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Establishment of a new genus for *Panopeus bermudensis* Benedict & Rathbun, 1891 and several other xanthoid crabs from the Atlantic and Pacific oceans (Crustacea: Decapoda: Xanthoidea)

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Abstract.—The new genus *Acantholobulus* is proposed to accommodate several brachyuran crab species formerly assigned to the genera *Panopeus* H. Milne Edwards, 1834 and *Hexapanopeus* Rathbun, 1898, with *Panopeus bermudensis* Benedict & Rathbun, 1898 as the type species. Characters of the carapace front, anterolateral dentition, male first pleopod, and larval stages define the new genus. Morphological findings are congruent with recently reported molecular evidence for distinction of this genus. The western Atlantic species *Hexapanopeus hemphillii* Benedict & Rathbun, 1891, *Panopeus gatunensis* Abele & Kim, 1989 and *Hexapanopeus heblingi* Rodrigues & de Loyola e Silva, 1998 are considered junior synonyms of *Acantholobulus bermudensis,* new combination. *Hexapanopeus schmitti* Rathbun, 1930 from the western Atlantic is assigned to the new genus, and *Panopeus margentus* Williams & Boschi, 1990 is concluded to be a junior synonym of *Acantholobulus schmitti,* new combination. *Panopeus mirafloresensis* Abele & Kim, 1989 from the eastern Pacific and *Panopeus pacificus* Edmondson, 1931 from Hawaii and Tahiti are also assigned to *Acantholobulus.* While provisionally retained among the Panopeidae Ortmann, 1893, genetic studies and larval morphology distance *Acantholobulus,* new genus, from typical panopeid crab genera examined to date.

The genus *Panopeus* H. Milne Edwards, 1834 includes a number of extremely common and abundant intertidal and upper subtidal marine and estuarine crab species, especially along warm-temperate to tropical coasts of the Americas. Taxonomic history of this group is confusing, and superficial similarities in morphology of the adults often make species identifications particularly difficult. This is especially true for juveniles of those species that attain large size as adults, since immature stages of these crabs superficially resemble adults of smaller panopeid species. However, the complex armature of male first pleopods (gonopods) in mature individuals of the small-sized species often facilitates ready distinction from the larger forms, the latter of which tend to share a very characteristic and conserved gonopod morphology (Williams 1984a, b). A unique gonopod morphology has been reported for *Panopeus bermudensis* Benedict & Rathbun, 1891 (Monod 1956), *P. pacificus* Edmondson, 1931 (Forest & Guinot 1961), *P. gatunensis* Abele & Kim, 1989 (Abele & Kim 1989), *P. mirafloresensis* Abele & Kim, 1989 (Abele & Kim 1989), and *P. margentus* Williams & Boschi, 1990 (Williams & Boschi 1990). In addition, differences in carapace granulation and dentition, together with the shape of the male abdomen, distinguish this group from most

species of *Panopeus* and from other panopeid genera like *Hexapanopeus* Rathbun, 1898, *Rhithropanopeus* Rathbun, 1898, *Eurypanopeus* A. Milne-Edwards, 1881, and *Eurytium* Stimpson, 1859.

Earlier studies of larvae for American panopeid crabs, which included *P. bermudensis,* revealed unique characters in zoeal morphology for the latter species (Martin et al. 1984, 1985). More recently, one of us (DLF) has participated in comparative genetic studies that unambiguously position *P. bermudensis* apart from most panopeids for which mt16S DNA has been sequenced (Schubart et al. 2000). Finally, extensive collections from the Indian River lagoon, Florida, the Gulf of Mexico, and several Caribbean localities have facilitated studies of adult morphology that provided insight into variations in characters at both the specific and generic level. In view of our present evidence from adult morphology, larval characters, and molecular genetics, we herewith establish a new genus for this species and its closest relatives.

Materials examined include selected holdings from National Museum of Natural History Smithsonian Institution, Washington, D.C. (USNM), the Muséum national d'Histoire naturelle, Paris (MNHN), and the University of Louisiana, Lafayette Zoological Collections (ULLZ). Size is expressed as maximum carapace width (CW) measured in millimeters (mm) and includes the anterolateral teeth.

Acantholobulus, new genus

Type species.—*Panopeus bermudensis* Benedict & Rathbun, 1891.

Diagnosis of adult morphology.—Carapace (Fig. 1a) moderately convex, slightly elliptical in outline, regions well-defined by grooves, usually crossed by raised transverse lines of granules on anterior half. Frontal edge bilobed with distinct median fissure, thickened granulate margin usually with transverse concavity, sometimes defined as furrow between rows of granules above and below. Anterolateral teeth strongly developed, prominent, arrayed in distinct arc, third and fourth teeth with tips anteriorly directed, fifth tooth well defined, thick, acute. Abdomen of male with terminus rounded or weakly triangular, lateral extremities on third segment rounded, sixth segment slightly broader than long; lateral lobe of third segment not contacting coxa of fifth pereopod, seventh sternite distinctly exposed. Dactyl of major chela with strong basal tooth (Fig. 1b); color of immovable finger extended variably onto palm; carpus distally with distinct transverse groove. Fixed finger of major and minor chela in male deflected, less so in female. Male first pleopods (gonopods) terminally complex (Fig. 1c–f, 2a–l), subterminally with row of short denticles, field or row of a few strong setae, and strong subterminal tooth directed at right angle to shaft; terminal apex (accessory process) tapered, usually acute; soft, variously folded median lobe surrounding terminus of tract and bearing 1 to several strong, distally directed spines or setae.

