

NOTES ON MALE PLEOPOD MORPHOLOGY IN THE
BRACHYURAN CRAB FAMILY PANOPEIDAE ORTMANN, 1893,
SENSU GUINOT (1978) (DECAPODA)

BY

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INTRODUCTION

The heterogeneous assemblage of species that makes up the unwieldy family Xanthidae MacLeay, 1838, has proved to be taxonomically problematic at all levels. Indeed, the easiest way to establish the identity of many xanthids is first to determine the species and then to search the literature for their currently accepted generic placement. This difficulty is the result of two factors: (1) the extreme morphological similarity of so many xanthid species and (2) the lack of established criteria upon which generic distinctions are based. Although nothing can be done about the former, the latter has been the subject of several carcinological studies. Major works containing keys to or descriptions of xanthid genera include Alcock (1895), Guinot (1967a, b; 1978), Manning & Holthuis (1981), A. Milne Edwards (1880), Monod (1956), and Rathbun (1930).

Most of the characters employed in generic distinction are based on carapace and/or cheliped morphology and are distressingly vague. Carapace morphology often can be explained as adaptation to habitat and probably should not be considered a conservative character. Cryptic xanthids such as *Eurypanopeus depressus* (Smith) have flattened carapaces, which allow movement among oyster clumps; burrowing xanthids such as *Eurytium limosum* (Say) have rounded, smooth carapaces with reduced or rounded anterolateral teeth. Yet these two species are closely related by both zoeal and pleopodal characters. Similarly, cheliped armature, including form of the fingers, may reflect adaptation to different foods and not phylogenetic distance.

Guinot's approach dealt with several characters including placement of the male genital openings, structure of the male first pleopod, and characters of the sternal plastron, endophragmal system, and "bouton-pressure" apparatus. The resulting classification given by Guinot (1978) is a superfamily, Xanthoidea, containing 8 families (Panopeidae, Pilumnidae, Menippidae, Xanthidae, Carpiliidae, Platyxanthidae, Trapeziidae, and Geryonidae). Because

first pleopod armature is unlikely to reflect adaptation to habitat, we agree with Guinot (1967a, b) in placing emphasis on the male first pleopod (hereafter referred to simply as pleopod) as a generic character in the Xanthidae (*sensu lato*). Unfortunately, this approach necessitates major changes in the currently accepted taxonomy of adults (see Historical Summary). Before accepting such an ambitious revision, we feel it is necessary to examine closely the characters upon which Guinot's Panopeidae is based. In this paper, we examine male pleopod morphology in the family Panopeidae *sensu* Guinot (1978) and in possibly related genera that Guinot excluded from the assemblage and comment on the generic placement of those species in which the pleopod is known. In addition, we remove two species from the genus *Neopanope* and place them in a new genus on the basis of pleopod morphology.

HISTORICAL SUMMARY

Systematically, the genus *Panopeus* H. Milne Edwards has a long-standing reputation as a problem group. The type-species selected by Desmarest (1852) is actually a member of the genus *Sphaerozius* Stimpson; *Panopeus herbstii* H. Milne Edwards became the type-species only after Holthuis (1979) recognized the errors of several earlier workers (see Manning & Holthuis, 1981). Erected by H. Milne Edwards (1834) to accommodate one new species, *P. herbstii*, and one new combination, *P. limosus* [originally *Cancer limosa* Say, now *Eurytium limosum* (Say)], the genus contained some 38 species by the time it was reviewed by Benedict & Rathbun (1891), but only 24 of those species were available for examination by them at that time. Benedict & Rathbun did not accept either the genus *Eurypanopeus* A. Milne Edwards, 1880, or *Eurytium* Stimpson, 1859, treating species earlier consigned to those genera as true *Panopeus*. Shortly thereafter, the species treated therein as *Panopeus* were reassigned to a variety of genera, and by the time of Rathbun's (1930) monograph the American species of the group had been placed in the following genera: *Eurypanopeus* A. Milne Edwards (8 species, 1 subspecies); *Hexapanopeus* Rathbun, 1898 (9 species); *Rithropanopeus* Rathbun, 1898 (1 species); *Eurytium* Stimpson (3 species); *Neopanope* A. Milne Edwards, 1880 (2 species, 1 subspecies); *Panopeus* H. Milne Edwards, 1834 (11 species, 6 forms). Many of these species have subsequently been referred to an assortment of genera, as various workers have attempted to reorder the assemblage (e.g., Menzies, 1948; Guinot, 1967a; Manning & Holthuis, 1981).

Guinot (1978) stated that the genus *Panopeus* and its allies "constituent une famille distinct, les Panopeidea," and thus elevated the subfamily Panopeinae Ortmann, 1893. Guinot's Panopeidae is a larger, more inclusive grouping than Ortmann's subfamily and consists of the following genera from the subfamily Xanthinae of Balss (1957): *Eurypanopeus* A. Milne Edwards, 1880, *Hexapanopeus* Rathbun, 1898, *Lophopanopeus* Rathbun, 1898, *Metopocarcinus* Stimp-

son, 1860, *Neopanope* A. Milne Edwards, 1880, *Panopeus* H. Milne Edwards, 1834, *Rhithropanopeus* Rathbun, 1898, and tentatively *Micropanope* Stimpson, 1871, s.s. (see Guinot, 1967a) and its allies. [Guinot (1967a) created the genera *Gonopanope* Guinot, 1967a, *Coralliope* Guinot, 1967a, *Nanocassiope* Guinot, 1967a, *Microcassiope* Guinot, 1967a, and *Nanoplax* Guinot, 1967a, to accommodate species formerly in the genus *Micropanope*. Under the heading "Remarks on the genus *Micropanope* Stimpson, 1871," she also created *Miersiella* Guinot, 1967a, to accommodate one former member of the genus *Medaeus* Dana, 1851. However, none of the above genera was meant to be considered an ally of *Micropanope*; rather, the allies of *Micropanope* were meant to include only those former *Micropanope* or related species that were not examined in Guinot's (1967a) paper or are yet to be described (D. Guinot, pers. comm.)]. The genus *Eurytium* Stimpson was removed from the Pilumninae of Balss and placed in the Panopeidae. All of the above genera (excluding Guinot's 1967a new genera) were placed by Guinot (1978) in the panopeid subfamily Panopeinae Ortmann, 1893, characterized by coxal genital openings in the male and a "xanthid facies". Guinot recognized a second subfamily of the Panopeidae, the Eucratopsinae Stimpson, 1871 (= Prionoplacinae Alcock, 1900), composed of the following genera previously placed by Balss (1957) in the family Goneplacidae: *Eucratopsis* Smith, 1869, *Prionoplax* H. Milne Edwards, 1852, *Cyrtoplax* Rathbun, 1914, *Tetraplax* Rathbun, 1900, and *Glyptoplax* Smith, 1870. Guinot (1978: 276) also noted that it may be necessary to include in the Eucratopsinae *Cycloplax* Guinot, 1969, *Malacoplax* Guinot, 1969, and perhaps *Panoplax* Stimpson, 1871. This subfamily was characterized by coxal or coxal-sternal male genital openings and a "goneplacid facies".

