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Phylogenetic significance of the brachyuran megalopa: evidence from the Xanthidae

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Synopsis

Existing classifications of the Brachyura are based almost entirely on characters of the adults. Because the planktonic larvae are thought to be adapted to a fairly uniform mid-water environment, several workers have, with some success, employed zoeal characters in attempts to elucidate brachyuran relationships. The megalopa stage, a morphologically unique phase in the brachyuran life cycle that is in some ways intermediate between zoeas and adults, has been all but ignored in systematic studies at levels above that of genus.

The family Xanthidae MacLeay, 1838 (= superfamily Xanthoidea of Guinot (1978) and Serène (1984)) is by far the largest family of crabs and may lie at or near the stem of the higher eubrachyurans. In this paper all published and several unpublished descriptions of the megalopa stage in the Xanthidae are reviewed. Descriptions are given for the megalopa stage of each of five groupings based on the zoeas. For approximately 50 species for which adequate information exists, 28 megalopal characters were scored, 16 of which are presented in tabular form and employed in a numerical phenetic analysis. The resulting phenogram does not strongly reflect previous groupings of adults or zoeas, but lends some support to the classification of Balss (1957) and the zoeal groupings of Rice (1980). The lack of congruence between larval and adult classifications, and the need for improved standards in megalopal descriptions, are discussed.

Introduction

The brachyuran megalopa (= decapodid; see Felder, Martin & Goy 1985) is a unique morphological stage transitional between the planktonic zoeas and the benthic adults. The megalopa is characterized by having functional setose natatory pleopods on abdominal segments 2 to 6 (with some exceptions), a somewhat dorsoventrally flattened carapace, functional thoracic appendages, and in many species long serrate setae on the dactylus of the

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fifth pereiopod (Williamson 1969, 1982; Felder *et al.* 1985). Thus, some characters seem intermediate between zoeal and juvenile crab stages, whereas others are unique to the megalopa. Despite this interesting combination of features, the megalopa has been virtually ignored in studies of brachyuran systematics. This may be in part because early students of zoeal morphology considered the megalopa a 'post-larval' stage (after Gurney 1942; see review by Williamson 1982), and therefore did not include it or gave only a brief sketch of the megalopa at the end of a larval description; carcinologists working with adults probably considered it a larval stage. Whatever the reason, there are very few detailed descriptions of the megalopa stage for any crab family. Consequently, while there is a fairly rich literature on the use of zoeal characters in brachyuran systematics (see Rice 1980, 1981a, 1983), there have been few attempts to employ characters of the megalopa at taxonomic levels higher than genus. An exception is a paper by Williams (1980), in which megalopal characters were used in establishing the superfamily Bythograeoidea; other examples are given in Felder *et al.* (1985). Keys to identification of megalopas, or tables comparing megalopal characters, exist only for restricted geographic areas (e.g. Lebour 1928; Williamson 1957; Bourdillon-Casanova 1960; Wear & Fielder 1985) and/or restricted taxa (e.g. Rice & Ingle 1975; Jewett & Haight 1977; Ingle & Clark 1980; Andryszak & Gore 1981; Salman 1982; Quintana 1986a, b; Quintana & Saelzer 1986). The most thorough treatments of the brachyuran megalopa as an aid to systematics are those of Rice (1981b) on Guinot's Podotremata and Quintana (1986a) on the Leucosiidae (see also Rice, this volume).

Arguments for examining the megalopa in a phylogenetic context are of two types. First, as noted by Rice (1981b), it is the only phase of the brachyuran life cycle that has not been subjected to scrutiny, and since both adult and zoeal phases may have been affected by convergence 'any classificatory evidence from other sources is likely to be of value' (Rice 1981b). Second, the megalopa and juvenile crab stages are the first to exhibit brachyurization and general attainment of the adult body plan, yet they are mostly free from the features developed later in adults. It is therefore possible that the megalopa and/or early crab stages will show more conservative and phylogenetically significant characters than either zoeas or adults (see Martin, Felder & Truesdale 1984; Felder *et al.* 1985).

