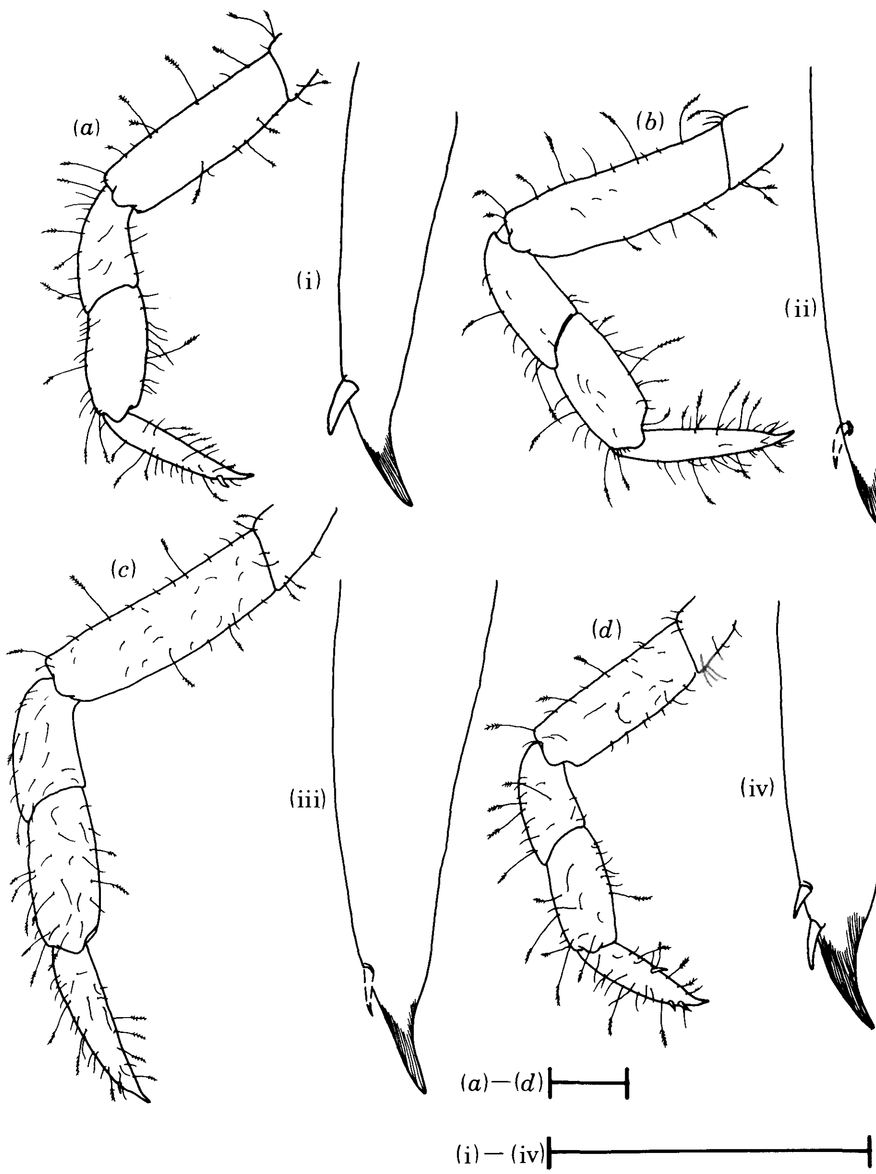


FIGURE 23. Pereopod 5 of third crab stages. (*a*)–(*e*) Entire pereopod; (i)–(iv) dactyl with setae removed. (*a*i) *Panopeus bermudensis*; (*b*ii) *Panopeus herbstii*; (*c*iii) *Panopeus turgidus*; (*d*iv) *Eurypanopeus depressus*. Scale = 0.25 mm.

Pereopods. Chelipeds (figure 21*c*) with fingers white. Movable finger without evidence of a basal tooth. Pereopod 5 (figure 23*a*i) with 1–2 dorsal subterminal spines on dactyl.

(xiii) Panopeus herbstii, *third crab stage*

Carapace. (Figures 24*a*, *b*.) Mesogastric region obvious, branchial regions subdivided. Anterolateral teeth displaced anteriorly, ending in a short, sharp spine, occasionally with lateral spinules. Occasionally with 1–2 granules on branchial region. Posterolateral borders straight, usually with granules on ventral margin.

Abdomen and telson. (Figure 24*c*.) As described for general panopeid third crab.

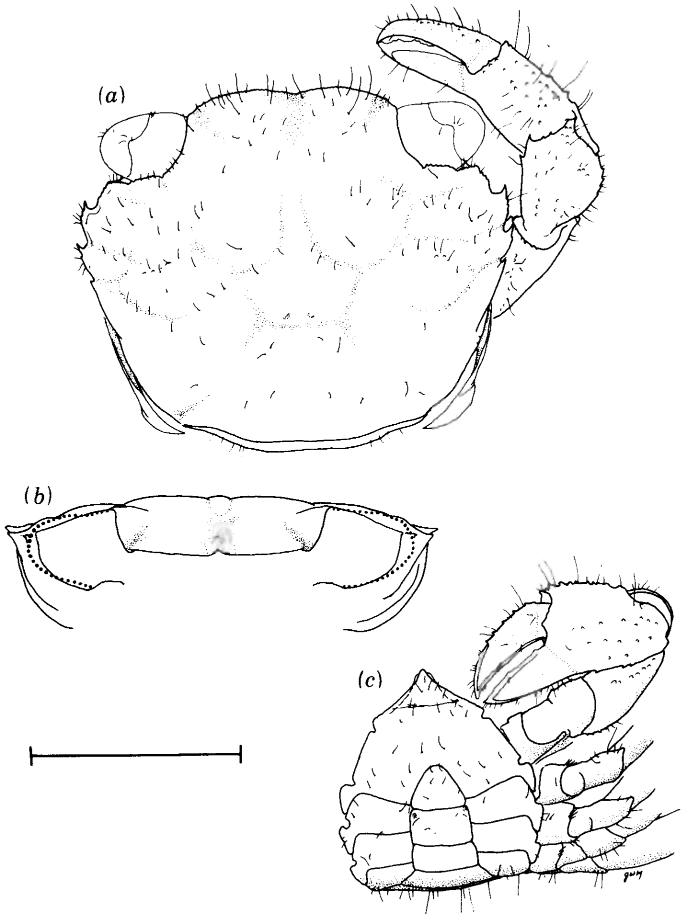


FIGURE 24. *Panopeus herbstii*, third crab stage. (*a*) Carapace, eyes, and right chela, dorsal view; (*b*) carapace, frontal view; (*c*) sternum and left pereopods, ventral view. Scale = 1.0 mm.

Mandible. (Figure 25*e*.) Palp setation 3–4, 8–10 (usually 9).

Maxillule. (Figure 25*f*.) Endopod with 6–7 setae, arranged 3–4, 3. Protopodite area with 3–4 setae. Basal and coxal endites with 20–22 and 15–16 spines and setae, respectively.

Maxilla. (Figure 25*d*.) Endopod with 1–6 setae. Setation of basal and coxal endites 15 + 8–9, 7 + 4, respectively. Scaphognathite with 62–70 fringing setae and 18–20 setae on blade.

Maxilliped 1. (Figure 25*c*.) Exopod setation 3–4, 5–6. Endopod with 17–24 setae, 10–12 of which are short terminal spines. Basal and coxal endites with 39–41 and 27–30 setae, respectively. Epipod with 25–33 long setae.

Maxilliped 2. (Figure 25*b*.) Exopod setation 11–12, 5–6. Endopod setation 10–11, 2, 7–11, 12. Epipod with 7–8 plumose setae and 7–13 long setae.

Maxilliped 3. (Figure 25*a*.) Exopod setation 9–13, 6–7. Endopod setation 40–42, 30–31, 18–19, 14, 10–11. Epipod with 22–26 plumose setae and 24–28 long setae.

Pereopods. Chelipeds (figure 24*c*) with brown fingers. Movable finger without evidence of a basal tooth. Pereopod 5 (figure 23*b* ii) with 0–1 (usually 0) dorsal subterminal spines on dactyl.

FIGURE 25. *Panopeus herbstii*, third crab stage mouthparts. (*a*) Maxilliped 3; (*b*) maxilliped 2; (*c*) maxilliped 1; (*d*) maxilla; (*e*) mandible; (*f*) maxillule. Scale = 0.25 mm.

(xiv) Panopeus turgidus, *third crab stage*

Carapace. (Figures 26*a*, *b*.) Ovate; posterolateral borders rounded. Anterolateral teeth terminating in a sharp spine; posterior two teeth directed more or less outward. Occasionally with 2–4 granules forming an oblique line on the branchial region, rarely with many granules on branchial region and additional granulated lines on protogastric, mesogastric and mesobranchial regions. Deep, robust in frontal view; carapace slightly dorsally inflated. Usually without shallow medial notch in frontal margin in frontal view.

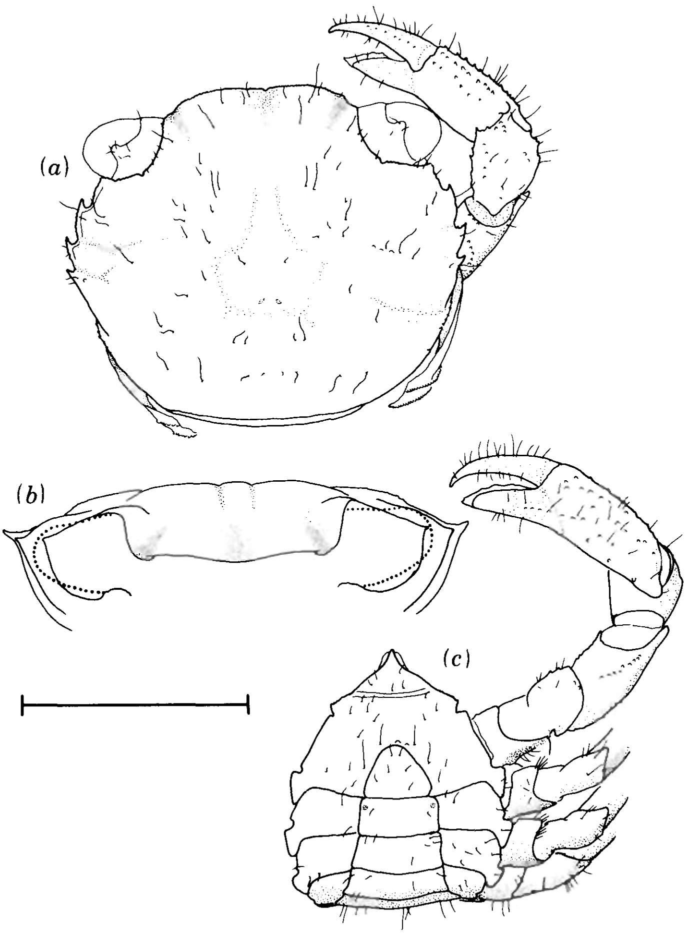


FIGURE 26. *Panopeus turgidus*, third crab stage. (*a*) Carapace, eyes, and right chela, dorsal view; (*b*) carapace, frontal view; (*c*) sternum and left pereopods, ventral view. Scale = 1.0 mm.

Abdomen and telson. (Figure 26*c*.) As described for general panopeid third crab.

Mandible. (Figure 27*e*.) Palp setation 1–3, 7–8 (usually 8).

Maxillule. (Figure 27*f*.) Endopod with 7 setae, arranged 3, 4. Basal and coxal endites with 18–20 and 12–13 spines and setae, respectively. Protopodite area with 1–2 long plumose setae.

Maxilla. (Figure 27*d*.) Endopod with 3–6 setae. Setation of basal and coxal endites 9–11 + 8–9 and 5 + 7, respectively. Scaphognathite with 50–67 fringing setae and 10–12 setae on blade.

Maxilliped 1. (Figure 27*c*.) Exopod setation 2–3, 5–6. Endopod with 18–24 setae, 3–10 of

FIGURE 27. *Panopeus turgidus*, third crab stage mouthparts. (*a*) Maxilliped 3; (*b*) maxilliped 2; (*c*) maxilliped 1; (*d*) maxilla; (*e*) mandible; (*f*) maxillule. Scale = 0.25 mm.

which are short terminal spines. Medial edge of distal border of endopod often produced into a blunt process with additional setae (illustrated). Basal and coxal endites with 35–41 and 20–22 setae, respectively. Epipod with 23–36 long setae.

Maxilliped 2. (Figure 27*b*.) Exopod setation 9–22, 5–7. Endopod setation 4, 1–2, 7–8, 11–13. Epipod with 2–4 plumose setae and 5–11 long setae.

Maxilliped 3. (Figure 27*a*.) Exopod setation 8–15, 5–7. Endopod setation 27–28, 20–22, 12, 10, 8–10. Epipod with 11–15 plumose setae and 18–23 long setae.

Pereopods. Cheliped (figure 26*c*) with brown fingers, light toward the distal end. Pereopod 5 (figure 23*c*iii) with 0–2 subterminal dorsal spines on dactyl.