It would seem that the family name should be Eucratopsidae Stimpson, 1871, rather than Panopeidae Ortmann, 1893, based on Article 23(d) (i) of the International Code of Zoological Nomenclature, if Guinot's classification is to be followed.

Below we describe male first pleopod morphology in the panopeid genera based upon earlier illustrations and upon our own observations (table I, figs. 1-3).

Subfamily PANOPEINAE Ortmann, 1893

Panopeus H. Milne Edwards, 1834. — In every species illustrated (table I) the pleopod is distinctly trilobed. A large, tapering, minutely spinulose and usually curved process (the accessory process) extends caudally from the apex. Usually shorter than this process is a less calcified, distally rounded or hooded process (the median process), always with a central depression or groove facing the accessory process. A lateral tooth, usually bifid, extends at an approximately 90° angle from the main shaft. The caudal margin of the shaft just below the accessory process is armed with an irregular row of short, blunt

spines. A row of shorter, sharper spines extends proximally from the lateral surface of the lateral tooth around the anterior margin of the shaft.

Manning & Holthuis (1981) surveyed all the species of *Panopeus* in the Smithsonian Institution, finding males of all save *P. convexus* represented, and noted that the "typically trilobed male pleopod" is universal.

Variations. — The pleopod of *P. bermudensis* Benedict & Rathbun has the lateral tooth entire. The median process is more rounded than in other species and bears 1 or 2 elongate spines [Monod (1956) shows 1 spine; our illustration (fig. 1K) shows 2 spines]. The accessory process is relatively shorter than in other species and is not so curved. *Panopeus turgidus* Rathbun has an accessory process with a bifurcated tip (fig. 1B); the resulting branches may themselves occasionally be bifid (Darryl L. Felder, University of Southwestern Louisiana, Lafayette, pers. comm.).

Eurypanopeus A. Milne Edwards, 1880. — The pleopod is essentially similar to that of *Panopeus*, having a trilobed apex. Our figure (1H) of *E. abbreviatus* (Stimpson) differs from that of Williams (1965) in the development of the median lobe. In our specimen, this lobe is laterally reflexed and not visible in median view, whereas in Williams' figure this lobe is erect and more similar to that of *Panopeus*. Monod's (1956) figure of *E. blanchardi* (A. Milne Edwards) is closer to Williams' figure of *E. abbreviatus* than it is to our figure. All species of *Eurypanopeus* so far described appear to have an accessory process bent sharply over the median process. This is also the case in *Panopeus turgidus*, a species that some believe to be more closely allied to *Eurypanopeus* (see discussion in Powers, 1977).

Hexapanopeus Rathbun, 1898. — The pleopods of *H. angustifrons* (Benedict & Rathbun) are similar to those of *H. paulensis* Rathbun, but differ from those of *Panopeus*. The accessory process is absent, and the median process is reduced and flattened. The pleopod of *H. paulensis* is slightly more sculptured than that of *H. angustifrons*. Garth (1961) described but did not illustrate the pleopod of *H. beebei* Garth. In this species, the pleopod does not resemble that of either *H. angustifrons* or *H. paulensis*. Garth described it as having a "long, backward-pointing medial spine [our lateral tooth], an equally long and oppositely directed lanceolate lobe [our accessory process], and a rimmed hood bearing three terminal setae [our median process]". Examination of *H. beebei* in our collections (fig. 2D) confirms this description. Thus, this genus presently contains at least two very different pleopod types.

Neopanope A. Milne Edwards, 1880. — The pleopod of *N. packardii* (Kingsley) (the type-species) is of the *Panopeus* form, but with an entire (not bifid) stout lateral tooth. The accessory process is curved over the median process, as in *Eurypanopeus*. We have examined the pleopod of the holotype of *N.*

TABLE I

Descriptions of male first pleopods within the family Panopeidae sensu
Guinot (1978)

PANOPEINAE Ortmann, 1893

- Dyspanopeus sayi* (Smith, 1857): Abele, 1972, fig. 3D; Williams, 1965, fig. 183F, G (as *Neopanope*).
Dyspanopeus texanus (Stimpson, 1858): Abele, 1971, pl. 1; 1972, figs. 3B, C; Lemaitre, unpublished, figs. 30A, B (as *Neopanope*); present study, fig. 1F.
Eurypanopeus abbreviatus (Stimpson, 1860): Williams, 1965, fig. 183K; present study, fig. 1H.
Eurypanopeus blanchardi (A. Milne Edwards, 1881): Monod, 1956, figs. 424, 426-429, 431-434, as *Panopeus parvulus*¹), fig. 428 reproduced here as 3B.
Eurypanopeus depressus (Smith, 1859): Williams, 1965, fig. 183L; present study, fig. 1C.
Eurypanopeus sp.: present study, fig. 2C.
Eurytium limosum (Say, 1818): Williams, 1965, fig. 1830; present study, fig. 1J.
Hexapanopeus angustifrons (Benedict & Rathbun, 1891): Williams, 1965, fig. 183D; present study, fig. 1G.
Hexapanopeus beebii Garth, 1961: Garth, 1961 (not figured); present study, fig. 2D.
Hexapanopeus paulensis Rathbun, 1930: Williams, 1965, fig. 183E.
Lophopanopeus bellus bellus Stimpson, 1860: Menzies, 1948, pl. 1 fig. 1, reproduced here as 1L.
Lophopanopeus leucomanus leucomanus (Lockington, 1876): Menzies, 1948, pl. 1 fig. 9, reproduced here as 1M.
Lophopanopeus frontalis (Rathbun, 1893): Menzies, 1948, pl. 4 figs. 30-32, fig. 32 reproduced here as 1N.
Lophoxanthus erosus Parisi, 1916: Menzies, 1948, pl. 4 fig. 33.
Metopocarcinus truncatus Stimpson, 1860: Holthuis, 1954, fig. 11c, d, reproduced here as 2E.
Micropanope lobifrons A. Milne Edwards, 1881: Guinot, 1967a, fig. 5a, b, reproduced here as 3D.
Micropanope sculptipes Stimpson, 1871: Guinot, 1967a, fig. 4a-c, fig. 4a and 4c reproduced here as 3E.
Neopanope packardii (Kingsley, 1879): Abele, 1971, pl. 1; 1972, fig. 3A; Lemaitre, unpublished, fig. 22A-B, present study, fig. 1D.
Panopeus africanus A. Milne Edwards, 1867: Capart, 1951, fig. 54, pl. 3 fig. 3; Monod, 1956, figs. 410-412, and figs. 436-437 as *Panopeus* sp.¹), fig. 410 reproduced here as 3A.
Panopeus bermudensis Benedict & Rathbun, 1891: Monod, 1956, figs. 439-440, fig. 440 reproduced here as 3C; present study, fig. 1K.
Panopeus chilensis H. Milne Edwards & Lucas, 1844: present study, fig. 1E.
Panopeus herbstii H. Milne Edwards, 1834: Williams, 1965, fig. 183M.
Panopeus herbstii forma *obesa* Rathbun, 1930: present study, fig. 1A.
Panopeus occidentalis Saussure, 1857: Williams, 1965, fig. 183N.
Panopeus turgidus Rathbun, 1930: present study, fig. 1B.
Panopeus sp. 1: present study, fig. 2A.
Panopeus sp. 2: present study, fig. 2B.
Rhithropanopeus harrisi (Gould, 1841): Williams, 1965, fig. 183C; present study, fig. 1I.