Diagnosis of zoeal morphology.—Zoeal development (known for the former *Panopeus bermudensis* and *Hexapanopeus schmitti*) consisting of 4 stages; all stages lacking lateral carapace spines or with, at most, a small lateral protrusion of the carapace where such spines exist in other xanthoid larvae (Fig. 3a, b, e, h, i). Antennal protopod unarmed and slightly dilated at tip; antennal exopod absent or greatly reduced; antennal endopod absent or reduced (Fig. 3c, f, j). Arms of telson furca each with 1 dorsal spine located below (posterior to) insertion point of, and sometimes posterior to, furthest distal extent of telson marginal setae; other telson spines may be located anterior to this (e.g., Fig. 3g). Other characters as in the "Group I" xanthid zoeas (Rice 1980, Martin 1984, Martin et al. 1985).

Etymology.—Combines prefix "acantho-," meaning thorny as in a thorny plant, with "lobulus," meaning small lobe, in ref-

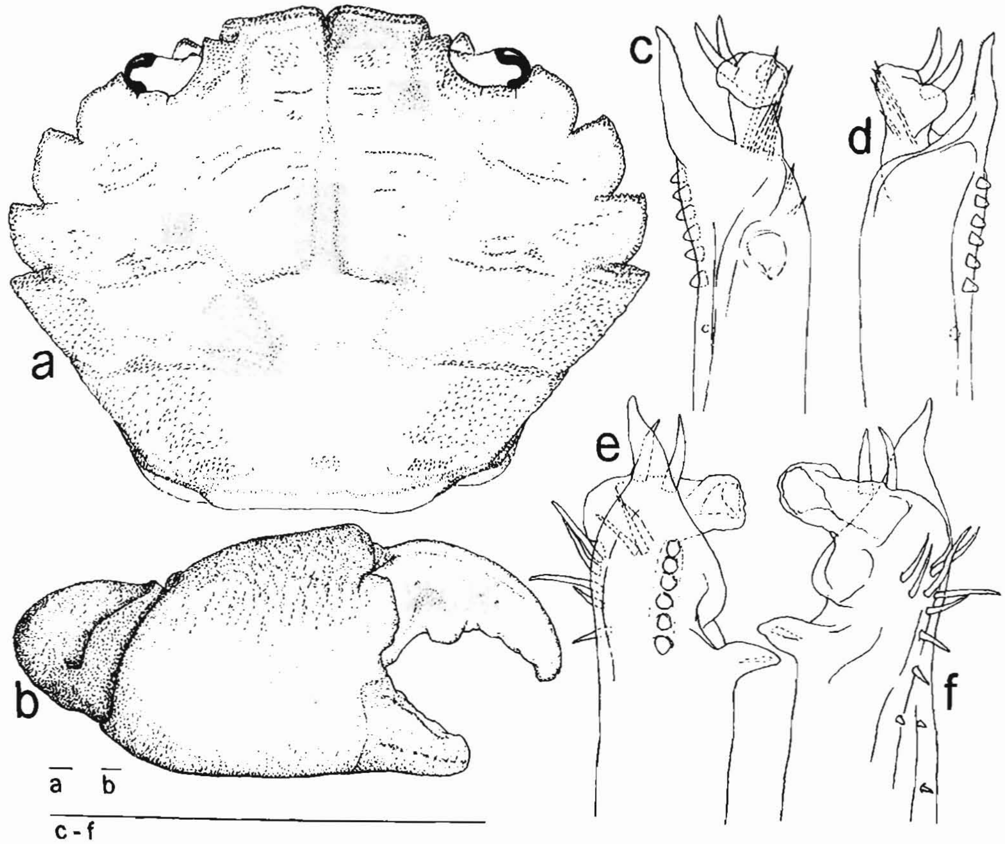

Fig. 1. *Acantholobulus bermudensis* (Benedict & Rathbun, 1891), new combination, syntypic specimens from Bermuda, USNM 42804. Male, CW 12.5 mm: a, carapace and eyes, dorsal surface; b, major chela, external surface. Male, CW 7.6 mm: c–f, right gonopod mesial, lateral, abdominal and sternal surfaces, respectively. Scale lines indicate 0.5 mm.

erence to the median lobe of the male gonopod in this genus, which generally bears characteristic spiniform setae. The gender is masculine.

Assigned species.—Acantholobulus bermudensis (Benedict & Rathbun, 1891), new combination, formerly *Panopeus bermudensis,* senior synonym of *Hexapanopeus hemphillii* Benedict & Rathbun, 1891, *Panopeus gatunensis* Abele & Kim, 1989, and *Hexapanopeus heblingi* Rodrigues & de Loyola e Silva (1998), from throughout tropical to warm-temperate waters of the western Atlantic; *Acantholobulus mirafloresensis* (Abele & Kim, 1989), new combination, formerly *Panopeus miraflorensensis,* including former eastern Pacific records of *P. bermudensis,* from throughout coastal waters of the tropical eastern Pacific region; *Acantholobulus pacificus* (Edmondson, 1931), new combination, formerly *Panopeus pacificus,* including "*Neopanope* sp. ?" of Edmondson, 1931), from Hawaii and Tahiti; and *Acantholobulus schmitti* (Rathbun, 1930), new combination, formerly *Hexapanopeus schmitti,* senior synonym of *Panopeus margentus* Williams & Boschi, 1990, from warm temperate Atlantic coastal waters of South America.

Acantholobulus bermudensis (Benedict & Rathbun, 1891), new combination

Figs. 1a–f, 2a–f, 3a–d

Panopeus herbstii var. *serratus* Miers, 1886:129.