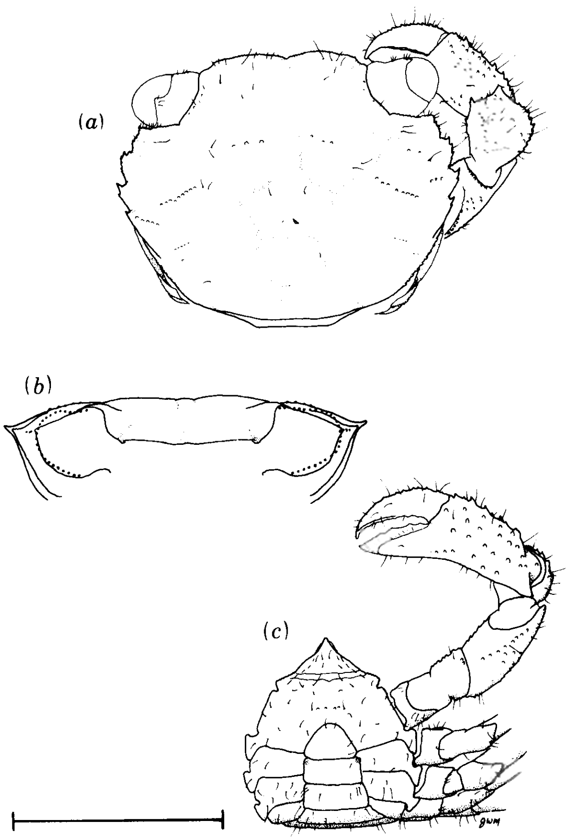


FIGURE 28. *Eurypanopeus depressus*, third crab stage. (*a*) Carapace, eyes, and right chela, dorsal view; (*b*) carapace, frontal view; (*c*) sternum and left pereopods, ventral view. Scale = 1.0 mm.

(xv) Eurypanopeus depressus, *third crab stage*

Carapace. (Figures 28*a*, *b*.) Broadly ovate; posterolateral borders rounded. Anterolateral teeth always with lateral spinules; the first two teeth broad, the last two sharp and directed more or less outward. Always with granulated ridge on each branchial region, a shorter row of granules on each protogastric region, and several short rows extending from the posterior anterolateral tooth into the mesobranchial region. Thin, somewhat flattened in frontal view. Usually without medial notch in frontal margin in frontal view.

Abdomen and telson. (Figure 28*c*.) As described for general panopeid third crab.

Mandible. (Figure 29*e*.) Palp setation 1, 6–7 (usually 7).

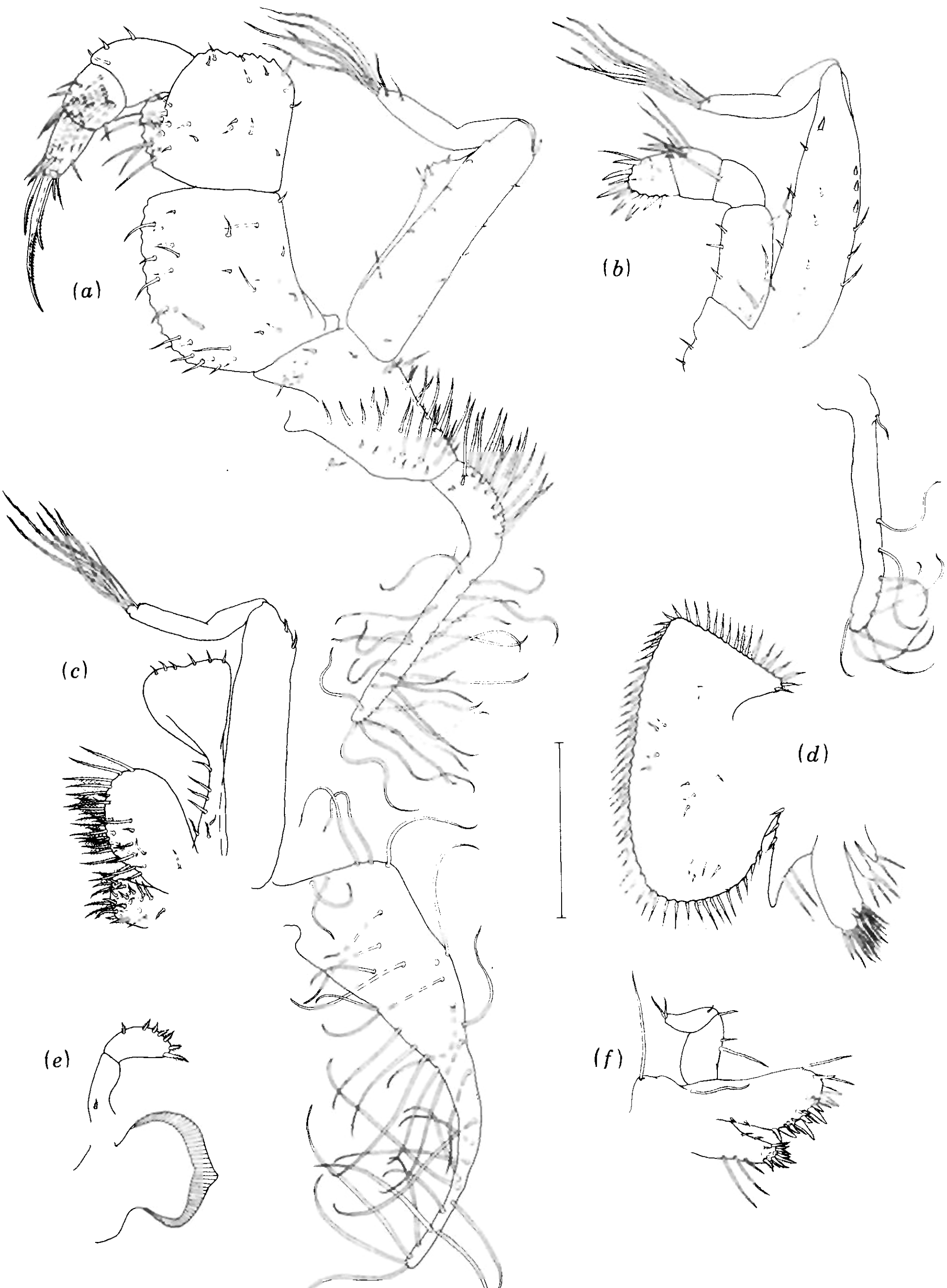


FIGURE 29. *Eurypanopeus depressus*, third crab stage mouthparts. (*a*) Maxilliped 3; (*b*) maxilliped 2; (*c*) maxilliped 1; (*d*) maxilla; (*e*) mandible; (*f*) maxillule. Scale = 0.25 mm.

Maxillule. (Figure 29*f*.) Endopod with 4–7 setae, arranged 1–4, 3. Protopodite area with 1–2 long plumose setae. Basal and coxal endites with 18–21 and 13–16 spines and setae, respectively.

Maxilla. (Figure 29*d*.) Endopod with 1–3 setae. Setation of basal and coxal endites 6–7 + 6–7 and 3–4 + 2–3, respectively. Scaphognathite with 50–60 fringing setae and 13–14 setae on blade.

Maxilliped 1. (Figure 29*c*.) Exopod setation 2–3, 5–6. Endopod with 13–15 setae, 5–6 of which are short terminal spines. Basal and coxal endites with 30–33 and 20–23 setae, respectively. Epipod with 27–35 long setae.

Maxilliped 2. (Figure 29*b*.) Exopod setation 12–18, 5–6. Endopod setation 6, 1, 7–8, 10–12. Epipod with 2–5 plumose setae and 9–10 long setae.

Maxilliped 3. (Figure 29*a*.) Exopod setation 8–13, 5–7. Endopod setation 29–30, 24–25, 9–14, 13, 8–9. Epipod with 16–17 plumose setae and 18–23 long setae.

Pereopods. Chelipeds (figures 28*a*, *c*) with brown fingers, pigment fading toward distal tip. Immovable finger with no evidence of 'spooning'. Pereopod 5 (figure 23*d*iv) with 2–4 subterminal spines on dorsal and ventral surfaces of dactyl.

(xvi) *General description of the panopeid fifth crab*

Carapace. Ovate to hexagonal, always wider than long. Five anterolateral teeth, the second is a rounded bulge on what was the posterior border of the first anterolateral tooth and is not always obvious. Other anterolateral teeth are sharp and may have spinules along anterior and posterior borders. The fifth tooth is much smaller than the first four teeth. Frontal margin slightly bilobed and minutely crenulate, with obvious medial depression. Areolations more obvious than in third crab stage. Mesogastric region always clearly defined. Granulated ridges always present on branchial regions, variably present on protogastric, mesogastric, mesobranchial and hepatic regions. Plumose setae scattered over carapace, with minute setae interspersed among them. Frontal view varies with species and may be deep and robust or thin and flattened. Posterolateral borders with ventral granulations, not always visible in dorsal view. Orbital groove now extends around and behind orbit. Posterior margin of orbit minutely crenulate. Anterolateral borders of carapace appear as a thin, transparent margin. Sternum broadly triangular, often with 2–5 tubercles just anterior to telson, and sparsely setose.

Eyes. Moderately large, never extending beyond second anterolateral tooth. Eyestalk with obvious blunt protrusion into corneal area, and with shallow wide groove just proximal to cornea.

Abdomen. Triangular, segments unfused. Sexual dimorphism not apparent, except in one example of *Panopeus bermudensis* where immature male gonopods were observed. Subterminal segment appears slightly longer than preceding segments.

Telson. Broadly triangular, posterior borders rounded. Setation variable.

Mandibles. Asymmetrical, with broad, spade-shaped cutting edge thickly cornified. Palp 2-segmented, setation 4–8, 8–18.

Maxillule. Endopod 2-segmented with 7–10 setae, usually arranged 4–6, 2–4. Distal segment of endopod always with two stout terminal setae; other setation variable. Basal and coxal endites with many heavy cuspidate spines and serrate setae. Spines do not appear as serrate as in earlier stages, smoother. Protopodite area with 2–5 long plumose setae.

Maxilla. Endopod with 1–6 setae, basal and coxal endites bilobed and with many plumose setae. Scaphognathite with 70–121 fringing setae and 22–59 setae on blade.

Maxilliped 1. Exopod 2-segmented, with 2–15 setae on proximal segment and 6–8 long plumose setae arranged in 3–4 tiers on flagellum. Epipod with 21–58 setae, several of which are short terminal spines. Medial edge of distal portion may be produced into a blunt process with 1–4 long setae (for example figure 38*a*); this condition may exist on one, both, or neither first maxillipeds in a single individual. Basal and coxal endites heavily setose. Epipod long and curved, with 52–98 long setae, some of which appear minutely serrulate; several short spines occasionally interspersed among these long setae.

Maxilliped 2. Exopod 2-segmented; proximal segment with 24–66 setae, flagellum with 6–7 long plumose setae arranged in 2–3 tiers. Setae on proximal segment always arranged as one medial row of short setae, one row of lateral setae which gives rise to thick serrate spines, one central row of short setae, and 1–3 thick distal spines. Endopod 4-segmented, distal segment with many heavy cuspidate spines that appear somewhat smoother than in earlier stages. Carpus with 3–4 setae, one of which extends beyond propodus. Epipod with several plumose setae and 19–45 long minutely serrulate setae.

Maxilliped 3. Exopod 2-segmented; proximal segment with 19–45 setae, flagellum with 7–9 long plumose setae arranged in 3–4 tiers, usually two setae per tier. Medial border of proximal segment of exopod with distinct row of tubercles and with prominent setose toothed projection about three quarters of the way distally along medial border. Lateral and medial borders of exopod with corneous border. Endopod 5-segmented; ischium with long diagonal groove on outer face, scalloped medial border and several corneous distal tubercles. Merus of endopod with medial circular depression on outer face, and several large tubercles. Inner face of merus with many plumose setae opposite the circular depression on outer face. Distal and medial borders of merus cornified and with several blunt teeth; lateral border cornified but without teeth. Distal two segments with long, heavy spines which are serrate along distal half. Many minute setae scattered over outer face of endopod and exopod. Epipod with many plumose setae and 25–63 long minutely serrulate setae. No oval red spot seen on inner face of ischium of endopod.

Pereopods. Chelipeds still with thin transparent cutting edge on fingers, and more or less symmetrical. Occasionally the beginnings of a basal tooth detectable on movable finger. Colour of fingers obvious. Carpus and manus tuberculate; carpus with prominent anteromedial tooth and several small spinules along anteromedial border. Merus and basi-ischium with ventral row of granules. Dorsal edge of manus with shallow proximal-distal groove bordered on either side by a distinct row of tubercles. Pereopod 5 with 0–7 subterminal spines on dactyl, variable with species.

(xvii) Panopeus bermudensis, *fifth crab stage*

Carapace. (Figures 30*a*, *b*.) Distinct areolations defined by deep grooves. Anterolateral teeth broad and spatulate, curved slightly dorsally at tips, and with many spinules on borders. Always with granulated ridges on the branchial region, hepatic region, mesobranchial region along the fifth anterolateral tooth, and one to two granulated ridges on each protogastric region. Posterior (fifth) anterolateral tooth directed more or less outward, not forward. Deep in frontal view; distinct regions of the carapace more apparent in frontal view; granulated ridges on branchial region obvious. Frontal margin usually with wide shallow medial notch in frontal view. Distinct double row of granules along frontal margin not yet developed. Posterolateral borders drop sharply away from fifth anterolateral tooth toward posterior border.

Abdomen and telson. (Figure 30*b*.) As described for general panopeid fifth crab.

Mandible. (Figure 31*b*.) Palp setation 3–4, 14–17.

Maxillule. (Figure 32*c*.) Endopod with 7–9 setae, arranged 4–6, 3. Protopodite area with 2–3 setae. Basal and coxal endites with 33–35 and 20–21 spines and setae, respectively.