This paper looks at the use of the megalopa for within-family systematics of the higher Brachyura (the Heterotremata and Thoracotremata of Guinot (1978); Eubrachyura of Saint Laurent (1980a, b)). The family chosen for study is the Xanthidae MacLeay, 1838 (*sensu lato*, the Xanthoidea of Guinot 1978, minus the geryonids). The Xanthidae were chosen for two reasons. First, it is the largest family of the Brachyura, and more papers on larvae of xanthids exist than on any other group (see Martin 1984). Second, and more important, some xanthids very likely lie at or near the stem group of the higher brachyuran families, excluding possibly the majids (see Rice 1980, 1983, this volume). Any clarification of systematics in this taxon should therefore shed light on evolutionary derivations of other crab families that, on the basis of zoeal characters, appear to be more advanced than the xanthids.

Previous classifications and phylogenies of the Xanthidae

The Xanthidae, with more than 130 genera and 1000 species (Powers 1977; Rice 1980), is the largest family of the Decapoda, and there have been numerous attempts at subdivision. Manning & Holthuis (1981) list no fewer than 32 family and subfamily names that have been proposed for various assemblages within the family, and Serène (1984) employs additional names. Early classifications were based entirely upon characters of the adults. Perhaps the most widely used classifications were those of Alcock (1898) and Balss (1957). Alcock (1898), following Dana (1852), recognized two sections within the family. The Hyperomerista, with efferent branchial chambers separated by a buccal ridge, were further divided by Alcock into the subfamilies Menippinae, Oziinae, Pilumninae, and Eriphiinae. The Hyperolissa, with buccal ridges reduced or absent, were divided among the Xanthinae, Actaeinae, and Chlorodinae. This classification enjoyed moderate acceptance until the introduction of the somewhat simpler scheme of Balss (1957), which admitted only four subfamilies: Xanthinae, Menippinae, Pilumninae, and Trapeziinae. Recent workers have realized that the Xanthidae is a far more complex assemblage than depicted by either Alcock or Balss. Takeda (1976) recognized 14 subfamilies and tentatively arranged them in the following order, primitive to advanced: Galeninae, Carpiliinae, Xanthinae, Actaeinae, Zosiminae, Euxanthinae, Chlorodiinae, Etisinae, Cymoinae, Pseudoziinae, Eriphiinae, Pilumninae, Polydectinae and Trapeziinae. Unfortunately, Takeda did not give detailed accounts of the characters upon which this arrangement is based. Guinot (1978), primarily on the basis of the location of the male gonopores but including several other characters, elevated the Xanthidae to superfamily level and included as constituent families the Carpiliidae, Menippidae, Platyxanthidae, Xanthidae (restricted, and including as subfamilies the Xanthinae, Trichiinae, Actaeinae, Polydectinae and Euxanthinae), Pilumnidae, Trapeziidae, Panopeidae, and tentatively the Geryonidae. (Glaessner (1969) also recognized a superfamily Xanthoidea, but as a much larger category, to include, along with the Xanthidae *sensu lato*, the potamonids, geryonids, goneplacids, pinnotherids, grapsids, and gecarcinids.) Guinot (1978) felt that two families, the Pilumnidae and Panopeidae, were advanced in relation to the other six, but she refrained from making any phylogenetic statements, instead pointing out that these were grades of development rather than evolutionary lineages. Serène (1984) felt that Guinot's classification was an improvement but that it was still incomplete. His classification of the xanthids of the Indian Ocean and Red Sea included a superfamily, Xanthoidea, divided into the families Xanthidae (with 10 subfamilies), Trapeziidae (with two subfamilies), Pilumnidae (with five subfamilies), Carpiliidae (not further divided) and Menippidae (with three subfamilies); Guinot's Panopeidae, Platyxanthidae and Geryonidae were not included.