EUCRATOPSINAE Stimpson, 1851

- Cycloplax pinnotheroides* Guinot, 1969: Guinot, 1969, fig. 32, reproduced in part here as 4A²).
Cyrtoplax schmitti Rathbun, 1935: Guinot, 1969, fig. 20, reproduced in part here as 4B.
Cyrtoplax spinidentata (Benedict, 1892): Guinot, 1969, fig. 21-22, reproduced in part here as 4C.
Eucratopsis crassimanus (Dana, 1851): Guinot, 1969, fig. 25, reproduced in part here as 4D.
Glyptoplax pugnax Smith, 1870: Guinot, 1969, fig. 23, reproduced in part here as 4E.
Glyptoplax smithii A. Milne Edwards, 1880: Guinot, 1969, fig. 24, reproduced in part here as 4F.
Malacoplax californiensis (Lockington, 1877): Guinot, 1969, fig. 27, reproduced in part here as 4G.
Panoplax depressa Stimpson, 1871: Guinot, 1969, figs. 28-29, reproduced in part here as 4H.
Prionoplax ciliata Smith, 1870: Guinot, 1969, figs. 18-19, reproduced in part here as 4I.

Prionoplax spinicarpus H. Milne Edwards, 1852: Guinot, 1969, fig. 17, reproduced in part here as 4J.

Tetraplax quadridentata (Rathbun, 1898): Guinot, 1969, fig. 26, reproduced in part here as 4K.

Subfamily uncertain (possibly not in Panopeidae); removed from *Micropanope* by Guinot (1967a)

Coralliopae parvula (A. Milne Edwards, 1869): Monod, 1956, figs. 397-400, as *Micropanope*; Guinot, 1967a, fig. 11, reproduced here as 3H.

Gonopanope angusta (Lockington, 1877): Guinot, 1967a, fig. 6a, b, reproduced here as 3F.

Gonopanope areolata (Rathbun, 1898): Guinot, 1967a, fig. 7a, b, reproduced here as 3G.

Microcassiope minor (Dana, 1852): Guinot, 1967a, fig. 15, as *M. rufopunctata*¹⁾ reproduced here as 3I; Monod, 1956, figs. 387-392; Chace, 1966, fig. 8, as *Micropanope rufopunctata*.

Nanocassiope alcocki (Rathbun, 1902): Guinot, 1967a, fig. 12, reproduced here as 3K.

Nanocassiope granulipes (Sakai, 1939): Guinot, 1967a, fig. 14, reproduced here as 3M.

Nanocassiope melanodactyla (A. Milne Edwards, 1867): Guinot, 1967a, fig. 13, reproduced here as 3L; Capart, 1951, pl. 3 fig. 15; Monod, 1956, figs. 403-405; Chace, 1966, fig. 7, as *Micropanope*.

Nanoplax xanthiformis (A. Milne Edwards, 1880): Guinot, 1967a, fig. 16, reproduced here as 3N.

¹⁾ See Manning & Holthuis, 1981.

²⁾ Placement tentative; see Guinot, 1978.

peterseni Glassell, 1933 (USNM 124804), and found it essentially identical to that of *N. packardii*. A very different situation exists for *N. sayi* and *N. texana*. These two species differ only slightly in pleopod morphology (see Abele, 1972), but are not at all similar to *N. packardii*, and for these two species we create the following new genus.

Dyspanopeus new genus

Type. — *Panopeus texanus* Stimpson, 1859.

Carapace subhexagonal, similar to that of *Neopanope*. Third to fourth anterolateral teeth directed anteriorly, more so than in *Neopanope*. Front advanced, arcuate. Anterolateral teeth not so acute as in *Neopanope*. Posterolateral border lacking weak notches just posterior to fifth anterolateral tooth. Chelipeds unequal, major chela without basal tooth on dactyl. Male pleopod strongly deflexed laterally at apex, not obviously trilobed; more simple than *Panopeus* form. Antennal segment forming lower mesial portion of orbit never more than 1½ times as long as wide, usually as long as wide or only slightly longer than wide. Anterolateral border of same antennal segment produced distally far beyond anteromesial border. Otherwise as in *Panopeus*.

Species. — *Dyspanopeus texanus* (Stimpson, 1859), *Dyspanopeus sayi* (Smith, 1869). See Abele (1972) for recent descriptions and synonymies.

Lophopanopeus Rathbun, 1898. — The pleopod is trilobed, with the accessory process extending from the shaft at an acute angle (except for *L. bellus bellus* Stimpson). The median lobe appears deeply furrowed, and the lateral tooth is simple. It is not clear from the illustration of *L. bellus bellus* by Menzies