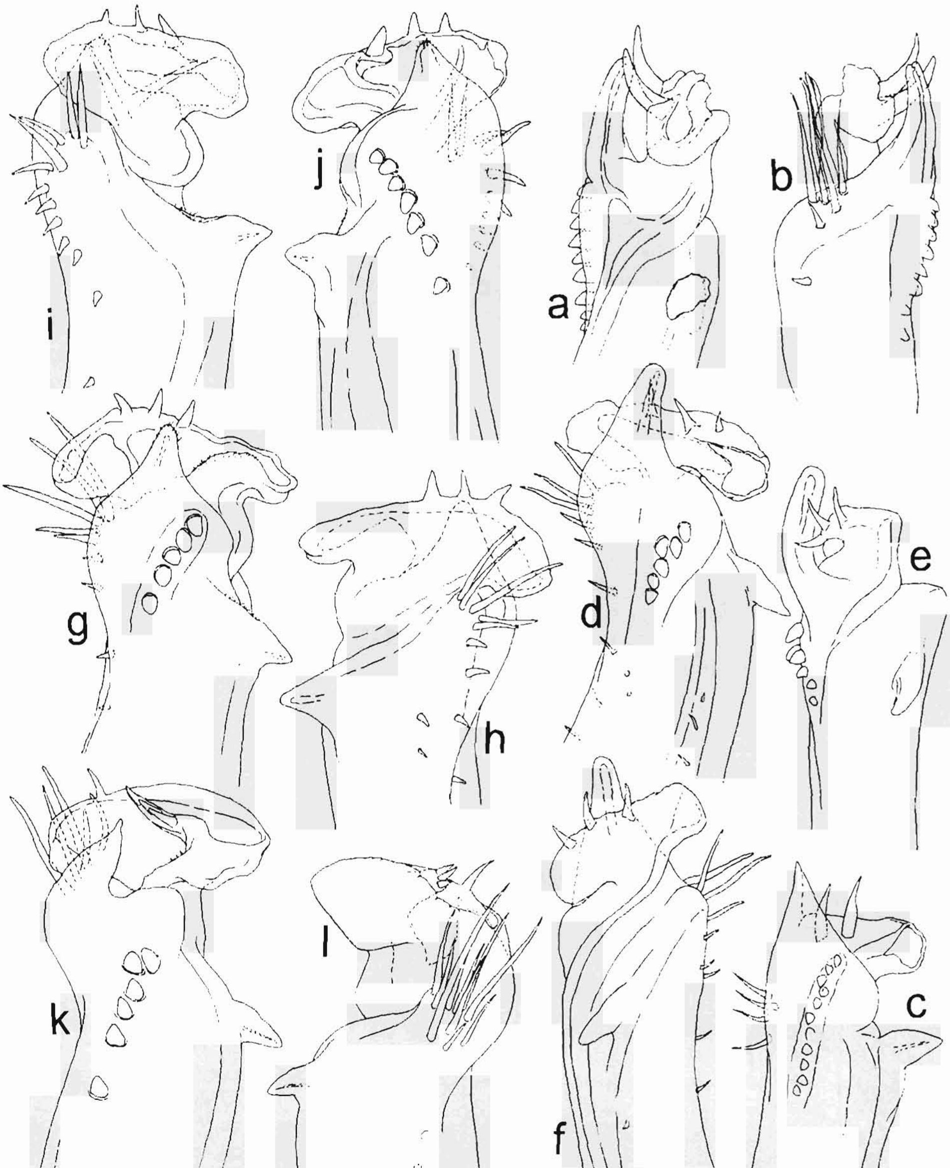

Fig. 2. *Acantholobulus bermudensis* (Benedict & Rathbun, 1891), new combination: a, b, syntypic male from Bermuda, USNM 42804, CW 12.5 mm, right gonopod mesial and lateral surfaces, respectively (subterminal tooth broken and missing from specimen, shown as dotted line); c, male from Macau, Rio Grande do Norte, Brazil, USNM 307299, (one of several specimens reported as "*Panopeus mirafloresensis*" by Ferreira & Sankarankutty 1997), CW 7.5 mm, right gonopod; d–f, male from Indian Key, Florida, USNM 15649 (holotype of *Hexapanopeus hemphillii* Benedict & Rathbun, 1891), CW 9.7 mm, right gonopod abdominal, mesial, and sternal surfaces, respectively. *Acantholobulus schmitti* (Rathbun, 1930), new combination: g, h, holotype male, Rio de Janeiro, Brazil, USNM 59831, CW 12.8 mm, right gonopod abdominal and sternal surfaces, respectively; i, j, male from Escollera Norte, Mar del Plata, Argentina, USNM 239191 (holotype of *Panopeus margentus* Williams & Boschi, 1990), CW 10.6 mm, left gonopod sternal and abdominal surfaces, respectively; k, l, male from Escollera Norte, Mar del Plata, Argentina, USNM 239195 (paratype of *Panopeus margentus* Williams & Boschi, 1990), CW 14.8 mm, right gonopod abdominal and sternal surfaces, respectively. Scale line indicates 0.5 mm.