Maxilla. (Figure 31*c*.) Endopod with 0–2 setae. Basal endite with 18 + 11–12 setae, coxal endite with 6 + 5 setae. Scaphognathite with 87–105 fringing setae and 35–40 setae on blade.

Maxilliped 1. (Figure 32*a*.) Exopod setation 12–13 on proximal segment, flagellum with 7–8 setae. Endopod with 31–39 setae, 10–12 of which are short terminal spines. Basal and coxal endites with 67–68 and 35–39 setae, respectively. Epipod with 73–93 long setae.

Maxilliped 2. (Figure 32*b*.) Exopod setation 35–45 on proximal segment, flagellum with 6–7 setae. Endopod setation 16, 4, 12–14, 14–15. Epipod with 7–10 plumose setae and 23–29 long setae.

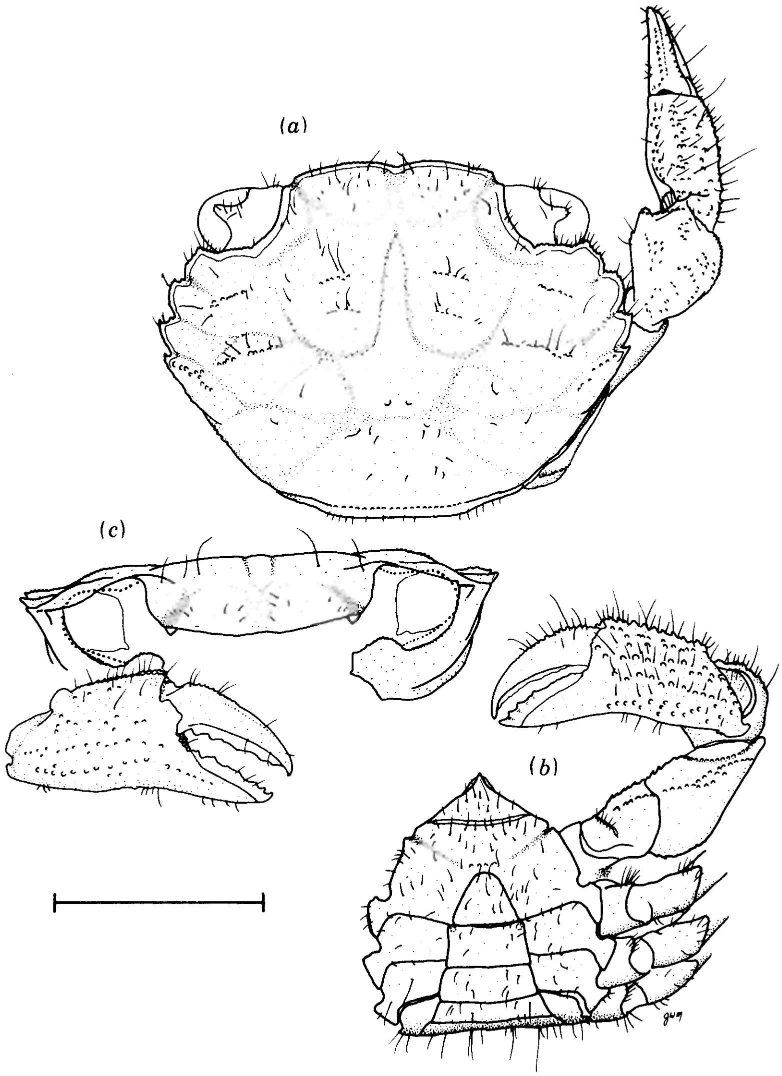


FIGURE 30. *Panopeus bermudensis*, fifth crab stage. (*a*) Carapace, eyes, and right chela, dorsal view; (*b*) carapace and right chela, frontal view; (*c*) sternum and left pereopods, ventral view. Scale = 1.0 mm.

Maxilliped 3. (Figure 31*a*.) Exopod setation 21–27 on proximal segment, flagellum with 7–9 setae. Endopod setation 56–64, 38–40, 32–33, 20–22, 12–14. Epipod with 34–35 plumose setae and 35–42 long setae.

Pereopods. Chelipeds (figures 30*a–c*) with light-coloured or white fingers. Movable finger with no evidence of basal tooth. Pereopod 5 (figure 33*a*i) with 1–3 subterminal spines on dorsal surface of dactyl, never on ventral surface.

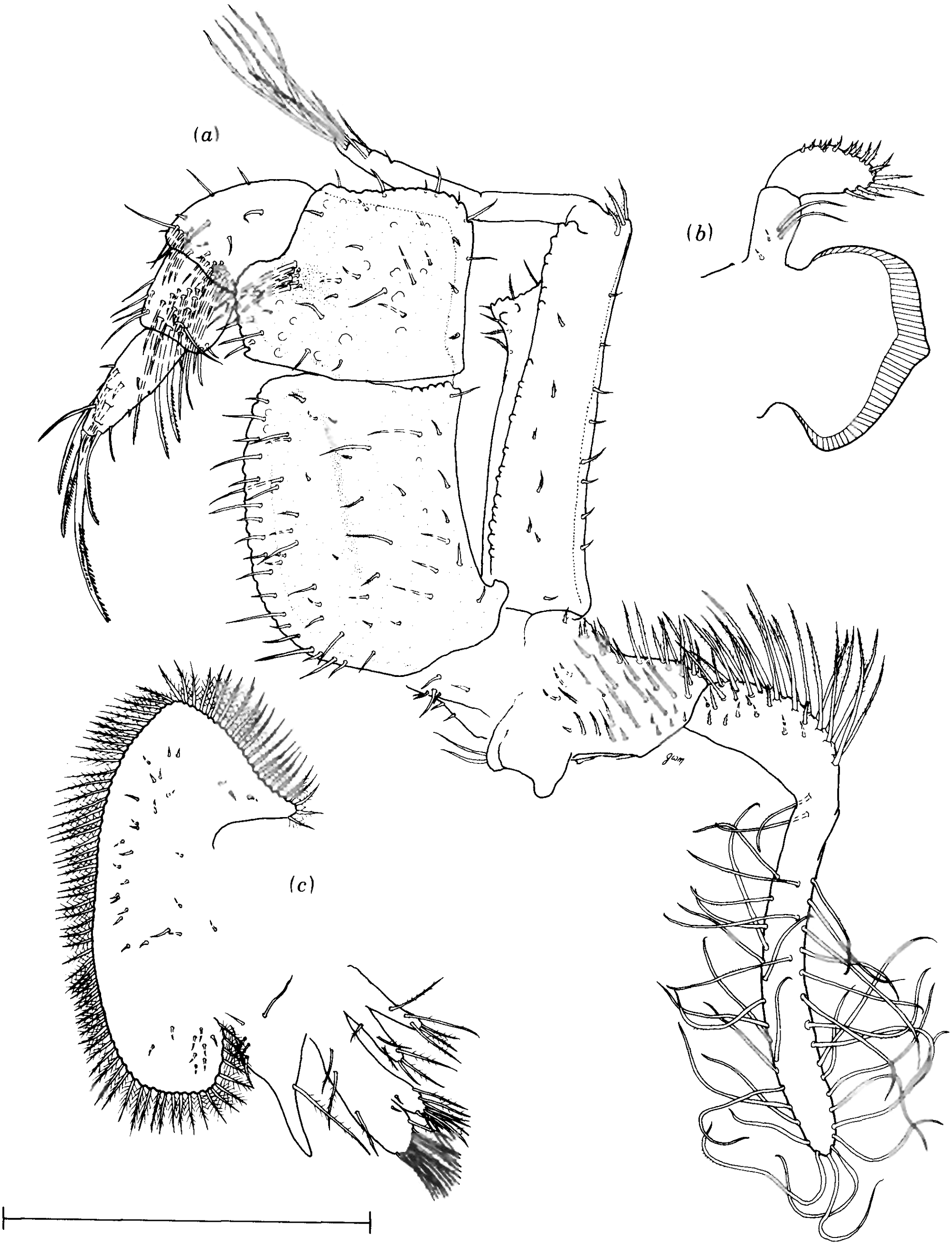


FIGURE 31. *Panopeus bermudensis*, fifth crab stage mouthparts. (*a*) Maxilliped 3; (*b*) mandible; (*c*) maxilla. Scale = 0.50 mm.

(xviii) Panopeus herbstii, *fifth crab stage*

Carapace. (figures 34*a–c*.) Anterolateral teeth displaced anteriorly and directed more or less forward, tapering broadly at base but terminating in a short, sharp spine; teeth one to three occasionally with lateral spinules. Posterolateral borders longer in proportion to carapace than in other three species. Granules always present in branchial regions, usually absent in other regions. Flattened in frontal view, areolations not distinct.

FIGURE 32. *Panopeus bermudensis*, fifth crab stage mouthparts. (*a*) Maxilliped 1; (*b*) maxilliped 2; (*c*) maxillule. Scale = 0.50 mm.

Abdomen and telson. (Figure 34*b*.) As described for general panopeid fifth crab.

Mandible. (Figure 35*b*.) Palp setation 6–7, 11–15.

Maxillule. (Figure 36*c*.) Endopod with 8–10 setae, arranged 4–6, 4. Protopodite area with 3–5 setae. Basal endite with 33–35 spines and setae, coxal endite with 20–22 spines and setae.

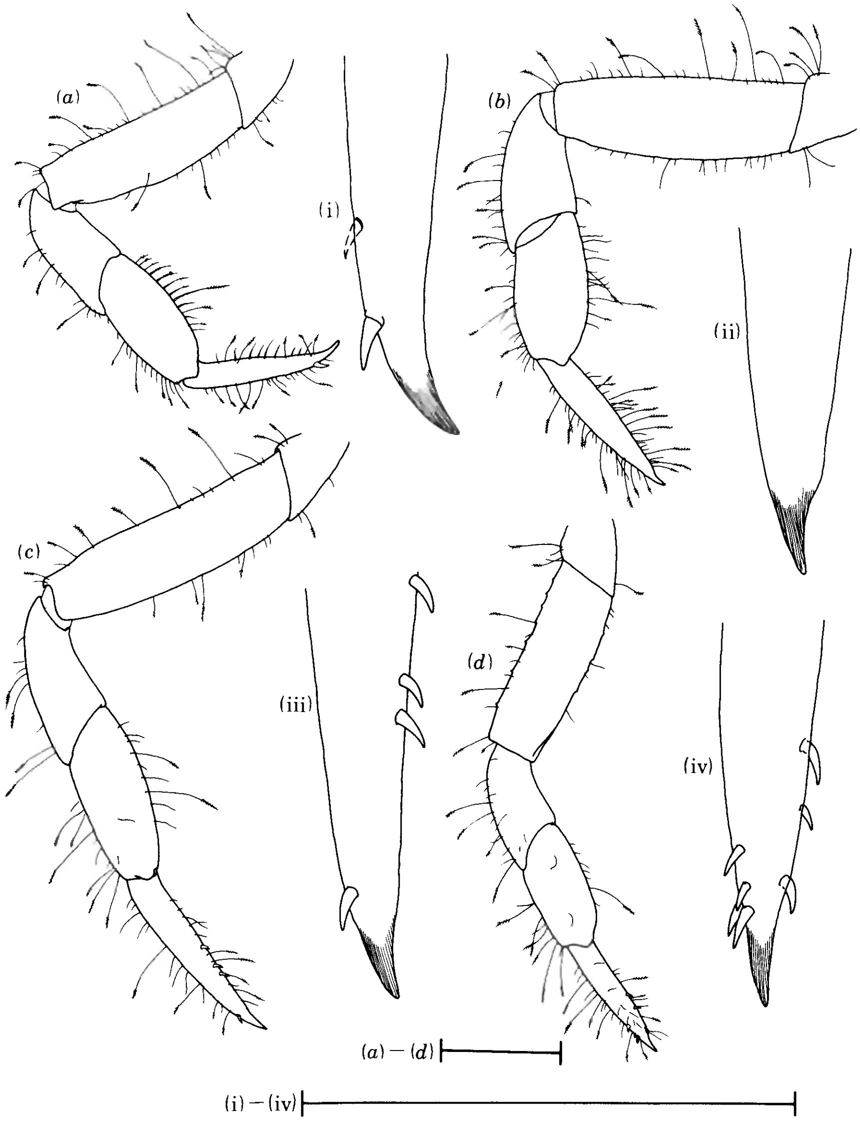


FIGURE 33. Pereopod 5 of fifth crab stages. (*a*)–(*d*) Entire pereopod; (i)–(iv) dactyl with setae removed. (*a*i) *Panopeus bermudensis*; (*b*ii) *Panopeus herbstii*; (*c*iii) *Panopeus turgidus*; (*d*iv) *Eurypanopeus depressus*. Scale = 0.25 mm.

Maxilla. (Figure 35*c*.) Endopod with 1–6 setae. Basal endite setation 16–17 + 10–12 setae, coxal endite with 8 + 8–9 setae. Scaphognathite with 80–102 fringing setae and 36–42 setae on blade.

Maxilliped 1. (Figure 36*a*.) Exopod with 12–15 setae on proximal segment and 6–7 setae on flagellum. Endopod with 31–48 setae, 18–20 of which are short terminal spines. Basal and coxal endites with 67–72 and 49–52 setae, respectively. Epipod with 53–69 long setae.

Maxilliped 2. (Figure 36*b*.) Exopod with 25–43 spines and setae on proximal segment and 5–7 setae on flagellum. Endopod setation 22–23, 4, 12–13, 15–17. Epipod with 6–8 plumose setae and 24–35 long setae.