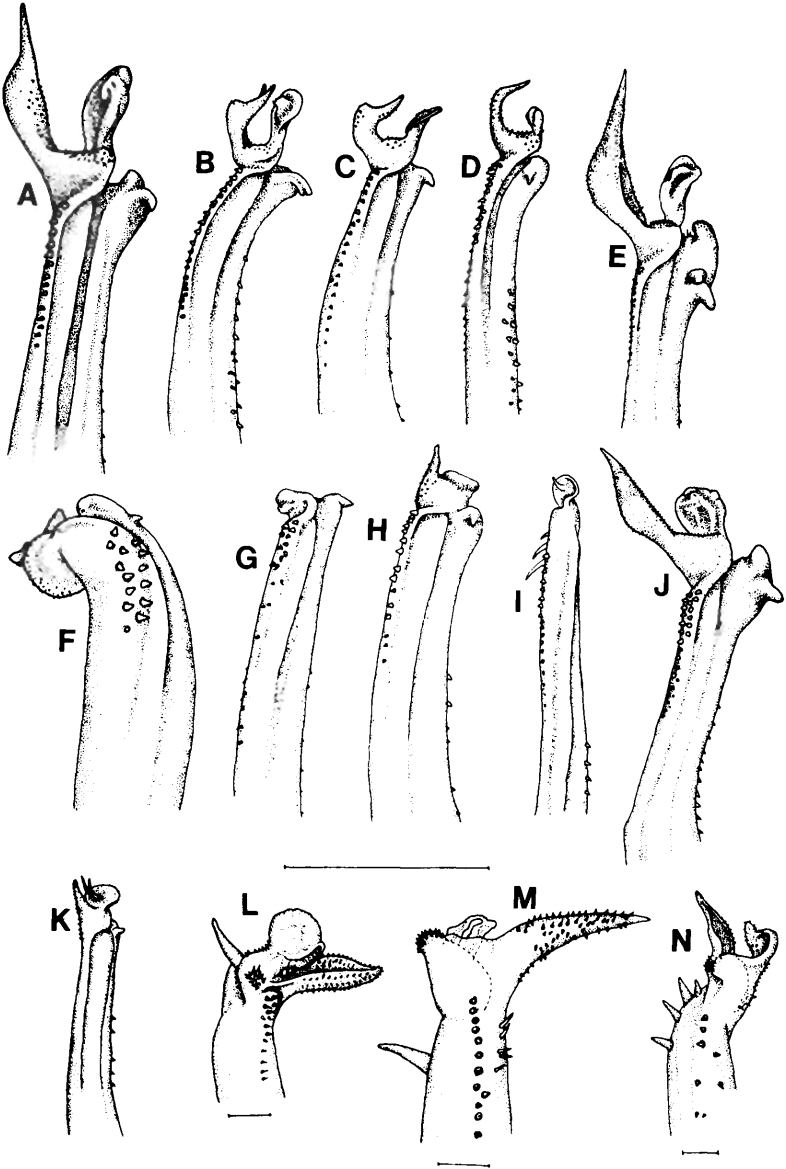


Fig. 1. Male first pleopods of the Panopeinae. A, *Panopeus herbstii*, forma *obesa*; B, *Panopeus turgidus*; C, *Eurypanopeus depressus*; D, *Neopanope packardii*; E, *Panopeus chilensis*; F, *Dyspanopeus texanus*; G, *Hexapanopeus angustifrons*; H, *Eurypanopeus abbreviatus*; I, *Rhithropanopeus harrisi*; J, *Eurytium limosum*; K, *Panopeus bermudensis*; L, *Lophopanopeus bellus bellus*; M, *Lophopanopeus leucomanus leucomanus*; N, *Lophopanopeus frontalis*. L, M, and N from Menzies, 1948. Scale = 1.0 mm for A-K, 0.1 mm for L-N. C and K are from laboratory-reared adults.

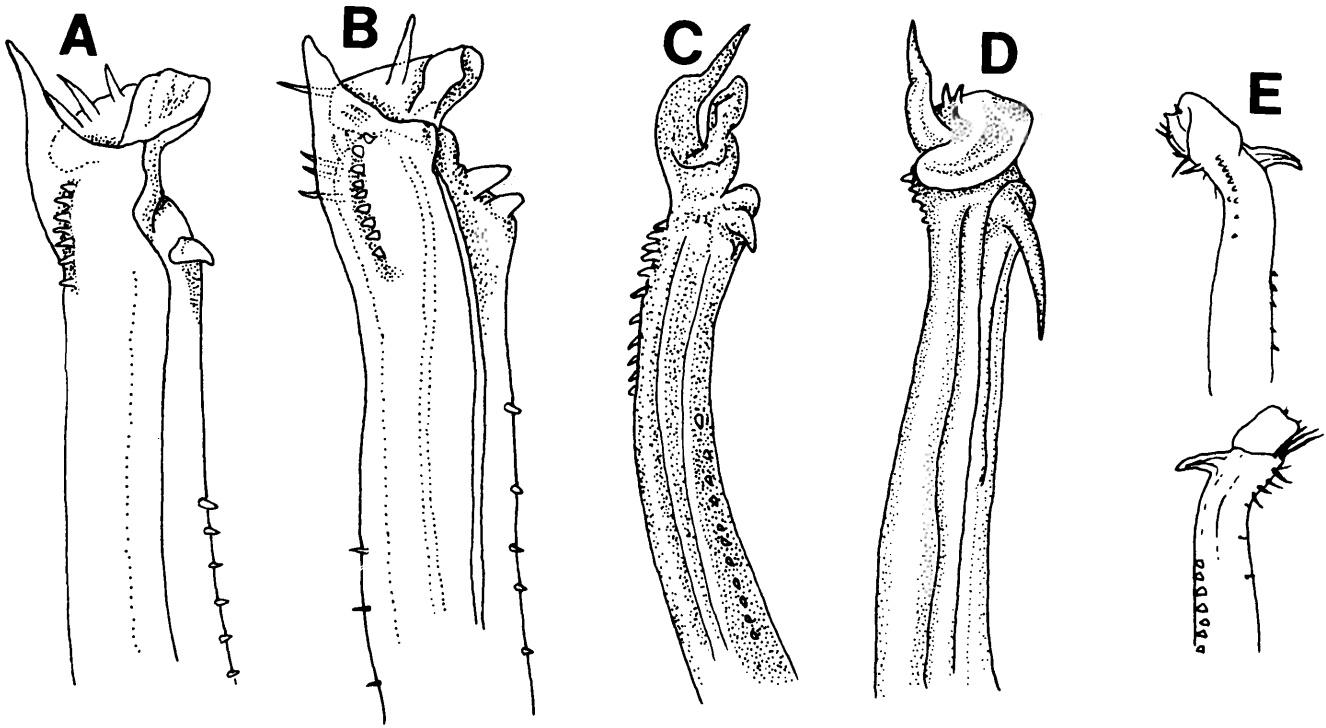


Fig. 2. Male first pleopods of the Panopeinae. A, *Panopeus* species 1, Pacific side of Panama Canal; B, *Panopeus* species 2, Atlantic side of Panama Canal (these two species possibly synonymous); C, *Eurypanopeus* sp., Pacific side of Panama Canal; D, *Hexapanopeus beebei*; E, *Metopocarcinus truncatus*. A-C after Kim & Abele (unpublished manuscript); D after Won Kim (unpublished data); E after Holthuis, 1954.