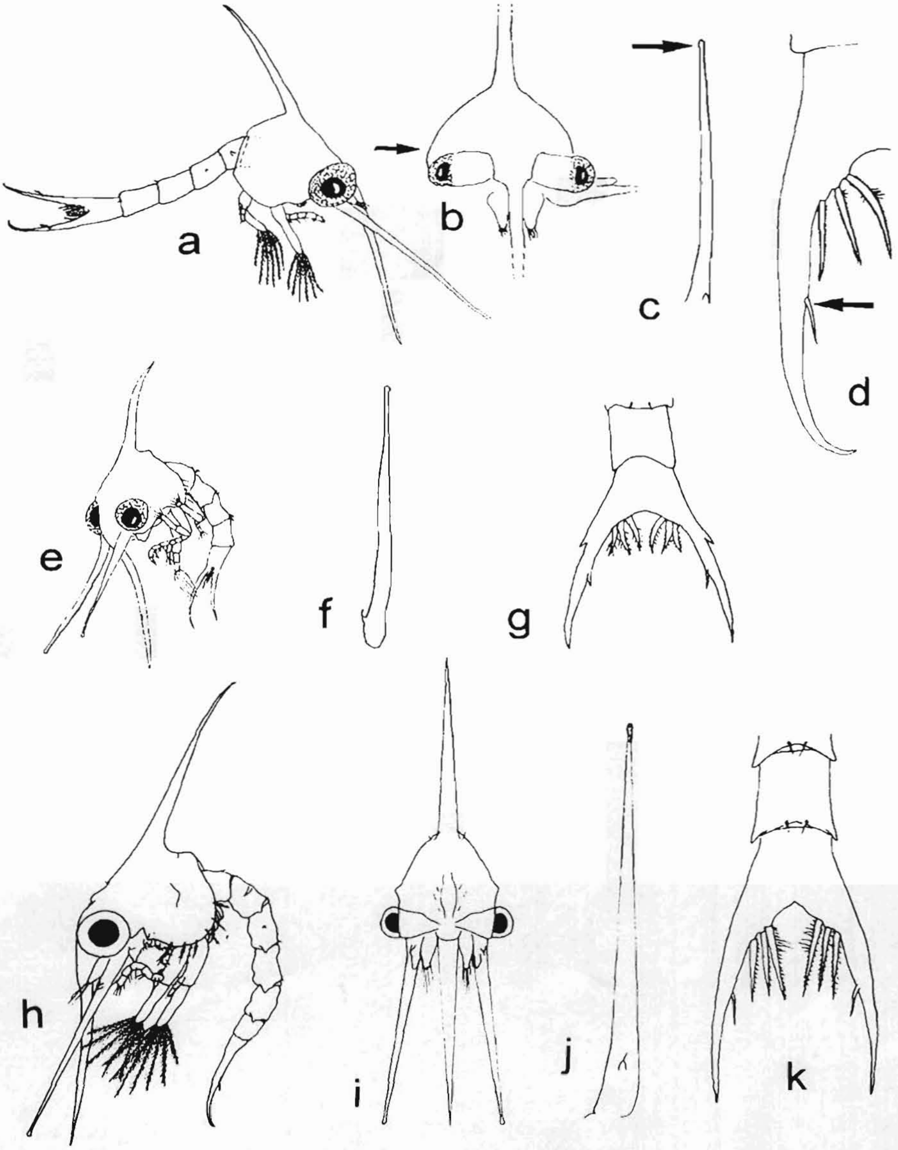

Fig. 3. Zoeal characters of *Acantholobulus*, new genus. a–d, *Acantholobulus bermudensis* (Benedict & Rathbun, 1891): a, second zoeal stage, lateral view; b, fourth zoeal stage, frontal view, arrow showing diagnostic lack of lateral carapace spine; c, second zoeal stage, antenna, arrow showing diagnostic dilated tip of protopod; d, left telsonal furca, dorsal view, arrow showing diagnostic posterior dorsal spine of furcal arm (from Martin et al., 1985, as *Panopeus bermudensis* Benedict & Rathbun, 1891). e–g, *Acantholobulus schmitti* (Rathbun, 1930), all figures of second zoeal stage: e, frontolateral view; b, antenna; c, telson, dorsal view (from Bakker et al., 1989, as *Hexapanopeus schmitti*). h–k, *Acantholobulus schmitti*: h, second zoeal stage, lateral view; i, third zoeal stage, frontal view showing lateral protrusions of carapace; j, second zoeal stage, antenna; k, second zoeal stage telson, dorsal view (from Rodríguez & Spivak 2001, as *Panopeus margentus* Williams & Boschi, 1990). Not drawn to scale.

Panopeus wurdemannii Benedict & Rathbun, 1891:357, 372, pl. 24, figs. 6, 7.

Panopeus bermudensis Benedict & Rathbun, 1891:357, 376, pl. 20, fig. 2, pl. 24, figs. 14, 15.—Rathbun 1930 (part): vii, 334 (key), 360–363, 365, 394, 583, fig. 56, pl. 165.—Rathbun 1933:60, 62.—Monod 1956:325, 336, figs. 439–440.—Felder 1973:5, 69, pl. 9, fig. 20.—Powers 1977:101.—Camp et al. 1977:35, 52, table 36.—Gore et al. 1978:221, 224, 228, 231–235, 237, 242–243, 248, table 2–4, figs. 8, 9, App. I.—Felder & Chaney 1979:15.—Martin 1984:227, 229, 230, 232, 233 (key to zoea), table 1.—Lemaitre 1981 (part, not Pacific range): 253–255, fig. 5a.—Markham & McDermott 1981:1273.—Martin et al. 1984:537–542, 544–549, 555–559, 563–564, 577–581, 589, 592–595, 597, 598, figs. 2–5, 10a, 11a, 12–13a, i, 17, 21–23a, i, 30–33a, i, 43–48, tables 4, 5.—Felder et al. 1985: 186, 208, fig. 14.—Martin et al. 1985: 84–103, figs. 1–7, tables 1, 2.—Abele & Kim 1986:xv, 59, 610 (key), 630, 631c.—Martin & Abele 1986:190, fig. 1K (not fig. 3C).—Martin 1988:76, 82, 89, 90, fig. 2f–h, j, k, 7, table 1.—Abele & Kim 1989:31, 36.—Williams & Boschi 1990:599.—Melo 1996 (part, not Pacific range):368 (key), 371, 598.—Camp et al. 1998:149, 212.—Schubart et al. 2000: 1168–1169, 1171, fig. 1, tables 1, 3.

Panopeus hemphillii Benedict & Rathbun, 1891:357, 374, pl. 24, figs. 12, 13.

Eupanopeus bermudensis.—Rathbun, 1898: 273.—Rathbun 1901:29.