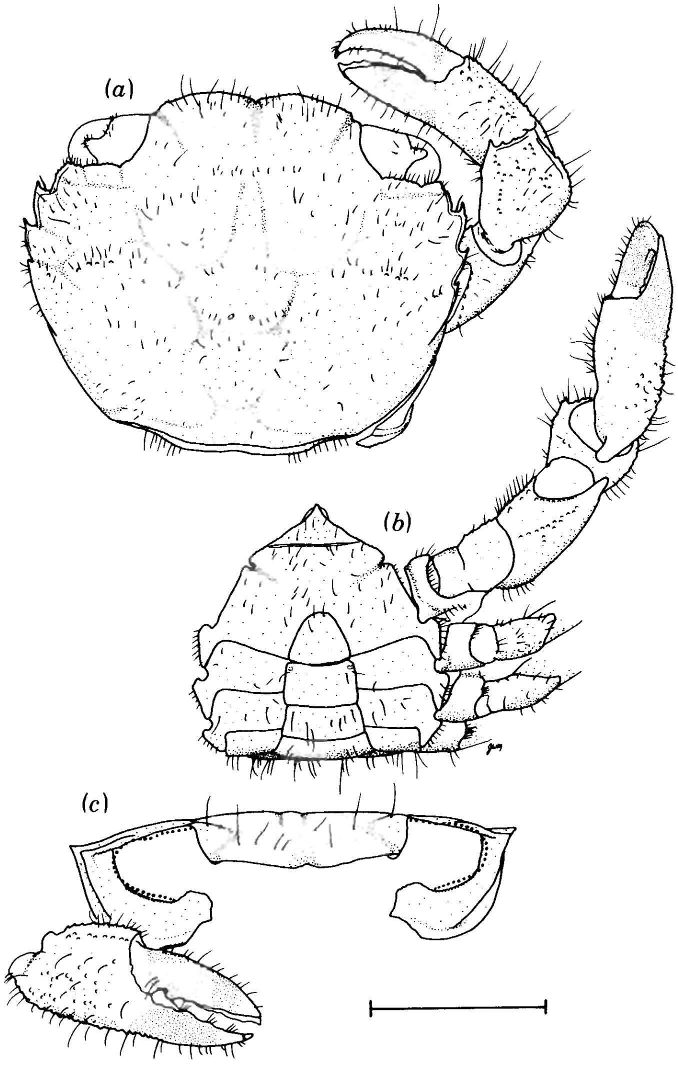


FIGURE 34. *Panopeus herbstii*, fifth crab stage. (*a*) Carapace, eyes, and right chela, dorsal view; (*b*) sternum and left pereopods, ventral view; (*c*) carapace and right chela, frontal view. Scale = 1.0 mm.

Maxilliped 3. (Figure 35*a*.) Exopod with 26–27 setae on proximal segment and 7–8 setae on flagellum. Endopod setation 68–72, 42–47, 38–40, 27–30, 17–18. Epipod with 37–41 plumose setae and 35–53 long setae. No red spot on inner surface of ischium of endopod.

Pereopods. Chelipeds (figure 34*a–c*) with brown fingers, pigment fading toward distal tips of fingers. Movable finger occasionally with a small blunt basal tooth. Pereopod 5 (figure 33*b*ii) with no subterminal spines on dactyl.

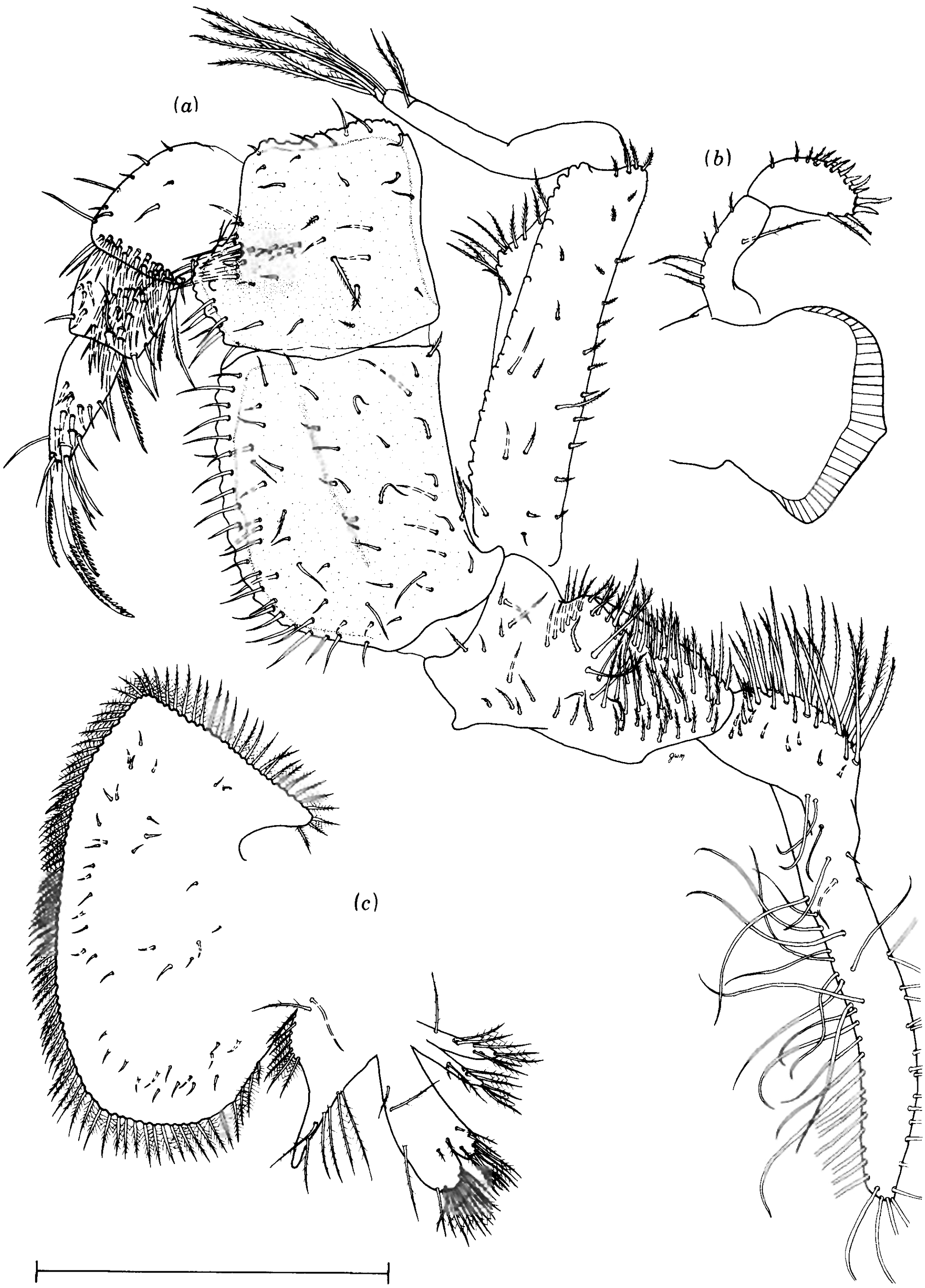


FIGURE 35. *Panopeus herbstii*, fifth crab stage mouthparts. (*a*) Maxilliped 3; (*b*) mandible; (*c*) maxilla. Scale = 0.50 mm.

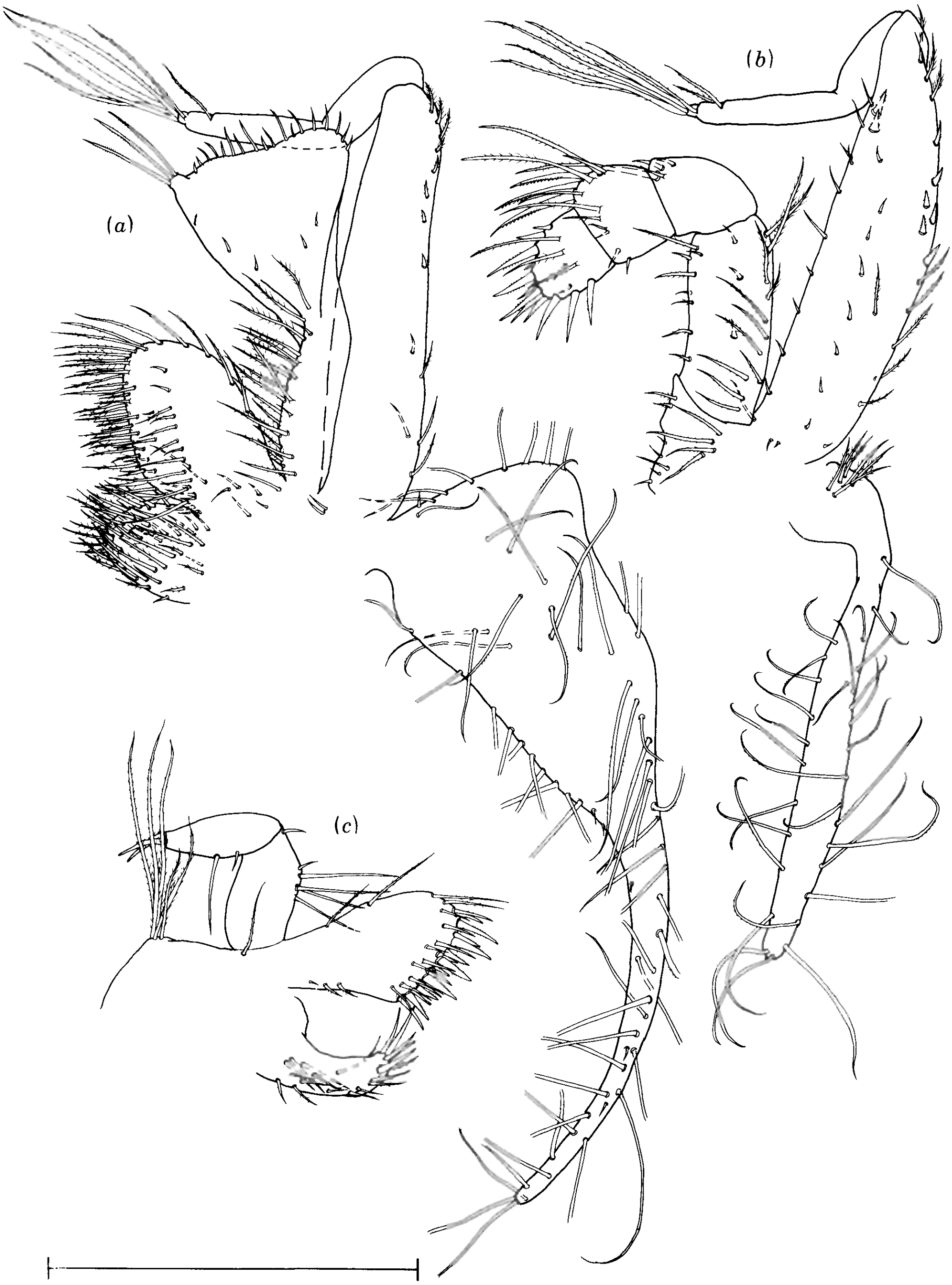


FIGURE 36. *Panopeus herbstii*, fifth crab stage mouthparts (*a*) Maxilliped 1; (*b*) maxilliped 2; (*c*) maxillule. Scale = 0.50 mm.

(xix) Panopeus turgidus, *fifth crab stage*

Carapace. (Figures 37*a*, *c*.) Ovate; anterolateral teeth not displaced anteriorly, posterior two teeth terminating in a short sharp spine and directed more or less outward. Granulated ridges always present on branchial regions, sometimes on protogastric, mesobranchial and mesogastric

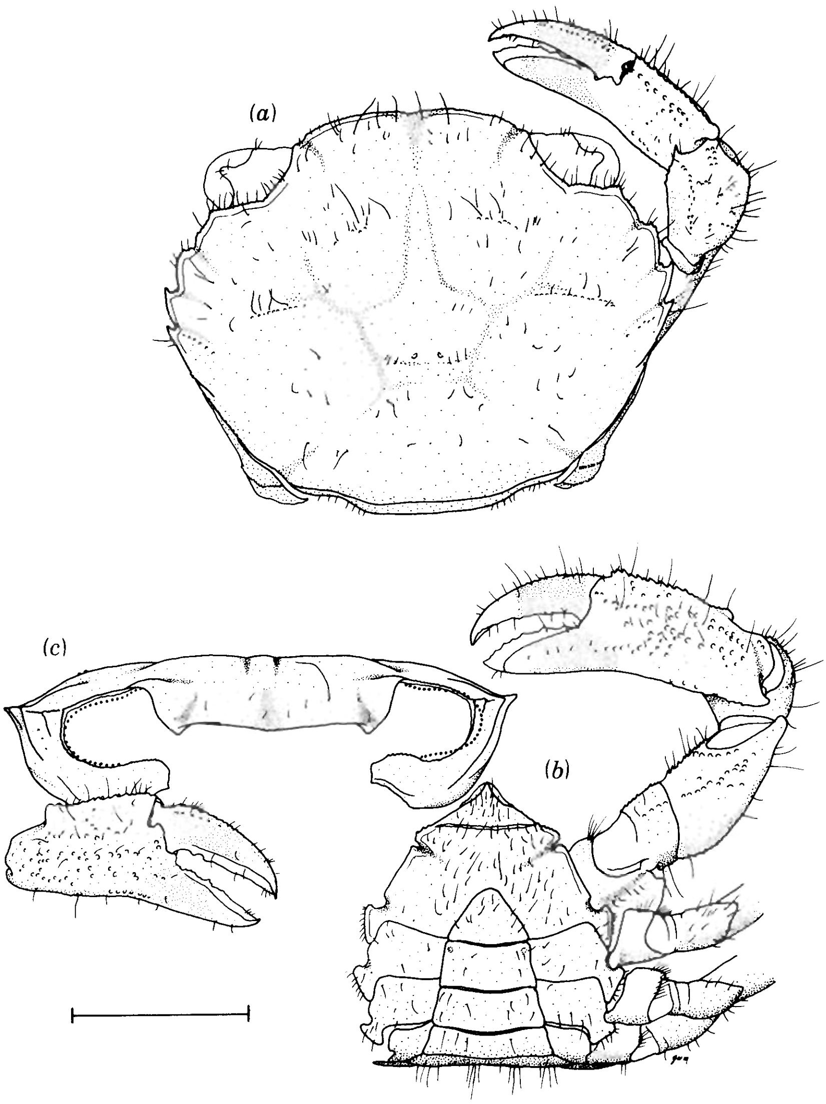


FIGURE 37. *Panopeus turgidus*, fifth crab stage. (*a*) Carapace, eyes, and right chela, dorsal view; (*b*) sternum and left pereopods, ventral view; (*c*) carapace and right chela, frontal view. Scale = 1.0 mm.

regions. Frontal margin without medial notch in frontal view. Deep in frontal view, carapace somewhat dorsally inflated. Areolations not distinct; carapace relatively smooth.