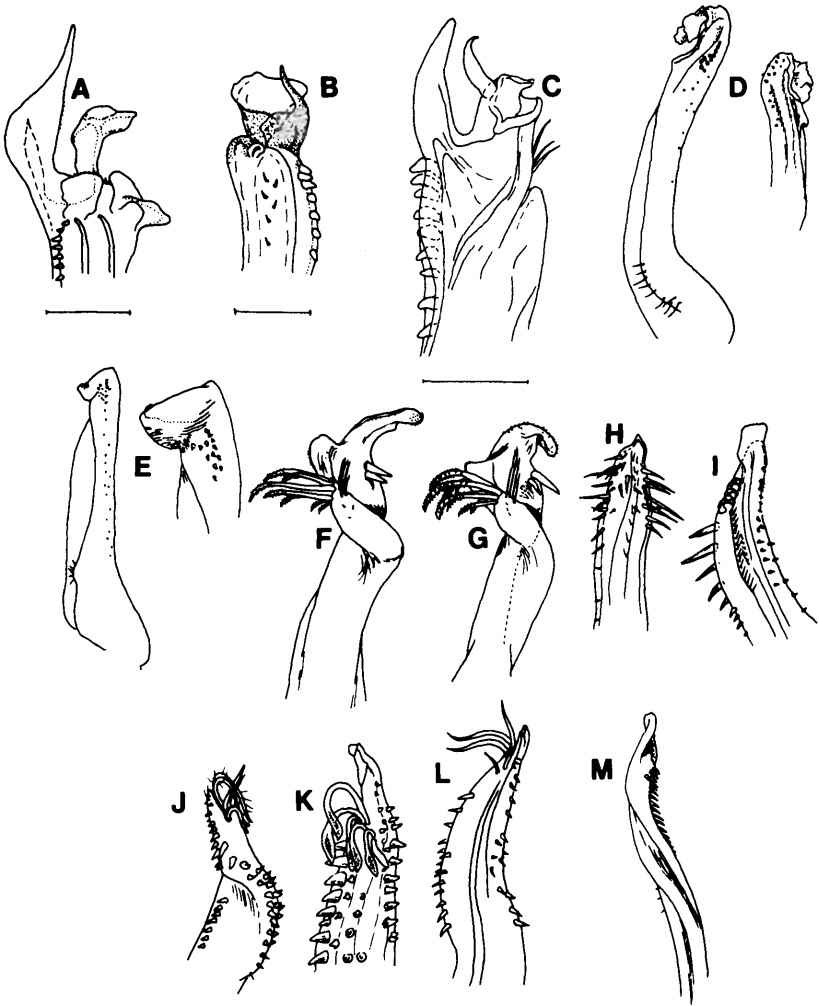


Fig. 3. Male first pleopods of the Panopeinae (A-E) and of species formerly in *Micropanope* (F-M). A, *Panopeus africanus*; B, *Eurypanopeus blanchardi*; C, *Panopeus bermudensis*; D, *Micropanope lobifrons* (2 views); E, *Micropanope sculptipes* (2 views); F, *Gonopanope angusta*; G, *Gonopanope areolata*; H, *Coralliopoe parvula*; I, *Microcassiope minor*; J, *Nanocassiope alcocki*; K, *Nanocassiope melanodactyla*; L, *Nanocassiope granulipes*; M, *Nanoplax xanthiformis*. A-C from Monod, 1956; D-M from Guinot, 1967a. Scale = 0.1 mm for A, B, and C.

whether the lateral tooth is absent in this species (fig. 1N), although Menzies stated (1948: 4) that this pleopod is "characteristic"; therefore, we assume that the lateral tooth is present.

Rhithropanopeus Rathbun, 1898. — The pleopod of *R. harrisii* (Gould) (fig. 1I) is unlike that of *Panopeus*. There is no accessory process or lateral tooth.

The median process is rounded and bears one long spine arising from the center. Three to four long thin spines project laterally from the main shaft.

Eurytium Stimpson, 1859. — The pleopod of *E. limosum* (Say) (fig. 1J) is identical to that of most species of *Panopeus*. A slight bend in the shaft, proximal to the apex, is the only character that appears unique to *Eurytium*. Examination of *E. tristani* Rathbun revealed pleopod morphology identical to that of *E. limosum*. Kurata et al. (1981) noted very little difference between early zoeas of *E. limosum* and *P. herbstii*; it may be that the genus *Eurytium* should be synonymized with *Panopeus* again.

Micropanope Stimpson, 1871. — Guinot (1967a) restricted this genus to two species, *M. sculptipes* Stimpson and *M. lobifrons* A. Milne Edwards. The pleopod of *M. sculptipes* (fig. 3E) is not at all similar to that of *Panopeus*. There is no indication of a trilobed condition. Instead, the tip is blunt and strongly recurved. The pleopod of *M. lobifrons* (fig. 3D) is similar, lacking a trilobed apex.

Lophoxanthus A. Milne Edwards, 1879. — Menzies (1948) reproduced Parisi's (1916) illustration of the pleopod of *Lophoxanthus erosus* Parisi. Although the figure is not detailed, the pleopod is clearly not of the panopeid form. The apex appears long and thin and not trilobed. Indeed, Menzies (1948) used this character as evidence that this species did not belong to the genus *Lophopanopeus* and transferred it to *Lophoxanthus*.

Metopocarcinus Stimpson, 1860. — The pleopod of *M. truncatus* Stimpson (fig. 2E) is basically trilobed but without the accessory process of *Panopeus*. It resembles the pleopod of *Rhithropanopeus harrisi* (compare to fig. 1I) but has a well developed lateral tooth not seen in *R. harrisi*.

EUCRATOPSINAE Stimpson, 1871

Cycloplax Guinot, 1969. — The pleopod of *C. pinnotheroides* Guinot (fig. 4A) is a modification of the trilobed *Panopeus* condition. The accessory process is greatly reduced, and the medium lobe is recurved. The overall shape is similar to that seen in some species of *Hexapanopeus* (compare fig. 4A to fig. 1G).

Cyrtoplax Rathbun, 1914. — The pleopods of *C. schmitti* Rathbun (fig. 4B) and *C. spinidentata* (Benedict) (fig. 4C) are essentially identical to that of *Panopeus* (compare to fig. 1A).

Eucratopsis Smith, 1869. — The pleopods of *E. crassimanus* (Dana) (fig. 4D) are of the *Panopeus* form, but with elongate medial spines. The accessory process is shorter than in most species of *Panopeus*.