Hexapanopeus hemphillii Rathbun, 1898: 273.—Rathbun 1901:31.—Rathbun 1930: 384 (key), 400–402, pl. 171, figs. 1, 2, 6.—Rathbun 1933:63.—Abele & Kim 1986:xiv, 57, 608 (key), 620, 621c–e.—Camp et al. 1998:148, 221.

Eupanopeus bermudensis var. *sculptus* Verrill, 1908:357.

Panopeus bermudensis? (juvenile).—Felder, 1973:62.

Panopeus species 2.—Martin & Abele, 1986:189, fig. 2B.

Panopeus gatunensis Abele & Kim, 1989: 3, 31, 32, 41, fig. 15a–h, table 3.

Panopeus permudensis (sic).—Sankarankutty & Manning, 1997:254.

Panopeus mirafloresensis.—Ferreira & Sankarankutty, 1997:153–155, fig. 1a–f (Brazilian specimens only; not *Panopeus mirafloresensis* Abele & Kim, 1989).

Hexapanopeus heblingi.—Rodrigues & de Loyola e Silva, 1998:263–270, figs. 1–20.

[not "*Panopeus bermudensis*" of Lebour, 1944:119, fig. 9a–d].

Material examined.—Type series, 16 specimens, of *Panopeus bermudensis* from Bermuda, USNM 42804; holotype male of *H. hemphillii* from Indian Key, Florida (USNM 15649); holotype male of *P. gatunensis* from Gatun Locks of Panama Canal, Caribbean side, Republic of Panama (USNM 237647); 2 males, 1 female reported as "*P. mirafloresensis*" by Ferreira & Sankarankutty (1997) from Macau, Rio Grande do Norte, Brazil (USNM 307299).

Diagnosis and common variations of adults.—Carapace (Fig. 1a) broadly oval; anterolateral teeth broadly developed, tending to lobiform, obtuse in small specimens, first and second broadly fused together with separation sometimes obscure; dorsal outline for each lobe of front arcuate near midline, becoming truncate or weakly concave laterally. Lines of granules on carapace usually including distinct short ridge (sometimes paired by short parallel ridge) on either half of epigastric region, composed of enlarged granules about same size as those of hepatic or branchial ridges. Color of movable finger (Fig. 1b) variably extended onto palm, varying from brown to tan, yellowish, or ivory; if dark, tips of fingers faded to near white. Palm usually with light, nearly white area distally near base of movable finger. Gonopod (Fig. 1c–f, 2a–f) with median lobe of terminus variously tubiform, slightly folded toward terminal apex (accessory process), not exceeding terminal apex distally, usually bearing 2–3 elongate,

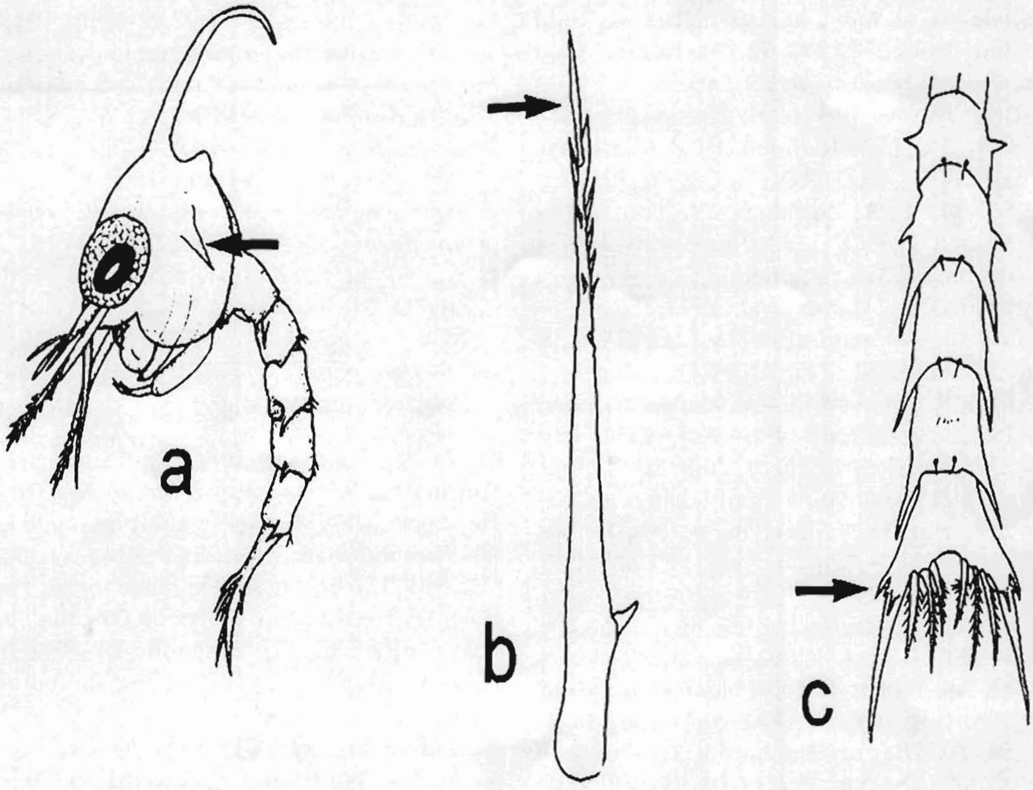

Fig. 4. Typical zoeal characters of the genus *Panopeus* H. Milne Edwards, 1834 and related genera in the family Panopeidae. a, second zoeal stage, lateral view, arrow showing well developed lateral carapace spine; b, second zoeal stage, antenna, arrow showing tapered distal extremity (note presence of spines and relative exopod/endopod sizes); c, third zoeal stage, telson in dorsal view, arrow showing placement of furcal spines (redrawn from Montú et al. 1998, as *Panopeus austrobesus* Williams 1984a).

curved spines. Zoeal stages (Fig. 3a–d) with arms of telsonal furca lacking lateral spination, each arm bearing single dorsointernal spine originating posterior to distal tips of internal marginal setae of furca. Occasional variants of adults include specimens having front a thickened lip, lacking transverse furrow on frontal lobes; bearing obscurely developed lines of granules dorsally on carapace; lacking dimorphism in chelae, with both being developed as enlarged minor chelae lacking basal tooth on movable finger; or bearing more or less than 2 or 3 spines on the median lobe of the gonopod terminus.