Abdomen and telson. (Figure 37*b*.) As described for general panopeid fifth crab.

Mandible. (Figure 38*b*.) Palp setation 7–8, 15–18.

Maxillule. (Figure 39*c*.) Endopod with 7–10 setae, arranged 5–8, 2. Protopodite area with 3–4 setae. Basal endite with 34–35 spines and setae, coxal endite with 21–22 setae.

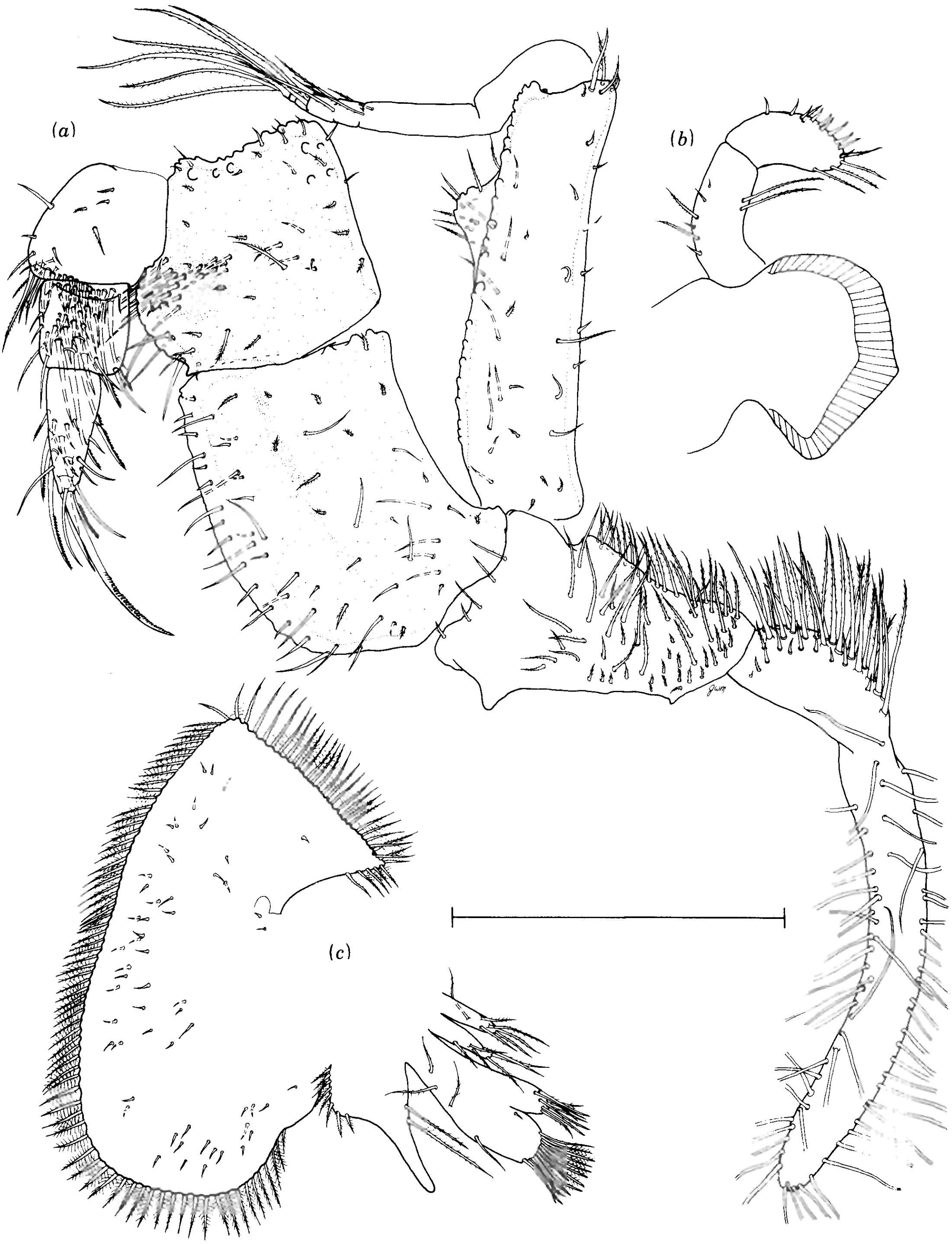


FIGURE 38. *Panopeus turgidus*, fifth crab stage mouthparts. (*a*) Maxilliped 3; (*b*) mandible; (*c*) maxilla. Scale = 0.50 mm.

FIGURE 39. *Panopeus turgidus*, fifth crab stage mouthparts. (*a*) Maxilliped 1; (*b*) maxillipd 2; (*c*) maxillule. Scale = 0.50 mm.

Maxilla. (Figure 38*c*.) Endopod with 2–6 setae. Basal endite with 15–18 + 9–10 setae, coxal endite with 6 + 5–6 setae. Scaphognathite with 106–121 fringing setae and 50–60 setate on blade.

Maxilliped 1. (Figure 39*a*.) Exopod with 13–14 setae on proximal segment and 6–8 setae on flagellum. Endopod with 43–58 setae, 10–14 of which are short terminal spines. Basal and coxal endites with 67–77 and 51–62 setae, respectively. Epipod with 93–98 long setae.

Maxilliped 2. (Figure 39*b*.) Exopod with 50–65 spines and setae on proximal segment, and 7–8 setae on flagellum. Endopod setation 17–19, 3–4, 17, 17–18. Epipod with 10–12 plumose setae and 39–45 long setae.

Maxilliped 3. (Figure 38*a*.) Exopod with 37–45 setae on proximal segment and 7–9 setae on flagellum. Endopod setation 55–58, 47–53, 34–36, 25–26, 25–28. Epipod with 36–41 plumose setae and 60–63 long setae.

Pereopods. Chelipeds (figures 37 *a–c*) with fingers brown, pigment fading toward tips of fingers. Pereopod 5 (figure 33*c*iii) with 3–5 subterminal spines on dorsal and ventral surface of dactyl.

(xx) Eurypaneous depressus, *fifth crab stage*

Carapace. (Figures 40*a*, *c*.) Widely ovate; posterior (fifth) anterolateral tooth closer to posterior border than in other three species. Distinct granulated ridges always present on branchial, mesobranchial and protogastric regions, usually on hepatic, gastric and mesogastric regions as shown. First three anterolateral teeth broad, last two ending in a sharp spine. Thin and flattened in frontal view; areolations not distinct.

Abdomen and telson. (Figure 40*b*.) As described for general panopeid fifth crab.

Mandible. (Figure 41*b*.) Palp setation 4–5, 8–10.

Maxillule. (Figure 42*c*.) Endopod with 7–10 (usually 7) setae, arranged 4–6, 3–4. Protopodite area with 3–4 setae. Basal endite with 26–30 spines and setae, coxal endite with 15–17 spines and setae.

Maxilla. (Figure 41*c*.) Endopod with 2–4 setae. Basal endite setation 10–12 + 8–9, coxal endite setation 4 + 3–5. Scaphognathite with 70–82 fringing setae and 20–27 setae on blade.

Maxilliped 1. (Figure 42*a*.) Exopod with 2–7 setae on proximal segment and 6–7 setae on flagellum. Endopod with 21–32 setae, 10–12 of which are short terminal spines. Basal and coxal endites with 51–55 and 35–40 setae, respectively. Epipod with 52–66 long setae.

Maxilliped 2. (Figure 42*b*.) Exopod with 24–34 spines and setae on proximal segment and 5–7 setae on flagellum. Endopod setation 12, 2–3, 10–12, 14–15. Epipod with 5–8 plumose setae and 19–28 long setae.

Maxilliped 3. (Figure 41*a*.) Exopod with 19–26 setae on proximal segment and 8–9 setae on flagellum. Endopod setation 41–47, 30–32, 25–28, 16–18, 10–13. Epipod with 25–27 plumose setae and 25–44 long setae. Ischium of endopod without oval red spot on inner face.

Pereopods. Chelipeds (figure 40*a–c*) do not show obvious 'spooning' of immovable finger. Fingers brown, fading to white toward distal tips. Pereopod 5 (figure 33*d*iv) with 4–7 dorsal and ventral subterminal spines on dactyl.

(*c*) *Later stages and adult morphology*

Beyond the fifth crab stage, study of sequential instars was discontinued; remaining individuals were placed in 20 l aquaria. All crabs that remained after approximately one year were mature adults; these were preserved in 70% (by volume) ethanol and found to be morphologically consistent with descriptions of the adults by Rathbun (1930), Williams (1965), and Felder (1973). There were some abnormalities. The major chelae of the two surviving *Panopeus bermudensis* did not have a large basal tooth on the movable finger; this finger appeared thin. In one surviving male *Eurypanopeus depressus*, two major chelae developed. Other characters appeared normal.

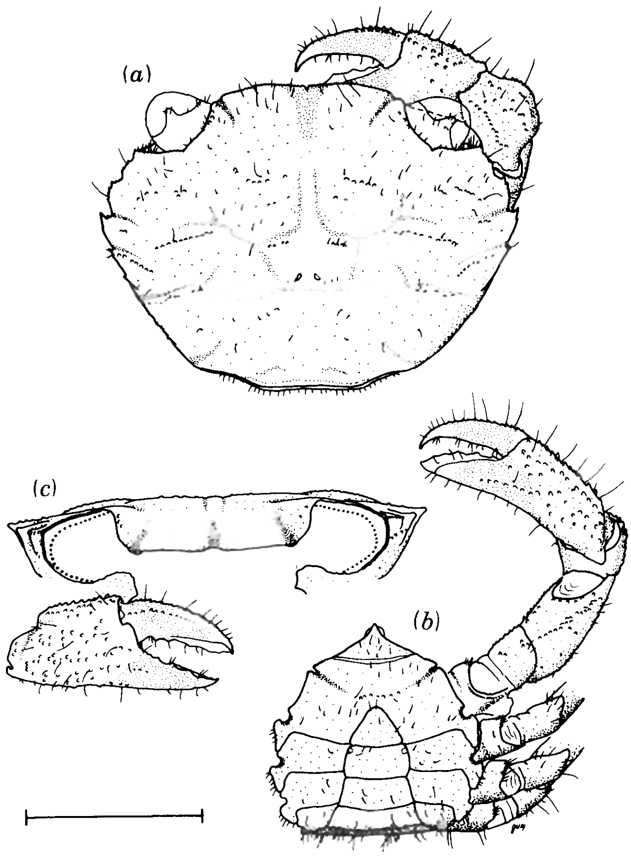


FIGURE 40. *Eurypanopeus depressus*, fifth crab stage. (*a*) Carapace, eyes, and right chela, dorsal view; (*b*) sternum and left pereopods, ventral view; (*c*) carapace and right chela, frontal view. Scale = 1.0 mm.

The gonopods of adult laboratory-reared male *E. depressus* (USL ARcMd 1079) closely resemble those figured by Williams (1965); gonopods of adult laboratory-reared male *P. bermudensis* (USL ARcMd 1076) and *P. turgidus* (USL ARcMd 1610) were compared to and found to be consistent with U.S.N.M. type male specimens. The single laboratory-reared *P. herbstii* that survived to maturity was a female (USL ARcMd 1077).

The inner face of the ischium of the endopod of the third maxilliped of the adult laboratory-reared male *E. depressus* had an obvious raised red oval spot, faded in one of the two surviving individuals; this spot had not yet developed in *E. depressus* at the tenth crab stage. Although this spot is also characteristic in adult males of *P. herbstii*, it was not evident in an adult laboratory-reared female *P. herbstii*; its absence in females is also the case in natural populations of *P. herbstii* forma simpsoni.