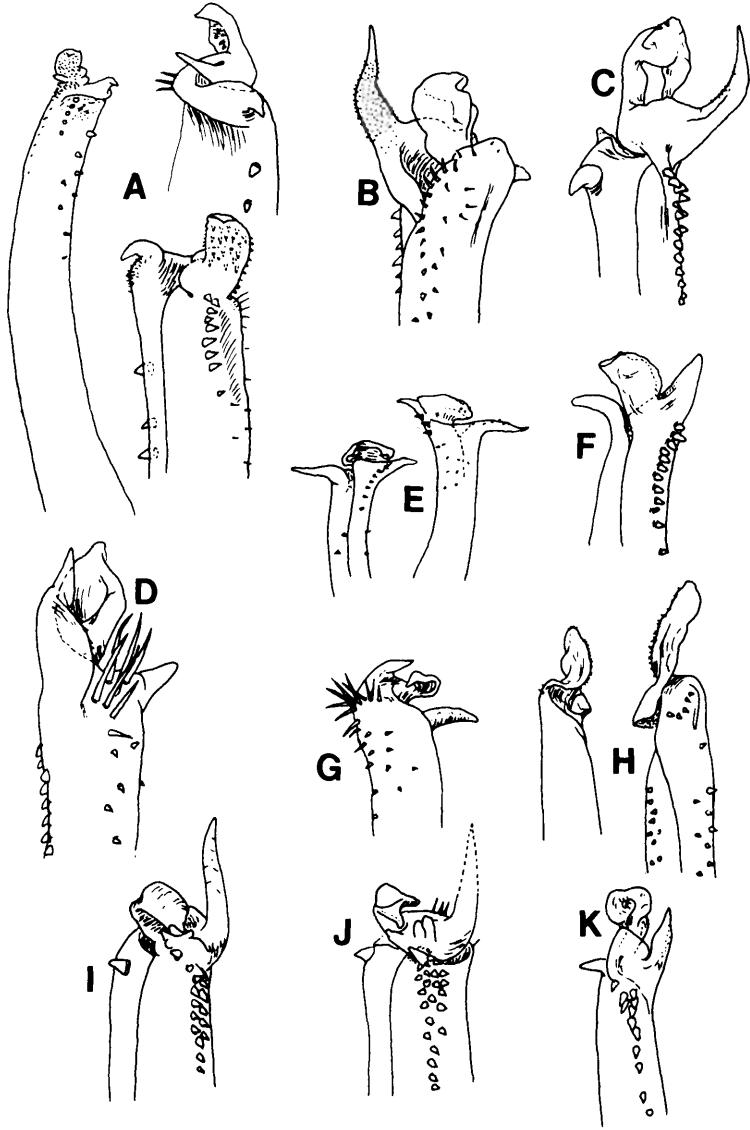


Fig. 4. Male first pleopods of the Eucratopsinae. A, *Cycloplax pinnotheroides* (3 views); B, *Cyrtoplax schmitti*; C, *Cyrtoplax spinidentata*; D, *Eucratopsis crassimanus*; E, *Glyptoplax pugnax*; F, *Glyptoplax smithi*; G, *Malacoplax californiensis*; H, *Panoplax depressa* (figure on right questionable; see Guinot, 1969); I, *Prionoplax ciliata*; J, *Prionoplax spinicarpus*; K, *Tetraplax quadridentata*. All after Guinot, 1969. Placement of some genera in Eucratopsinae questionable (see text and Guinot, 1978).

Glyptoplax Smith, 1870. — The pleopod of *G. pugnax* Smith (fig. 4E) has the accessory process deflected at a right angle to the main shaft, somewhat similar to that of *Lophopanopeus* (compare fig. 4E to fig. 1L-M). The condition in *G. smithii* A. Milne Edwards (fig. 4F) is similar, but the accessory process is not so strongly deflected, and the median lobe is more erect.

Malacoplax Guinot, 1969. — The pleopods are trilobed, as in *Panopeus*, with long sharp lateral spines (*M. californiensis* (Lockington), fig. 4G) and with a reduced and curved accessory process.

Panoplax Stimpson, 1871. — The pleopod of *P. depressa* Stimpson (fig. 4H, possibly not the illustration on the right [see Guinot, 1969]) appears to be lacking an accessory process and possibly the lateral tooth as well. A recurved portion of the medial wall may represent a reduced lateral tooth. There is very little similarity to the pleopods of *Panopeus*.

Prionoplax H. Milne Edwards, 1852. — The pleopods of *P. ciliata* Smith (fig. 4I) and *P. spinicarpus* H. Milne Edwards (fig. 4J) are trilobed, with a fairly small lateral tooth, a straight, thin accessory process, and a reduced or folded median process. This condition is very like that found in some species of *Eurypanopeus* (see fig. 1H).

Tetraplax Rathbun, 1900. — The pleopods are *Panopeus*-like, with a reduced accessory process (see fig. 4K).

No assigned subfamily (formerly *Micropanope*)

The following genera were created by Guinot (1967a) to accommodate species that she removed from *Micropanope* s.s. They were not explicitly assigned to any subfamily within the Panopeidae, nor did Guinot intend to infer placement even in the Panopeidae (pers. comm.). We include descriptions of the pleopods of these genera because there is some evidence (see Martin, 1984) that at least a few former *Micropanope* species may not be far removed from *Micropanope* s.s.

Coralliope Guinot, 1967. — The pleopod of *C. parvula* (A. Milne Edwards) (fig. 3H) bears numerous long sharp spines and terminates in an acute process. It bears no resemblance to the typical trilobed panopeid pleopod.

Gonopanope Guinot, 1967. — The pleopods of *G. angusta* (Lockington) and *G. areolata* (Rathbun) (figs. 3F and 3G, respectively) are distally twisted and bear several elongate spinulose setae on the lateral margin. The two stout medially-directed spines may be analogous and homologous to the spines of the

median process in some *Panopeus* (e.g. *P. bermudensis*). However, if the *Gonopanope* pleopod is derived from the trilobed condition, the accessory process and lateral tooth have been lost.

Microcassiope Guinot, 1967. — The pleopod of *M. minor* (Dana) (= *M. rufopunctata* (A. Milne Edwards)) (fig. 3I) bears no resemblance to the trilobed condition of other panopeid pleopods. The lateral spines and reduced medial process are somewhat similar to the pleopod of *Rhithropanopeus harrisii* (compare to fig. 1I).

Nanocassiope Guinot, 1967. — The pleopods of *N. alcocki* (Rathbun) (fig. 3K), *N. melanodactyla* (A. Milne Edwards) (fig. 3L), and *N. granulipes* (Sakai) (fig. 3M) all bear elongate subterminal setae; these appear distally spatulate in *N. melanodactyla*. There is no resemblance to "typical" panopeid trilobed pleopods.