Distribution.—Warm-temperate and tropical shallow waters of the western Atlantic, from Bermuda and Florida, throughout the Gulf of Mexico and Caribbean Sea, the Antilles, and northern coastlines of South America to the state of Santa Catarina, Brazil.

Remarks.—No holotype was designated in the published original description of *Panopeus bermudensis* by Benedict & Rathbun (1891), though a "large male" was reported be 12 mm CW. Subsequently, Rathbun (1930) indicated that the type series consisted of 15 specimens "including holotype" and indicated that the "type male" as 14.4 mm CW. We presently find no specimen larger than a male of 12.5 mm CW in the type series of 16 specimens that comprise USNM 42804. We must surmise that the presumed holotype is either missing or that the size of the largest specimen and presumed holotype was in error as reported by Rathbun (1930). While 16 specimens remain in this lot, which exceeded the number reported by Rathbun, a small, possibly original tag with this lot does appear to indicate that the collection consists of "15+" specimens. In absence of any more definitive evidence that a designated holotype ever existed, we regard this series as syntypes.

Monod (1956:325) first noted the potential significance of the gonopod of *Panopeus bermudensis* as a generic-level character. Subsequent workers also called attention to the unique terminal gonopod morphology and its possible generic significance in both *P. bermudensis* and *Panopeus miraflorensensis* (Martin & Abele 1986; Martin et al. 1984, 1985; Abele & Kim 1989). In addition, *Panopeus gatunensis,* herein recognized as a junior synonym of *Acantholobulus bermudensis,* was shown to have a gonopod similar to the aforementioned two species, differing primarily in having a supernumerary lateral spine. Without question, all three of these species share gonopod morphology diagnostic of *Acantholobulus.* However, we place no significance in the observation of a supernumerary lateral spine on the gonopod of *P. gatunensis* that was originally illustrated by Abele & Kim (1989: fig. 15f–h) especially since the holotype male (USNM 237647, the only known specimen) has only a single lateral spine on the opposite gonopod from that illustrated. Furthermore, supernumary lateral spines are occasionally seen among large series of specimens assignable to *A. bermudensis* from the Indian River region of Florida (ULLZ collections); when these occur, they are usually on only one side of the male. The holotype of *P. gatunensis* also appears to have a regenerated major chela, an atypically smooth carapace, and a very poorly defined transverse frontal furrow. These are, however, again features seen in a small percentage of specimens assignable to *A. bermudensis* from Florida, and none occur in such combination and consistency as to suggest that they are likely characters of a separate species.

Records of *Hexapanopeus hemphillii* are not to be found in the literature since Rathbun (1930), and our attempts to collect from habitats described in that work consistently yield only specimens assignable to *Acantholobulus bermudensis.* Examination of the male holotype of *H. hemphillii* (USNM 15649) revealed that it is clearly assignable to *Acantholobulus.* Its gonopod (Fig. 2d, e) differs from the typical form in *A. bermudensis* in that it bears three smaller, rather than two larger, spines on the medial lobe. This condition, however, is not uncommon among males in large samples of *A. bermudensis.* Also, white coloration on the fingers of the chelipeds, relative widths of the anterolateral teeth on the carapace, and the carapace shape, as used in the description and later diagnosis of *H. hemphillii* (see Benedict & Rathbun 1891, Rathbun 1930), all can be found among larger series of *A. bermudensis.* In the absence of dependable diagnostic characters for *H. hemphillii,* we must treat it as a junior synonym of *A. bermudensis.*

Likewise, no characters are offered in the description by Rodrigues & de Loyola e Silva (1998) that would differentiate *Hexapanopeus heblingi* from *A. bermudensis,* and interspecific comparisons they make are limited to western Atlantic species of *Hexapanopeus.* We have not been able to examine type materials of this species, but both the text and figures in the published description clearly detail features diagnostic of *Acantholobulus,* new genus, well within the range of variation that we have observed in *A. bermudensis.* At least for the present, we conclude that this species is also a junior synonym of *A. bermudensis,* a finding supported by the strong similarity of its larvae (Rodrigues 1997) to those of *A. bermudensis* (see Discussion below).

A report of *Panopeus miraflorensensis* from Brazil (Ferreira & Sankarankutty 1997) is interpreted to also represent *Acantholobulus bermudensis* rather than the aforementioned species, which appears to be restricted to Pacific coastlines. Specimens upon which this Brazilian record was based were furnished to the late R. B. Manning prior to publication and (as noted by Ferreira & Sankarankutty 1997:157) he could not confirm that they represented *Panopeus mirafloresensis*. We have examined these specimens (USNM 307299), illustrated the male gonopod (Fig. 2c) and found them indistinguishable from *A. bermudensis*. We also observe, however, that the Pacific species *Acantholobulus mirafloresensis* (as herein assigned) is itself not readily distinguishable from *A. bermudensis* on the basis of characters reported to date, especially given the range of variation that we have observed in populations of the latter species. Records from the eastern Pacific region include mention of both *Panopeus bermudensis* (see Rathbun 1930, Garth 1961, Lemaitre 1981, Abele & Kim 1989, Lemaitre & Alvarez León 1992) and *P. mirafloresensis* (see Abele & Kim 1989: 36), and no attempt is herein made by us to resolve morphologically whether these eastern Pacific populations could represent more than one species. At least until further comparative study is undertaken and ongoing molecular analyses are completed, we recognize *A. mirafloresensis* as the eastern Pacific cognate of *A. bermudensis*. The natural range of latter species appears limited to warm-temperate and tropical shallow waters of the western Atlantic, as also concluded by Salgado Barragán & Hendrickx (1997).