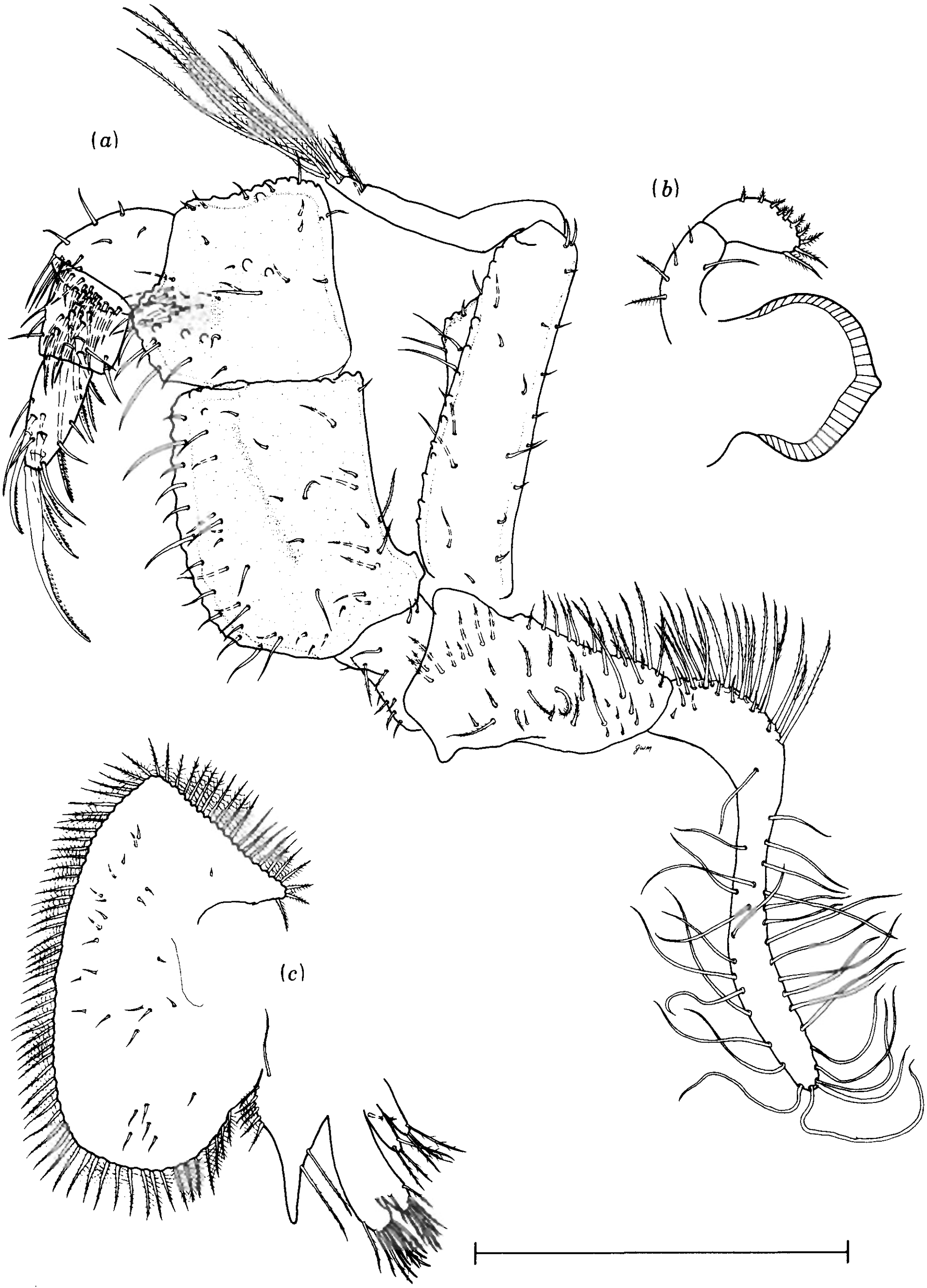


FIGURE 41. *Eurypanopeus depressus*, fifth crab stage mouthparts. (*a*) Maxilliped 3; (*b*) mandible; (*c*) maxilla. Scale = 0.50 mm.

FIGURE 42. *Eurypanopeus depressus*, fifth crab stage mouthparts. (*a*) Maxilliped 1; (*b*) maxilliped 2; (*c*) maxillule. Scale = 0.50 mm.

The carapaces of the parental females of *P. bermudensis* (USL ARcMd 1064), *P. turgidus* (USL ARcMd 1067), and *E. depressus*, (USL ARcMd 1074) agree with descriptions of adults by Rathbun (1930), Williams (1965), and Felder (1973).

(*d*) *Statistical results*

In all three crab stages examined, stepwise discriminant analysis showed a significant difference between all species pairs (table 5). However, the variables accounting for these interspecific differences were not the same at each stage. The first three variables selected by

TABLE 5. *F* STATISTICS (UPPER VALUES) AND SIGNIFICANCES (LOWER VALUES) BETWEEN PAIRINGS OF *PANOPEUS BERMUDENSIS*, *PANOPEUS HERBSTII*, *PANOPEUS TURGIDUS* AND *EURYPANOPEUS DEPRESSUS* AFTER COMPLETION OF STEPWISE DISCRIMINANT ANALYSIS

first crab	*P. bermudensis*	*P. herbstii*	*P. turgidus*
P. herbstii	25.661		
	< 0.0001		
P. turgidus	3.3003	16.827	
	0.0121	< 0.0001	
E. depressus	17.773	43.189	11.077
	< 0.001	< 0.0001	< 0.0001
third crab	*P. bermudensis*	*P. herbstii*	*P. turgidus*
P. herbstii	22.026		
	< 0.0001		
P. turgidus	20.040	7.9134	
	< 0.0001	0.0002	
E. depressus	32.909	33.018	13.472
	< 0.0001	< 0.0001	< 0.0001
fifth crab	*P. bermudensis*	*P. herbstii*	*P. turgidus*
P. herbstii	31.061		
	< 0.0001		
P. turgidus	14.398	25.914	
	0.0001	< 0.0001	
E. depressus	23.722	70.926	42.414
	< 0.0001	< 0.0001	< 0.0001

approximate *F*, first crab: 10.94476
approximate *F*, third crab: 17.22621
approximate *F*, fifth crab: 26.99485

F values below matrices represent overall interspecific distances. Degrees of freedom (10, 19) first crab stage; (10, 16) third crab stage; (10, 11) fifth crab stage.

the stepwise discriminant analysis at the first crab stage were, in order of decreasing importance: (1) setation of the palp of the mandible; (2) number of setae on the epipod of the first maxilliped; (3) number of setae on the epipod of the third maxilliped. At the third crab stage, the first two variables included in the stepwise discriminant analysis were the same two as in the first crab stage (mandibular palp and epipod of first maxilliped), but the third variable included was the number of setae on the endopod of the first maxilliped. At the fifth crab stage, the most discriminating character was the spination of the dactyl of the fifth pereopod, and the second was again the epipod of the first maxilliped. The third variable included at the fifth crab stage was the setation of the epipod of the second maxilliped.

A scatterplot based on the first two discriminant functions demonstrates an increase in phenotypic expression as ontogeny proceeds. In the scatterplot of the first crab stage (figure 43)

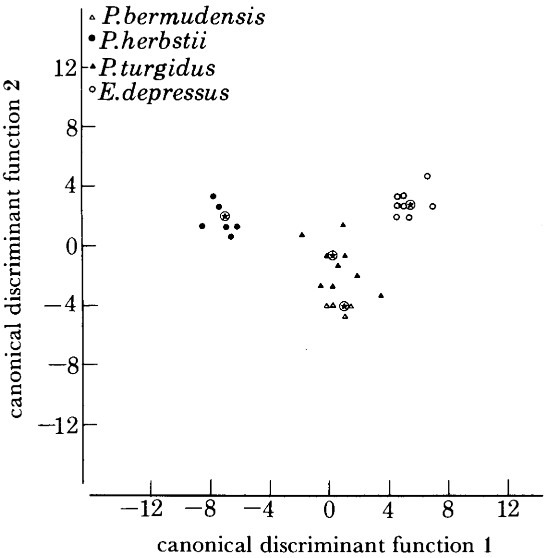
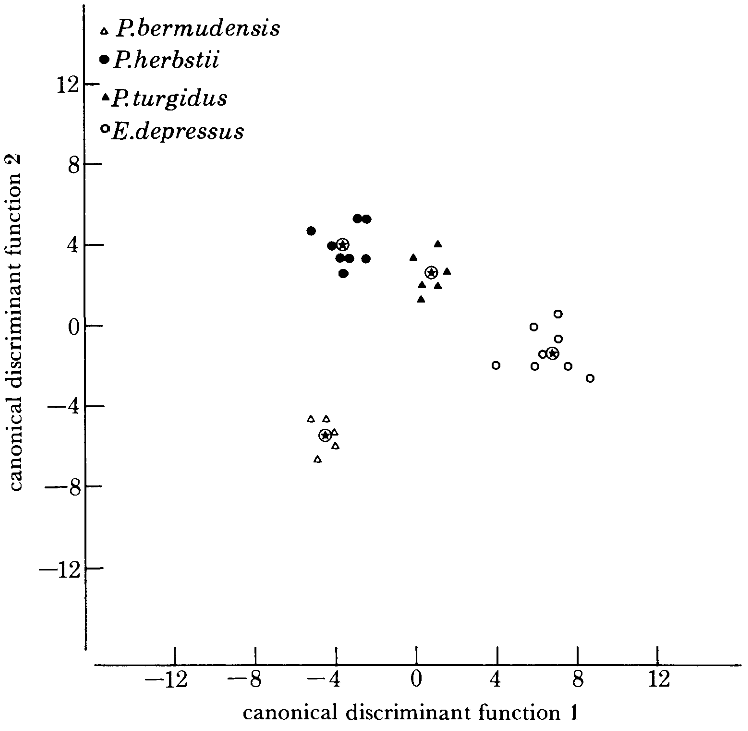


FIGURE 43. Scatterplot of *Panopeus bermudensis*, *Panopeus herbstii*, *Panopeus turgidus*, and *Eurypanopeus depressus* at the first crab stage, based on the first two discriminant functions; third function explains less than 11 % of variance. Stars represent species centroids.

44



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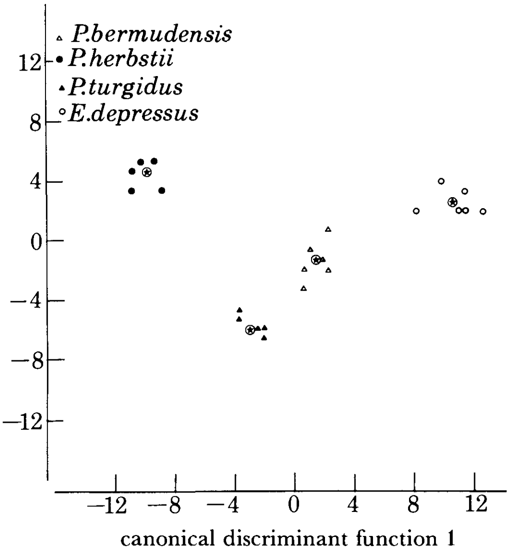

FIGURE 44. Scatterplot of *Panopeus bermudensis*, *Panopeus herbstii*, *Panopeus turgidus*, and *Eurypanopeus depressus* at the third crab stage, based on the first two discriminant functions; third function explains less than 10 % of variance. Stars represent species centroids.

FIGURE 45. Scatterplot of *Panopeus bermudensis*, *Panopeus herbstii*, *Panopeus turgidus*, and *Eurypanopeus depressus* at the fifth crab stage, based on the first two discriminant functions; third function explains less than 7 % of variance. Stars represent species centroids.

the species are shown to be distinct entities, but there is some overlap between *P. bermudensis* and *P. turgidus*. A scatterplot based on the first two discriminant functions at the third crab stage (figure 44) and at the fifth crab stage (figure 45) illustrates the greater distance between species centroids at later stages. Phenotypic expression can be seen as an increasing cline from the first crab stage scatterplot (figure 43) to the fifth crab stage scatterplot (figure 45).

4. Discussion

(*a*) *Recognition characters in early crab stages*

The first crab stages may be identified as being first crabs by a combination of characters. There are three anterolateral teeth; when a fourth is present, it is minute and directed laterally. The eyes are large, and the carapace is relatively quadrate and robust. The setation of the mouthparts is also indicative of the first crab stage; that of the epipods and scaphognathite of the maxillipeds usually differs from setation of the same mouthparts in a megalopa or third crab stage (the second crab mouthparts were not examined but are undoubtedly intermediate in form and meristics). Although statistical analyses indicated that the four species could be separated by a combination of characters, variation within any one species, both in meristics of the mouthparts and in shape and dentition of the carapace, makes positive identification to species level extremely difficult.

The second crab stages were not dissected; however, differences among carapaces of the four species are more apparent than in the first crab stage. The carapace of *P. bermudensis* is wide and the anterolateral teeth are broad and widely spaced. The carapace of *P. herbstii* is not as wide in relation to its length, and the anterolateral teeth are anteriorly displaced, or crowded toward the anterior of the crab. The carapace of *P. turgidus* is relatively ovate at this stage and somewhat intermediate in outline between *P. herbstii* and the more broadly ovate *E. depressus* second crabs. The carapace of *E. depressus* is wide, as in *P. bermudensis*; it is also granulate, as is occasionally the case with *P. bermudensis*. However, the anterolateral teeth are not as broad, and their borders not as spinulose, as in *P. bermudensis*. Although pigmentation is often indistinct, any dark colouration in the fingers of the chelipeds will rule out *P. bermudensis*.