Nanoplax Guinot, 1967. — *Nanoplax xanthiformis* (A. Milne Edwards) (fig. 3M) appears to have a reduced pleopod, twisted distally, with a medial row of spines. This condition is similar to that seen in *Microcassiope* (fig. 3I) and *Rhithropanopeus* (fig. 1I).

DISCUSSION

Guinot (1978: 276) stated that all of the Panopeidae possess, among other characters, a male first pleopod easily recognizable by its special ornamentation. This clearly is not the case for all species in which the pleopod is known. It is true that the majority of pleopods in the panopeid group appear trilobed, but there are notable exceptions. The two species of *Micropanope* do not conform to this pleopod morphology, nor does *Lophoxanthus erosus*, the only member of the genus *Lophoxanthus* with described pleopods. The pleopods of *Dyspanopeus sayi* and *Dyspanopeus texanus* are sufficiently different to warrant their placement in a new genus, although it is not difficult to derive the *Dyspanopeus* pleopod form from the basic *Panopeus* pleopod. Even more striking is the difference between the *Panopeus* pleopod and the pleopods of *Coralliope* and *Nanocassiope*, both of which Guinot (1978) removed from the genus *Micropanope*. Thus, her implied exclusion of these genera from the Panopeinae and her hesitancy to include them in the Panopeidae (D. Guinot, pers. comm.) are supported by pleopodal morphology. It is odd that some members of the subfamily Eucratopsinae show more similarities to the basic trilobed *Panopeus* pleopod than do other members of the Panopeinae sensu Guinot. An exception in the Eucratopsinae is the genus *Panoplax*; the pleopod of *P. depressa* (fig. 4H) appears non-panopeid. However, the carapace of *Panoplax depressa* more strongly resembles that of the Panopeinae, especially the genus *Hexapanopeus*, than do any of the other

eucratopsine genera. Guinot (1969: 265) noted that the affinities of *Panoplax* are at best uncertain and suggested as an alternative a gonoplacid relationship. In fact, she listed in that same paper the genera *Prionoplax*, *Cyrtoplax*, *Tetraplax*, *Eucratopsis*, *Glyptoplax*, *Malacoplax*, and *Cycloplax* as belonging to the panopeine lineage ("la lignée panopéenne") of the family Goneplacidae.

The transfer of several genera from the Goneplacidae to the Panopeidae illustrates the close morphological similarity between these two families. In fact it is often difficult to determine the familial affinities of a genus within the large and complex Xanthoidea.

Although most goneplacids differ from xanthids in having elongate eyestalks, this character could represent adaptation to environment rather than phyletic affinity; the goneplacid carapace may have evolved along with the development of elongate eyestalks (Barnes, 1968; von Hagen, 1970). It appears to us that certain goneplacids are more closely related to xanthids, and we agree with Guinot's (1978) removal of the goneplacid genera listed in table I from the Goneplacidae, with the possible exception of *Panoplax*. However, generalizations should be strictly avoided. The transfer of an entire genus from one family to another should be made only after all the evidence is in for all members of that genus. As male pleopods are not known for a large number of panopeid species, we recommend caution in accepting any generic or familial scheme that is not based on close examination of all species.

Zoal evidence may be of some help in resolving the problem at hand. The pleopod of *Panopeus bermudensis* differs from that of other *Panopeus*, and so do the zoeas (Martin, 1984). The pleopods of *Micropanope* s.s. are not panopeid-like, and the larvae of *Micropanope* species also differ from those of *Panopeus* and its allies (Martin, 1984). Unfortunately, zoeas of *Neopanope texana* (now *Dyspanopeus texanus*) and *N. sayi* (now *Dyspanopeus sayi*) are essentially similar to those of many other panopeid crabs with typical trilobed pleopods.

Less is known of goneplacid larvae, and unfortunately zoeas are not known from any of the genera that Guinot (1978) transferred to the Panopeidae, Eucratopsinae (table I). *Goneplax* and *Carcinoplax* both have four zoal stages, which appear similar to the majority of xanthid larvae, especially the Pilmuninae of the Group II xanthid zoeas of Rice (1980) and Martin (1984).

Lastly, if pleopod morphology is accepted as a strong generic character within the Panopeidae, then several genera within the panopeid group should be synonymized with genera acknowledged at present. For example, we see little reason to exclude the genera *Neopanope* (sensu stricto), *Eurypanopeus*, and *Eurytium* from the genus *Panopeus*. There is some reason to doubt the generic placement of *Panopeus bermudensis*, on pleopodal evidence and on the basis of the bizarre larvae of this species (see Martin et al., 1984). There is also reason to consider placing the former goneplacids *Prionoplax spinicarpus*, *P. ciliata*, *Cyrtoplax schmitti*, and *C. spinidentata* in the genus *Panopeus*, if only pleopod morphology is considered, and the remaining goneplacid species in related

panopeid genera as noted earlier. However, the carapace and eyestalks of these goneplacid species do differ dramatically from the *Panopeus* group, and retention in already recognized genera may eliminate confusion in future taxonomic works.

SUMMARY

Clearly, the taxonomic situation within the Xanthidae s.l. is confused and relationships among the presently accepted panopeid genera are complex. If pleopod characters are used to the exclusion of other characters such as carapace morphology, then the panopeid genera are in need of further revision. Specifically, the genus *Panopeus* could be expanded to include several species currently in other genera or other subfamilies (the Eucratopsinae), while some species placed by Guinot (1978) in the Panopeinae do not seem to warrant a close relationship to *Panopeus*. We hope that, rather than adding to the existing systematic confusion, our compilation of data will be of some benefit to future systematists attempting to elucidate panopeid phylogeny.

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RÉSUMÉ

La morphologie du pléopode de crabes de la famille des Panopeidae Ortmann *sensu* Guinot (1978) est examinée. La condition trilobée "typique" du genre *Panopeus* n'est pas évidente chez tous les membres de la famille. Les pléopodes de plusieurs espèces que Guinot a proposé de ranger dans la sous-famille des Eucratopsinae ressemblent davantage à ceux du genre *Panopeus* et d'autres espèces de Panopeinae, qu'à ceux des genres d'Eucratopsinae. Il est suggéré que la forme du pléopode est un caractère plus conservateur que la morphologie de la carapace ou des chélicèdes, et que des révisions ultérieures des Panopeidae sont souhaitables.