Systematic review of congeners.—Recognition of *Panopeus margentus* as a junior synonym of *Acantholobulus schmitti* (Rathbun, 1930), new combination, was based upon examination of the holotype (USNM 239191) and paratypes (USNM 239195) of *Panopeus margentus*, all from Mar del Plata, Argentina. The description of *P. margentus* by Williams & Boschi (1990) included no comparisons to or mention of *Hexapanopeus schmitti*, even though the latter species has been documented to range into warm-temperate waters of southern Brazil and Uruguay. Instead, the authors did note its resemblance to *Panopeus bermudensis* and the Pacific *P. mirafloresensis*, both of which are in the present work established as congeners of *Acantholobulus schmitti*. We have found no consistent features of general carapace and cheliped morphology that would serve to distinguish *P. margentus* from larger specimens of *Acantholobulus schmitti*. Furthermore, the right gonopod as figured in the original description (Williams & Boschi 1990: fig. 1e, d) appears to be highly aberrant and perhaps damaged. Our own examination of the damaged holotype revealed the left gonopod of this specimen to be intact (Fig. 2i, j) and almost identical in terminal morphology to that herein figured for the holotype of *Acantholobulus schmitti* (Fig. 2g, h). However, as discussed below, the description of larval development for this species (*Panopeus margentus*) by Rodríguez & Spivak (2001) included some differences from that presented by Bakker et al. (1989) for *Hexapanopeus schmitti*, which should not be the case if these two names indeed refer to the same species (further addressed in Discussion below).

Materials of *Panopeus pacificus* from Hawaii and Tahiti, along with some questionably assigned to "*Neopanope* sp. ?" by Edmondson (1931), were reviewed by Forest & Guinot (1961) who provided detailed illustrations of gonopods, chelae, and carapace dentition for these specimens, all of which appear to be typical of *Acantholobulus*. Our direct examination of topotypic specimens of *P. pacificus* (four males, two females) collected by C. H. Edmondson from Pearl Harbor (USNM 96304) confirms this generic reassignment. We have also reexamined the two males of *P. pacificus* reported from Tahiti (MNHN B13963) by Forest & Guinot (1961) and found no characters to distinguish them from the Hawaiian materials. Edmondson (1931) preceded his original description of *P. pacificus* by noting the possibility of this species being "transported to Hawaii through shipments of oysters or on the bottoms of ships," especially since he found it only in association with "sponges, barnacles and tunicates attached to buoys and floats in Pearl Harbor, Oahu." This is typical habitat for most of the known *Acantholobulus* spp., and may indicate a high potential for their dispersal and introduction among fouling materials. At very least, it could account for wide distributions, such as that for *A. pacificus,* which appears to encompass both Hawaii and Tahiti. However, except for the apparent larger size evident in most specimens of *A. pacificus,* there are also no obvious morphological characters to distinguish it from *A. mirafloresensis.* More definitive conclusions about the relationship between these species and their relationships to others of the genus should be facilitated by molecular genetic studies that we have in progress.

While we have not re-examined materials of the "*Neopanope* sp.?" reported by Edmondson (1931:14), from Pearl Harbor, the chelae of one large male in the lot of *Panopeus pacificus* that we examined (USNM 96304) appears to match Edmondson's description of the chelae in his specimen of "*Neopanope* sp.?". In addition, the figure of the gonopod for "*Neopanope* sp.?" provided by Forest & Guinot (1961: fig. 106) is clearly typical of *Acantholobulus* and well within the range of variation to be expected in gonopod morphology for species in this genus. We thus conclude that the peculiar cheliped dentition reported for "*Neopanope* sp.?" by Edmondson (1931) is likely the result of cheliped regeneration and that these materials represent additional specimens of *A. pacificus,* new combination. Cheliped variations like those observed by Edmondson are not uncommon in populations of *A. bermudensis* that we have sampled in Florida (ULLZ collections). These have also been illustrated for variant specimens of both *A. bermudensis* (as *Panopeus gatunensis,* Abele & Kim, 1989: fig. 15) and *A. mirafloresensis,* (as *Panopeus mirafloresensis,* Abele & Kim, 1989: fig 18) from Panama.

Our proposed revisions are summarized as follow:

Former name	New name
Panopeus bermudensis	*Acantholobulus bermudensis,* new combination
Hexapanopeus schmitti	*Acantholobulus schmitti,* new combination
Panopeus mirafloresensis	*Acantholobulus mirafloresensis,* new combination
Panopeus margentus	junior synonym of *A. schmitti*
Panopeus gatunensis	junior synonym of *A. bermudensis*
Hexapanopeus hemphillii	junior synonym of *A. bermudensis*
Hexapanopeus heblingi	junior synonym of *A. bermudensis*