By the third crab stage, some of the adult diagnostic characters are evident. The carapace of *P. bermudensis* is wide, with broad anterolateral teeth bordered by many spinules. The carapace of *E. depressus* is very similar to that of *P. bermudensis*; both have distinct granulated ridges on the branchial regions. The overall shape of the carapace of *P. herbstii* has not changed much from the second crab stage; *P. herbstii* differs from the other species in its anterior displacement of the anterolateral teeth, which gives the carapace a quadrate appearance. The anterolateral teeth in *P. herbstii* usually end in short spines. *P. turgidus* at the third crab stage appears intermediate between *P. herbstii* and *E. depressus*; all three species have dark fingers on the cheliped, not seen in *P. bermudensis*. By the third crab stage some of the mouthparts can be used to separate species; the palp of the mandible has seven or fewer setae in *E. depressus* and eight or more setae in the other three species. The epipod of the first maxilliped has more long naked setae in *P. bermudensis* (38–53) than in *E. depressus* (27–35), *P. herbstii* (25–33), and *P. turgidus* (23–36). Meristics of other appendages overlap and are therefore of little taxonomic value.

By the fifth crab stage, species can be separated with little difficulty. The regions of the carapace are clearly defined, the fingers of the chelae white, and granulations on the carapace obvious in *P. bermudensis*. The carapace of *P. herbstii* and *E. depressus* is depressed; anterolateral dentition is similar to the third crab stage but more pronounced. Granulated ridges are obvious on the carapace of *E. depressus* but usually not so in *P. herbstii*. *P. turgidus* again appears intermediate between *P. herbstii* and *E. depressus*, but has a deeper body and a slightly more inflated carapace. As in the third crab stage, mandibular palp setation distinguishes *E. depressus* (8–10 setae) from the other three species (11–18, usually 15–17 setae). However, the variable first selected in the stepwise discriminant analysis for the fifth crab stages of the four species compared was the spination of the dactyl of the fifth pereopod; spine numbers in *P. turgidus* (3–5), *E. depressus* (5–7), *P. herbstii* (0), and *P. bermudensis* (1–3) are significantly different in comparisons of any two species. The second most discriminating character at this stage is the number of setae on the epipod of the first maxilliped; the number of setae in *P. turgidus* (93–98) exceeds that in *P. bermudensis* (73–93), *P. herbstii* (53–69), and *E. depressus* (52–66).

(*b*) *Suggested relationships based upon early crab stages*

The four species selected for this study were chosen because of their close relationship, postulated on the basis of adult characters. The fact that recognition of morphological distinctions between these species is difficult even after five postlarval moults is probably indicative of their phylogenetic proximity to one another. On the basis of the carapacial characters and the pale terminal pigmentation of chelae, *P. bermudensis* is unique from the other three species. *P. turgidus* appears allied to *E. depressus* on the basis of spination on the dactyl of the fifth pereopod and overall shape of the carapace. The scatterplot (figure 43) suggests that at the first crab stage *E. depressus* is closer to *P. turgidus* than either species is to *P. herbstii*. The scatterplots at the third and fifth crab stages (figures 44, 45) suggest that *P. herbstii* is closer to *P. turgidus* than either species is to *E. depressus*. At all stages, *P. bermudensis* shared more characters with *P. turgidus* than with either *P. herbstii* or *E. depressus* (table 5). The species that share the fewest characters at all stages are *P. herbstii* and *E. depressus*; this is consistent with electrophoretic studies on these two species by Turner & Lyerla (1980).

There are virtually no other descriptions of early crab stage xanthids in the literature with which to compare mouthpart morphology. Hart (1935) illustrated the first maxilliped of the first crab stage for *Lophopanopeus bellus bellus* (Stimpson, 1860), and Hyman (1925, after Cano 1891) illustrated the third maxilliped of the same stage for '*Xantho* sp.'. Neither illustration adds insight to group relationships. Kurata (1970) illustrated the carapace of the first crab stage for *Rhithropanopeus harrisii* (Gould, 1841), *Neopanope sayi* (Stimpson, 1859), *Panopeus herbstii* H. Milne Edwards, 1834, '*Panopeus occidentalis*' Saussure, 1857, and *Eurytium limosum* (Say, 1818); these descriptions agree well with the present general panopeid first crab description. However, Kurata's (1970) illustrations of the first crab carapace of *Menippe mercenaria* and *Pilumnus sayi* do not fall into the panopeid category. *Pilumus sayi* apparently has no anterolateral teeth at the first crab stage, and *Meniipe mercenaria* has very broad, rounded lobes instead of sharp teeth at this stage. Obviously, there are discernable differences in the carapaces of xanthoids at the first crab stage; pilumnid and menippid lines do appear to differ from the panopeid line at the first crab stage. Kurata (1970) described what might be an atypical example of the first crab carapace of *Pilumnus sayi*; the first crabs of *Pilumnus hirtellus*, *Pilumnus novaezealandiae* and *Pilumnus* sp. all show anterolateral dentition and body shape essentially the same as the panopeids (Lebour 1928; Wear 1967; Hyman 1925). The first crab of *Lophopanopeus bellus bellus* figured by Hart (1935) also is of the general panopeid form.

Among the panopeid crabs illustrated by Kurata (1970), the carapace of the first crab of *Rhithropanopeus harrisii* is distinctive in having a very quadrate shape and anteriorly projecting anterolateral teeth. The carapace of '*Panopeus occidentalis*' figured is distinctive in having granulated ridges on the branchial region, that do not appear until later stages of the four species in the present study. It should be noted again that Kurata (1970) was very probably mistaken in his identification of this species, and the species listed as '*P. occidentalis*' is probably *Hexapanopeus angustifrons*.

Another xanthoid line might be represented by *Xantho incisus* Leach, 1814, the first crab of which is very elongate (as described by Lebour 1928). However, the first crab of an additional species, referred to by Hyman (1925, after Cano 1891) as '*Xantho* sp.' is more or less panopeid in form.

Several works˙ have dealt with descriptions of the early crab stages of non-xanthoid brachyuran crabs. These studies have also lacked detailed descriptions of the appendages and for the most part consist of line drawings of the first few crab stages, usually at the end of a larval rearing study. The major works of this type are the descriptions of the first few crab stages for *Liocarcinus puber*, *L. depurator*, *L. holsatus*, *L. marmoreus*, *L. pusillus*, *L. arcuatus*, *Xaiva biguttatas*, *Portumnus latipes*, *Cancer pagurus*, *Carcinus maenas*, *Goneplax rhomboides*, *Thia scutellata*, *Ebalia tuberosa*, *Atelecylus rotundatus*, *Maia squinado*, *Eurynome aspera*, *Hyas coarctatus*, *Inachus dorsettensis*, *Macropodia rostrata* and *M. deflexa* by Lebour (1928), the description of the first crab of *Portunus anceps*, *Planes minutus*, *Calappa flammea*, and *Cycloës bairdii* by Lebour (1944), the description of the first crab carapace of *Achaeus tuberculatus*, *Pugettia quadridens quadridens*, and *Acanthophrys longispinosus* (sic) by Kurata (1969), and the description of the first crab stage of *Parthenope serrata*, *Microphrys bicornutus*, *Libinia erinacea*, *Macrocoeloma camptocerum*, *Epialtus dilatatus*, and *Stenorhynchus secticornis* by Yang (1967, 1968, 1971). Kurata (1970) described the first crab carapace of *Callinectes sapidus*, *Uca pugnax*, *Libinia dubia*, and *Pinnotheres* sp. in addition to several xanthids (table 1); Novak & Salmon (1974) described the first and second crab carapaces of *Uca panacea*, Knight (1968) figured the first five crab stages of *Raninoides benedicti*, and Diaz & Ewald (1968) described the first two crab stages of *Metasesarma rubripes* and *Sesarma ricordi*. Special mention must be made of the thorough study by Morita (1974) on *Eriocheir japonica*, in which the first five crab stages were described and illustrated.

Of these studies, only Yang (1967, 1968, 1971), Diaz & Ewald (1968), and Morita (1974) described the mouthparts of the juvenile crabs. One of the most detailed studies of postlarval development of a brachyuran was the description by Shen (1935) of the early crab stages of *Carcinus maenas*; the emphasis of this study was on pleopod development. Other studies dealing with postlarval development of brachyurans are scattered throughout the literature dealing with brachyuran larvae and include such works as Bocquet (1965), Gamo (1958), Krefft (1952), Anderson & Ford (1976), Jones (1977), Ingle (1977, 1981), Ingle & Clark (1980), and Williamson (1910). A more thorough review of brachyuran postlarval development is included in a recent paper by Felder *et al.* (1984).

Comparison of xanthoid first crabs with those of other superfamilies reveals that many superfamilies can be easily distinguished from the xanthoid line at the first crab stage. Portunids all carry a stout lateral spine or at least a serrate anterolateral border at this stage; ocypodids (based on description of a first crab *Uca pugilator* by Kurata 1970, and the first two crabs of *Uca panacea* by Novak & Salmon 1974) have no anterolateral teeth. Grapsids (based on the description of the first crab of *Planes minutus* by Lebour 1944, and the description of the first two crab stages of *Metasesarma rubripes* and *Sesarma ricordi* by Diaz & Ewald 1968) have slight postorbital lobes but not true anterolateral teeth at the first crab stage. However, this is not the case for the first crab stage of *Eriocheir japonica* as described by Morita (1974). The excellent descriptions of juvenile majids by Yang (1967) show that although the majid first crab carapace is totally different from the panopeid first crab carapace, the mouthparts are very similar. Certain characters, such as the elongate seta on the endopodal carpus of the second maxilliped and the number of setae on the maxilla, and the general shape of the mouthparts, are virtually identical. There are differences among the majid species that are greater than the differences among the four panopeid species. Two majids, *Stenorhynchus seticornis* (Herbst, 1788) and *Epialtus dilatatus* A. Milne Edwards, 1878, lack the medial projection on the third maxilliped exopod, and these two species and *Libinia erinacea* (A. Milne Edwards, 1879) have a bilobed endopod on the maxilla. However, when compared to panopeid first crab stage mouthparts, these differences appear small in relation to the striking differences in carapace morphology. It must be surmised that mouthpart morphology in early crab stages is of less value as a discriminating character than overall carapace morphology. Another description of first crab mouthparts (Diaz & Ewald 1968) lends support to this belief; the mouthparts of the two grapsids (*Metasesarma rubripes* and *Sesarma ricordi*) are very similar to the panopeid first crab mouthparts, although the carapaces of the two groups differ. Mouthparts were not described by Kurata (1970) for the first crab stage of *Pinnotheres* sp., *Uca pugnax* (Smith, 1870), and *Libinia dubia* H. Milne Edwards, 1834; the carapaces of the first crab stages of these species are distinctly non-xanthoid.

(*c*) *Comparison of relationships based upon crab stages with those based on larval stages*

As noted above, comparisons at the early crab stages for the panopeid species under study revealed only a few subtle characters for distinction of juveniles; however, examination of the larval stages for the same species reveals immediate and obvious differences. First, the zoea of *Panopeus bermudensis* is markedly different from the zoeas of the other three species (figure 46). It is highly modified, with no lateral spines on the carapace. Furthermore, the telson is markedly longer, with only one pair of dorsal spines that are placed far down the caudal furcae. Among the other three species, the zoeal antennal spinous process is spinose and has a reduced exopod; in *P. bermudensis* the spinous process of the antenna is completely smooth, and the exopod is absent. It should be noted that the fourth zoea here attributed to *P. bermudensis* differs markedly from the sole previous description of a supposed *P. bermudensis* zoea; Lebour (1944) described a first zoeal stage which she reported to be that of *P. bermudensis*, but her figure is clearly that of a pilumnid zoea (group II xanthid zoeas of Rice (1980) and Martin (1984)). There is little reason to doubt that the parental females used in the present study (USL ARcMd 1063, 1064, 1067 and 1074) are correctly identified, so it can only be assumed that Lebour's (1944) parental female was not *P. bermudensis*.

Among the three similar zoeas in the present study (*P. herbstii*, *P. turgidus*, and *Eurypanopeus depressus*) the antenna is identical, but spination of the telson is not (figure 46). The telsonal armature could suggest that *P. herbstii* and *P. turgidus* are more closely related to each other than either species is to *E. depressus*, the zoea of which has only one pair of telsonal spines.

However, comparisons at the megalops stage could suggest a different relationship. The megalopas of *P. herbstii* and *P. bermudensis* are similar in having a sharp, curved anterolateral horn on each side of the carapace. These horns are conspicuously absent in the megalopas of

P. turgidus and *E. depressus*. Therefore, on the basis of megalopal carapace morphology, one might conclude that *P. turgidus* and *E. depressus* are closely related, and that *P. herbstii* is allied with *P. bermudensis*. Megalopal mouthpart morphology is of little use in distinguishing these four species. The megalopal telson is similar in all species except *P. bermudensis*, where it is rounded posteriorly and has no posterolateral spines.

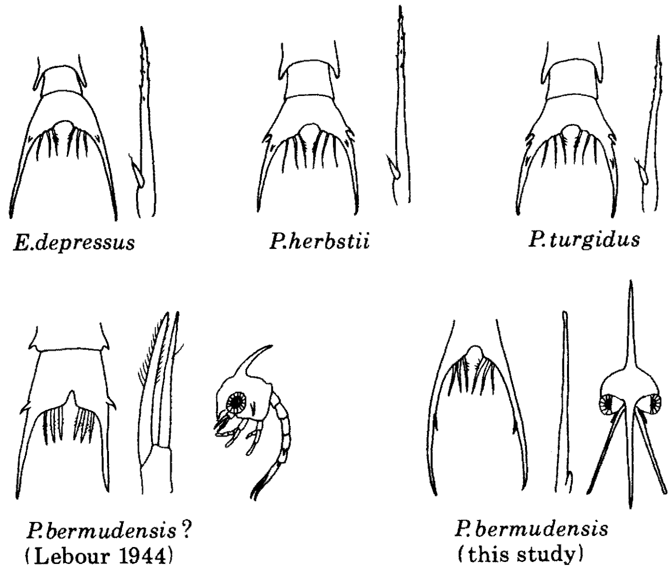

FIGURE 46. Comparisons of the zoeal types of *Panopeus bermudensis*, *Panopeus herbstii*, *Panopeus turgidus*, and *Eurypanopeus depressus*. Zoea of *Panopeus bermudensis* (present study) is a fourth stage zoea; of '*Panopeus bermudensis*?' (after Lebour 1944) and all other drawings are first stage zoeas.