LITERATURE CITED

- ABELE, L. G., 1971. Scanning electron photomicrographs of brachyuran gonopods. *Crustaceana*, **21**: 217-220.
- , 1972. A reevaluation of the *Neopanope texana-sayi* complex with notes on *N. packardii* (Crustacea: Decapoda: Xanthidae) in the western Atlantic. *Chesapeake Science*, **13**: 263-271.
- ALCOCK, A., 1895. Materials for a carcinological fauna of India, no. 3. The Brachyura Cyclometopa. Part I. The family Xanthidae. *Journal Asiatic Society Bengal*, **57** (2): 302-468 (1968 reprint).
- BALSS, H., 1957. Decapoda, Part VIII: Systematik. In: H. G. BRONN, *Klassen und Ordnungen des Tierreichs*, **5** (1) (7) (12): 1505-1672, figs. 1131-1199.
- BARNES, R. S. K., 1968. On the evolution of elongate ocular peduncles by the Brachyura. *Systematic Zoology*, **17**: 182-187.

- BENEDICT, J. E. & M. J. RATHBUN, 1891. The genus *Panopeus*. Proceedings U.S. National Museum, **14**: 355-385, pls. 19-24.
- CAPART, A., 1951. Crustacés Décapodes Brachyures. Expédition océanographique Belge dans les eaux côtières Africaines de l'Atlantique Sud (1948-1949), Résultats Scientifiques, **3**: 11-205, figs. 1-80, pls. 1-3.
- CHACE, F. A., JR., 1966. Decapod crustaceans from St. Helena Island, South Atlantic. Proceedings United States National Museum, **118**: 622-661, figs. 1-15, pls. 1, 2.
- DESMAREST, E., 1852. Crustacés, Mollusques, Zoophytes. In: J. CHENU, Encyclopédie d'histoire naturelle ou traité complet de cette science: 1-312, figs. 1-320, pls 1-40. (Paris).
- GARTH, J. S., 1961. Non-intertidal brachygnathous crabs from the west coast of tropical America. Part 2: Brachygnatha Brachyrhyncha. Eastern Pacific expeditions of the New York Zoological Society. XLV. Zoologica, **46**: 133-159, figs. 1, 2, pl. 1.
- GUINOT, D., 1967a. Recherches préliminaires sur les groupements naturels chez les Crustacés Décapodes Brachyures. II. Les anciens genres *Micropanope* Stimpson et *Medaues* Dana. Bulletin Muséum National Histoire Naturelle, (2) **39**: 345-374.
- , 1967b. Recherches préliminaires sur les groupements naturels chez les Crustacés Décapodes Brachyures. IV. Observations sur quelques genres de Xanthidae. Bulletin Muséum National Histoire Naturelle, (2) **39**: 695-727.
- , 1969. Recherches préliminaires sur les groupements naturels chez les Crustacés Décapodes Brachyures. VII. Les Goneplacidae. Bulletin Muséum National Histoire Naturelle, (2) **41**: 241-265.
- , 1978. Principes d'une classification évolutive des Crustacés Décapodes Brachyures. Bulletin biologique France Belgique, **112**: 211-292.
- HAGEN, H. O. VON, 1970. On the significance of elongated and horned eyes in ocypodid crabs (Decapoda, Brachyura). Forma et Functio, **2**: 13-57.
- HOLTHUIS, L. B., 1954. On a collection of decapod Crustacea from the Republic of El Salvador (Central America). Zoologische Verhandelingen Leiden, **23**: 1-43, pls. 1, 2.
- , 1979. *Panopeus* H. Milne Edwards, 1834 (Crustacea, Decapoda): proposed designation of type species under the plenary powers. Bulletin Zoological Nomenclature, **36**: 158-160.
- KURATA, H., R. W. HEARD & J. W. MARTIN, 1981. Larval development under laboratory conditions of the xanthid mud crab *Eurytium limosum* (Say, 1818) from Georgia. Gulf Research Reports, **7**: 19-25.
- MANNING, R. B. & L. B. HOLTHUIS, 1981. West African brachyuran crabs (Crustacea: Decapoda). Smithsonian Contributions Zoology, **306**: 1-379.
- MARTIN, J. W., 1984. Notes and bibliography on the larvae of xanthid crabs, with a key to the known xanthid zoaea of the western Atlantic and Gulf of Mexico. Bulletin of Marine Science, **34**: 220-239.
- MARTIN, J. W., D. L. FELDER & F. M. TRUESDALE, 1984. A comparative study of morphology and ontogeny in juvenile stages of four western Atlantic xanthoid crabs (Crustacea: Decapoda: Brachyura). Philosophical Transactions of the Royal Society of London, (B) **303**: 537-604.
- MENZIES, R. J., 1948. A revision of the brachyuran genus *Lophopanopeus*. Allan Hancock Foundation Publications, Occasional Paper, **4**: 1-27, figs. 1-3, pls. 1-6.
- MILNE EDWARDS, A., 1880. Études préliminaires sur les Crustacés. Ière Partie. Reports on the results of dredging under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877, '78, '79, by the U.S. Coast Survey Steamer "Blake", Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding. Bulletin Museum Comparative Zoology Harvard College, **8**: 1-68, pls. 1, 2.
- MILNE EDWARDS, H., 1834. Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux, **1**: 1-468. (Paris).
- MONOD, T., 1956. Hippidea et Brachyura ouest-africains. Mémoires Institut Français Afrique Noire, **45**: 1-674, figs. 1-884.
- ORTMANN, A., 1893. Abtheilung: Brachyura (Brachyura genuina Boas). II. Unterabtheilung: Cancroidea, 2. Section: Cancrinea, 1. Gruppe: Cyclometopa. Die Decapoden-Krebse des Strassburger Museums. VII. Theil. Zoologische Jahrbücher, (Syst.) **7**: 411-495, pl. 17.
- PARISI, B., 1916. Cyclometopa. I decapodi giapponesi del Museo di Milano IV. Atti Società Italiana Scienze Naturali, **40**: 153-190, textfigs. 1-4, pls. 7-11.

- POWERS, L. W., 1977. A catalogue and bibliography to the crabs (Brachyura) of the Gulf of Mexico. *Contributions in Marine Science*, **20** (suppl.): 1-190.
- RATHBUN, M. J., 1930. The Cancroid crabs of America of the families Euryalidae, Portunidae, Ateleycyclidae, Cancridae, and Xanthidae. *United States National Museum Bulletin*, **152**: i-xvi, 1-609, figs. 1-85, pls. 1-230.
- RICE, A. L., 1980. Crab zoeal morphology and its bearing on the classification of the Brachyura. *Transactions Zoological Society London*, **35**: 271-424.
- STIMPSON, W., 1871. Preliminary report on the Crustacea dredged in the Gulf Stream in the straits of Florida, by L. F. de Pourtalès, Assist. U.S. Coast Survey. *Bulletin Museum Comparative Zoology Harvard College*, **2**: 109-160.
- WILLIAMS, A. B., 1965. Marine decapod crustaceans of the Carolinas. *Fishery Bulletin, U.S. Fish Wildlife Service*, **65**: 1-298, figs. 1-252.