Attempts to subdivide the Xanthidae on the basis of zoeal characters also have a long history, and are summarized in Rice (1980), Martin (1984), and Martin, Truesdale & Felder (1985). Rice (1980) recognized four distinct groupings, one of which was recognized earlier by Hyman (1925) and Wear (1970) and corresponded roughly to the Hyperolissa of Alcock (1898). Genera in this group (Group I) belong to Balss's (1957) subfamily Xanthinae; the few exceptions listed by Rice are likely cases of misidentification (Martin, Truesdale *et al.* 1985). The Group II larvae correspond, with few exceptions, to the Pilumninae of Balss. However, other larval groupings of Rice (1980) and Martin (1984) do not appear to accurately reflect any existing adult classifications. Rice (1980) noted that the lack of congruence between zoeal groupings and earlier adult classifications might support the more complex subdivisions of Guinot (1978).

Rice (1980, 1983) felt that among the five recognized xanthid zoeal groupings (Groups I-V; see Martin 1984; Martin, Truesdale *et al.* 1985), the only group of larvae that could have given rise to the more advanced xanthids and to higher brachyuran families was Group III. Specifically, the genera *Homalaspis*, *Ozius* and *Eriphia*, and an unidentified zoea belonging to the Menippinae or Trapeziinae (ASM 26; Rice & Williamson 1977), were depicted as the most primitive of the xanthid larvae. Larval features of Group III are thought to have given rise to Groups I (the Xanthinae), II (the Pilumninae), and IV (*Menippe* and *Sphaerozius*), by reduction of the antennal exopod (Group I) and of the mouthpart setation (*Menippe* and *Sphaerozius*). A visual interpretation might resemble Fig. 1A. Martin, Truesdale *et al.* (1985) suggested that it is equally plausible that the Group II larvae are the most primitive, as pilumnine zoeas have an elongate antennal exopod and the full complement of setae on all appendages, and some species have dorsolateral knobs on abdominal somites 2 through 5. Groups I and III, with a reduced antennal exopod, and Group IV, with reduced appendage setation, would, in this scheme, be depicted as more advanced (Fig. 1B). The Group V larvae (*Micropanope sensu lato*; see Martin 1984) could have arisen from either lineage, because the antennal exopod is reduced but appendage setation is not so reduced as in Group IV. Martin, Truesdale *et al.* (1985) acknowledged that one serious drawback to this suggested phylogeny is that the Group II rostrum is nearly always reduced, a character state