The larvae of other panopeids described in the literature all fall among Rice's group I xanthid zoeas, except for the zoea that Lebour (1944) reported as '*Panopeus bermudensis*' (Rice 1980). The present study has shown that the zoea described by Lebour is not assignable to *P. bermudensis* and has established that *P. bermudensis* is indeed a member (albeit modified) of Rice's xanthid group I. Martin (1984) has placed the zoeas described here as *P. bermudensis* in a separate xanthid zoeal group, group VI, on the basis of their lack of lateral carapace spines.

Only three other species in Guinot's (1978) Xanthoidea have been found to have zoeas with lateral and rostral spines, or both, reduced or absent (Rice 1980). These are *Heteropanope glabra* Stimpson, *Pilumnopeus indicus* (de Man), and *Pilumnopeus serratifrons* (Kinahan) described by Aikawa (1929), Takeda & Miyake (1968), and Wear (1968) respectively. These three species are closely related on the basis of adult characters; the genera *Heteropanope* and *Pilumnopeus* were considered synonymous by Buitendijk & Holthuis (1949). The absence of lateral carapace spines in the zoea of *Panopeus bermudensis* is a departure from typical xanthoid zoeal morphology and may raise some question as to the correct generic placement of this species.

The panopeid megalopas vary in morphology and with some difficulty can be placed into two groups. The first group, which includes *Panopeus herbstii*, *P. bermudensis*, *Panopeus* sp. (Kurata 1970), '*Panopeus occidentalis*' (as described by Kurata 1970), *Neopanope packardi*, *N. texana*, *Micropanope sculptipes*, *Hexapanopeus angustifrons*, *Eurytium limosum*, and *Lophopanopeus bellus* *diegensis*, has megalopas with obvious anterolateral horns. The second group, which includes *Eurypanopeus depressus*, *Panopeus turgidus*, *Rhithropanopeus harrisii*, and *Neopanope sayi*, has megalopas without anterolateral horns. *Lophopanopeus bellus bellus* and *L. leucomanus leucomanus* are somewhat intermediate, having broad teeth, rather than narrowed horns, on the carapace (Hart 1935; Knudsen 1958).

(*d*) *Phylogenetic significance of early crab stages compared to zoeal stages*

It is usually accepted that zoeal stages would be more likely to exemplify conservative characters than would mature adults because adaptation to the adult environment involves considerable specialization. This hypothesis has led many workers to draw phylogenetic conclusions based upon zoeal morphology (see § 1). This approach applied to panopeid zoeas might, for example, suggest an evolutionary line in which there has been a gradual reduction in armature of the telson and the antennal exopod of larvae (figure 47). According to Rice (1980), however, zoeal groupings do little to clarify brachyuran systematics below the superfamily level. Indeed, panopeid genera are divided among several zoeal types (figure 47).

Giard (1905) gathered under the name 'poecilogenie' cases known to him in which similar adults developed from strikingly different larvae. Gould (1977) lists several other workers whose studies have shown that larval characters, instead of recapitulating ancestral phylogenies, may in fact represent larval adapatations. Although evidence pointing to this phenomenon in crustaceans is not entirely lacking, it has not been proven to occur in the Brachyura. The present study, which shows that two very different larval types metamorphose into extremely similar juveniles, may be a case of Giard's 'poecilogenie'.

If there are two definable sets of selective pressures, one acting upon the planktonic larvae and the other acting upon the benthic juveniles and adults, the groupings of larvae and adults need not closely correspond. In one instance, Rice considers this explanation untenable, and states that '... modern evolutionary theory would suggest that despite specializations to particular environments or life styles, larval and adult classifications should show a high degree of congruence if they are based on sufficient characters to avoid the superficial confusions resulting from adaptive convergence or radiation' (Rice 1980, p. 278). He proceeds to show that based upon detailed setation of zoeal appendages, brachyuran zoeas can be assigned at least to adult superfamilies with a few exceptions.

An alternative hypothesis is that both larvae and adults are often too highly modified to exemplify clearly conservative characters. As noted by Rice (1981 *b*), both adult and zoeal phases of brachyuran life cycles seem subject to convergent evolution, and similarities between zoeas of different brachyuran groups do not necessarily imply close relationship. On the basis of this observation, Rice (1981 *b*) deduced that classificatory evidence from other phases of the life cycle would likely be of value; he consequently undertook comparative studies of brachyuran megalopas. We suggest that there may also be value in applying early crab stages to classificatory studies of the Brachyura. These are the first stages to exhibit the fully brachyurized adult form and it is possible that, in at least some cases, they could exhibit more conservative, phylogenetically significant characters than would zoeas, megalopas, or mature adults. There are several reasons why this could be expected.

The megalopa is primarily or most typically a dispersal stage that achieves transition from a planktonic to a benthic existence. In the benthic habitat, the xanthid megalopa commonly moults to the first truly benthic instar, the first crab stage. Thereafter, a series of short duration instars (the early crab stages) follows. There is little evidence of morphological specialization in the earliest of these crab stages, but as later stages are transcended, structure and function are increasingly specialized. At later stages, different species phenotypically diverge as each species begins to exhibit its unique adaptations to the heterogeneous food substrates and habitats available in the benthic environment (figure 48). Transition of a xanthid from early crab to adult stages requires direction of energy to growth, thickening and calcification of

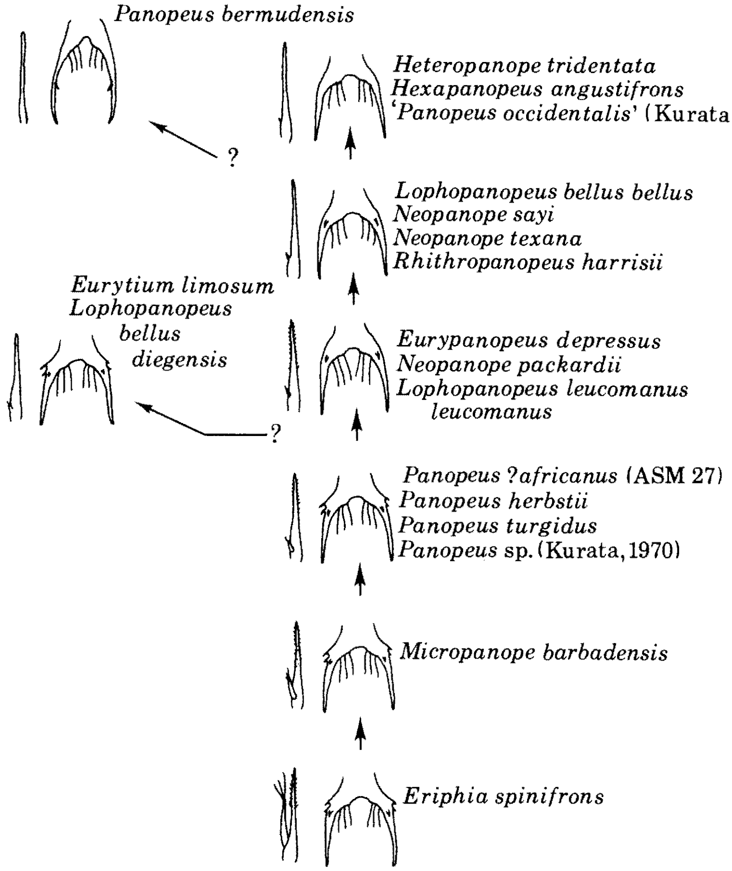

FIGURE 47. Possible evolutionary derivation of the various panopeid zoeal types, based upon spination of the telson and armature of the antenna and antennal exopod.

cuticular structures, increased complexity of musculature, and increased complexity of behaviour. Such developments are added incrementally during each juvenile's transition of crab stages and are little evident at the first crab stage. However, the model on which the features of maturation and specialization are superimposed is first exemplified in the first crab stage. It represents the most plesiomorphic brachyurized stage in the xanthid crab's developmental history. The statistical analysis in the present study, regardless of whether it provides sound taxonomic characters for distinction of early crab stages, does demonstrate one salient feature of successive crab stages: the crab stages phenotypically diverge as ontogeny proceeds.

The juvenile stages of brachyuran crabs have been much overlooked. If the proposed hypothesis, that these stages may indeed be more conservative than either larvae or mature adults, is true, then these stages are in need of considerably more investigative work. For ecological

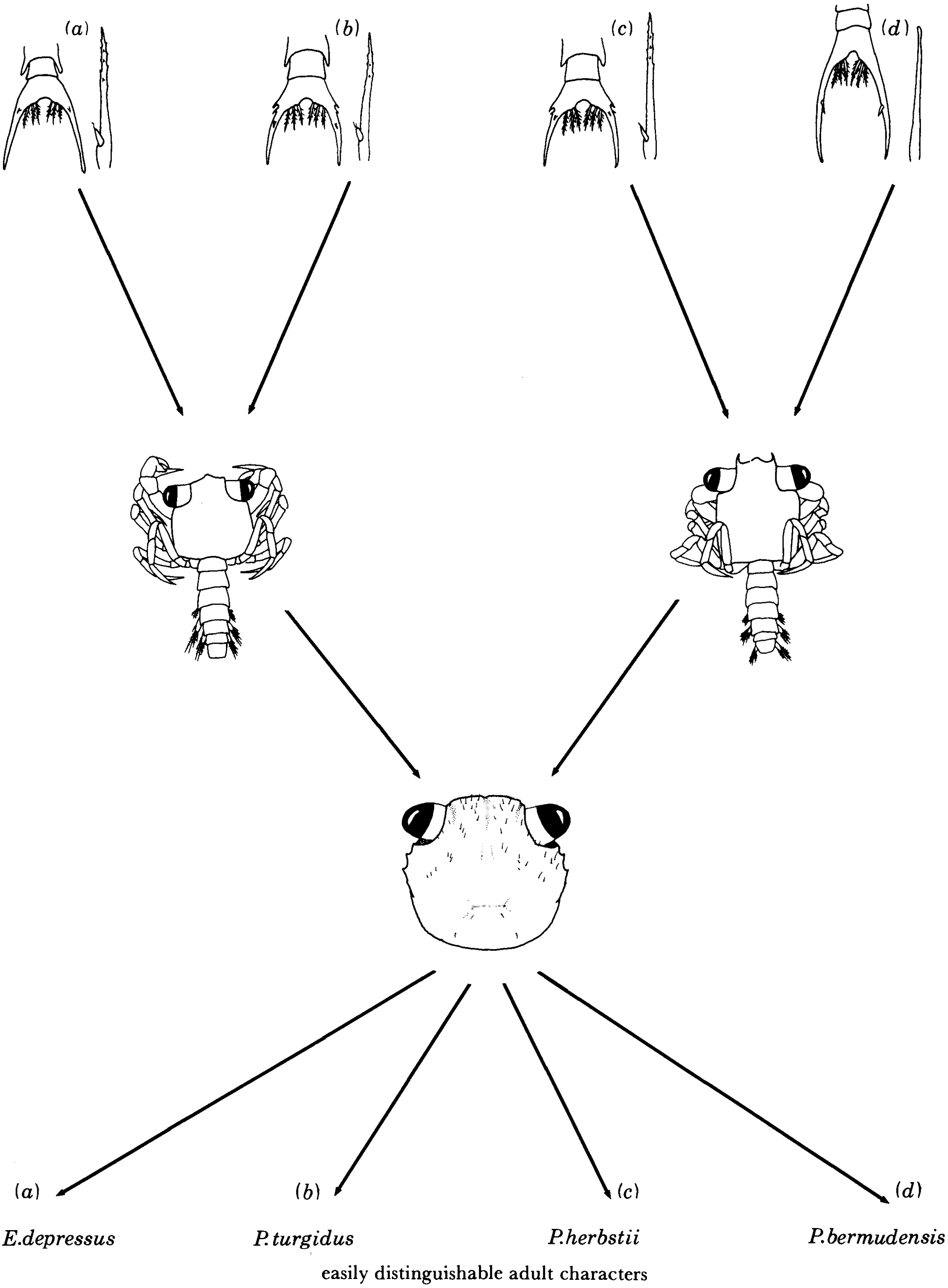

FIGURE 48. Diagrammatic representation of ontogenetic transition from zoeal stages to adult stages in (*a*) *Eurypanopeus depressus*, (*b*) *Panopeus turgidus*, (*c*) *Panopeus herbstii* forma simpsoni, and (*d*) *Panopeus bermudensis*. Zoeal stages (above) may be characterized by armature of the telson and antenna; development thereafter transcends one of two megalopal forms and a common first crab form before adult characters become evident.

purposes the identification of juvenile stage crabs is always desirable and should be facilitated. A comparison of the mouthparts of these four panopeids with the mouthparts of Yang's (1967) majids indicates that the mouthparts are probably poor characters, since mouthpart morphology is very similar despite obvious differences in panopeid and majid first crab carapaces. In view of the use of juvenile carapacial structure, in the distinction of both higher crab taxa and the closely related panopeid crabs in this study, further investigations should fully evaluate this character, at least in addition to mouthpart morphology.

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