Discussion

The use of brachyuran larval morphology, especially characters of the first zoeal stage, in elucidating systematic and phylogenetic questions is now relatively well established (e.g., see references in Clark et al. 1998). Larval morphology has been of particular value for resolving relationships within the enormous superfamily Xanthoidea MacLeay, 1838 (e.g., Clark & Al-Aidaroos 1996, Clark & Galil 1998, Clark & Ng 1998, Fransozo et al. 2001, and papers cited therein). Several workers (Rice 1980; Martin 1984, 1988), have proposed recognizable groupings of xanthoid larvae in attempts to address systematic or phylogenetic questions. Within the xanthoid family Panopeidae Ortmann, 1893 sensu Guinot 1978 (see also Martin & Davis 2001), larval morphology is diverse. Prior to 1985, however, all known species of the Panopeidae save *Panopeus bermudensis* were thought to have lateral carapace spines, which is true of nearly all known xanthoid larvae. "Typical" zoeal larvae of panopeid crabs have well developed (although sometimes short) lateral carapace spines, a tapering antennal protopod that is often armed distally (and is never distally inflated), and two or three small spines on the telsonal furcae, all located at approximately the level of insertion of the three paired telsonal setae (Fig. 4). The larvae of *P. bermudensis* were described as differing from all other panopeid larvae in lacking these lateral carapace spines (Martin et al. 1985), having an antenna that is dilated at the tip and that lacks an exopod (actually present, but greatly reduced, see Discussion), and in bearing a single pair of telsonal spines located posterior to the distal tip of the interior telsonal setae. Remarkably, the zoeal stages of *Hexapanopeus schmitti* as described by Bakker et al. (1989) also lack a lateral carapace spine, have an antennal protopod that is dilated at the tip, have a reduced antennal exopod, and bear a pair of posterior spines on the telsonal furca (although, in addition, there is also a pair of more anterior furcal spines).

Our decision to group the former *Panopeus bermudensis* and *Hexapanopeus schmitti*, along with the former *Panopeus mirafloresensis* and *P. pacificus*, into *Acantholobulus*, new genus, on the basis of adult morphology is thus supported by larval morphology for at least the first two of these species. We expect that larval characters of the former *P. mirafloresensis* and *P. pacificus*, which remain undescribed, should resemble those of the two other species of *Acantholobulus*. Given the similarities in adult morphology herewith reported for proposed members of *Acantholobulus*, new genus, shared characters in larval morphology to the extent known within this group, and the established genetic distinction for at least one of its members (Schubart et al. 2000), the generic revision herein proposed is strongly supported.

Even so, some problems remain in our assignment of species to the new genus *Acantholobulus*, decision to synonymize *Panopeus margentus* with *Acantholobulus schmitti*, and conclusion that *Hexapanopeus hemphillii* and *H. heblingi* must be synonymized with *Acantholobulus bermudensis*. In the case of *Panopeus margentus*, our reasons for placing this species into synonymy with *Acantholobulus schmitti* on the basis of adult features have been given earlier. One would thus expect that reported larval descriptions would prove to be identical, and to large extent this is true; Rodríguez & Spivak (2001:818) state that "*Panopeus margentus* larvae are very similar to those of *H. schmitti*." The larvae of *P. margentus* as described by Rodriguez & Spivak (2001) also lack lateral carapace spines, although a slight protrusion of the carapace can be seen (Fig. 1h, i), which may be a homologue of the lateral spine in typical panopeid zoeas. As described, however, the zoeal stages of *P. margentus* would appear to lack the second pair of telson furcal spines shown by Bakker et al. (1989) for *H. schmitti*.

In the course of our studies, we have reexamined the parental female (USNM 288046), as well as the larval stages of *P. margentus* (USNM 291175) described by Rodríguez & Spivak (2001). We cannot definitively separate the female from those of *A. schmitti*, though females of both of these species remain poorly described. Among the larvae, when mounted in glycerin and examined with differential interference contrast (DIC) optics, we do find zoeas at stages one through four in which a second, very small pair of telson furcal spines can be discerned at high magnifications (first called to our attention by J. Cuesta and B. Mahon). These, however, appear to be less conspicuous than those illustrated for zoeal stages of *A. schmitti* by Bakker et al. (1989), and it should be noted that they were not obvious on all specimens examined; in some cases, the small setal shaft appeared instead as a cluster of two or three miniscule setae or setal fragments and may have been worn or damaged.

For *Hexapanopeus heblingi* we examined

selected figures of the larvae illustrated by Rodrigues (1997, figs. 3–10). On the basis of these larval descriptions, zoeal stages of *H. heblingi* are essentially identical to those of *Panopeus bermudensis* described by Martin et al. (1984, 1985). The absence of a lateral carapace spine, the inflated tip of the antenna, the reduced antennal exopod, and other features are a nearly perfect match, supporting our synonymy of the two species under the name *Acantholobulus bermudensis.* Yet, descriptions of the megalopa appear to differ slightly. In the megalopa of *P. bermudensis,* described by Martin et al. (1984, 1985), the frontal region of the carapace bears anterolateral horns, and the cheliped bears a distinct recurved spine on the ischium. Neither of these characters is illustrated by Rodrigues (1997) for the species therein referred to as *H. heblingi.* Although frontal horns on the carapace are easily missed, especially if the carapace front is strongly deflected downward, the cheliped spine is a feature that rarely escapes notice.

We cannot further comment on this apparent discrepancy without directly re-examining the larvae referred to as *H. heblingi.* Minute structures are easily overlooked, and it is pertinent to note that Martin et al. (1985) also overlooked a diagnostic structure in the course of describing larvae that we now refer to *Acantholobulus bermudensis.* We have re-examined some of the actual larvae treated in that earlier study (ULLZ, uncatalogued slide mounts), and we must now report that the antenna does in fact possess a small exopod. It is entirely possible that other small features have also escaped the notice of previous workers, and a thorough reinvestigation of larval morphology in all of these xanthoid groups is warranted.

For the present, pending additional molecular studies to build on those of Schubart et al. (2000), we continue to treat species herewith assigned to *Acantholobulus,* new genus, as members of the Panopeidae. As noted above, however, both mtDNA sequences and larval morphology set this group apart from typical panopeid species, and definitive assignment must await improved understanding of familial separations among the Xanthoidea.

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