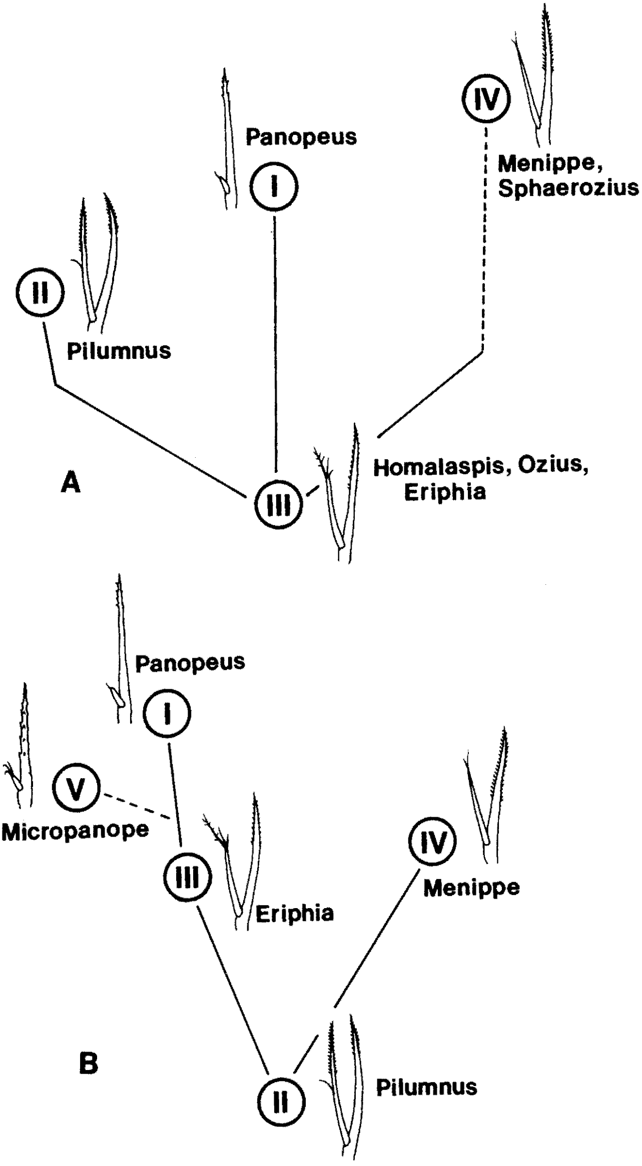

Fig. 1. Possible evolutionary pathways within the Xanthidae as indicated by zoeal morphology; antenna (diagrammatic) illustrated. Roman numerals refer to recognized groupings of zoeas (see text). A, with certain Group III larvae as the most primitive (adapted from Rice 1980); B, with Group II larvae as the most primitive (suggested by Martin, Truesdale *et al.* 1985). Only selected genera are given for each group.

that is probably derived (see primitive xanthid zoeal characters listed by Martin, Truesdale *et al.* 1985:102). However, some pilumnine zoeas (e.g. *Heteropanope glabra* as described by Lim, Ng & Tan 1984) have a fairly long rostrum that exceeds the length of the antennal protopod. Neither Rice's (1980) nor Martin's (1984) scheme) is completely satisfactory, as there are some species with 'advanced' and some with 'primitive' features in any given group.

The xanthid megalopa stage has not been examined in the detail in which Rice (1980) examined the zoeas. Tables with comparative characters of megalopas of certain assemblages within the family or from certain geographic regions exist, and Salman (1982) consulted published accounts of 23 species in the Xanthinae, Pilumninae and Menippinae of Balss (1957). However, an overview of the family has not been attempted.

Materials and methods

Literature surveyed

Martin (1984) listed 97 references to descriptions of xanthid larvae. These references included descriptions of the megalopa stage of about 50 species, some identified only to genus (Martin 1984: table I). Not included in table I of that paper, or published since its appearance, are the accounts of larvae of *Carpilius corallinus* (Herbst, 1783) by Laughlin, Rodriguez & Marval (1983); *Pilumnopeus serratifrons* (Kinahan, 1856) by Greenwood & Fielder (1984a); *Monodaeus couchii* (Couch, 1851), *Xantho incisus* Leach, 1814, and *Pilumnus hirtellus* (Linnaeus, 1761) by Ingle (1983); *Heteropanope glabra* Stimpson, 1858 by Lim *et al.* (1984) and also by Greenwood & Fielder (1984b); *Panopeus occidentalis* de Saussure, 1857 by Ingle (1985); *Panopeus americanus* de Saussure, 1857 by Negreiros-Fransozo (1986); *Panopeus bermudensis* Benedict & Rathbun, 1891 by Martin, Truesdale *et al.* (1985); *Pilumnopeus eucratoides* Stimpson, 1858 by Lim, Ng & Tan (1986); *Parapilumnus trispinosus* Sakai, 1965 by Fukuda (1978), Terada (1984), and Quintana (1986c); *Cycloxanthops truncatus* (de Haan, 1837), *Macromedaeus distinguendus* (de Haan, 1835) and *Gaillardiellus orientalis* (Odhner, 1925) (as *Paractaea rueppelli orientalis*) by Fukuda (1978); and *Pilumnopeus indicus* (de Man, 1887), *Pilumnus minutus* de Haan, 1835 and *Halimede fragifer* de Haan, 1835 by Terada (1980, 1984, 1985, respectively). In addition, descriptions of the larvae of *Eriphia gonagra* (Fabricius, 1781) and of *Eurypanopeus abbreviatus* (Stimpson, 1860) are available from the doctoral theses of A. Fransozo (1982) and M. L. Negreiros-Fransozo (1984), respectively. Larvae described by Aikawa (1937) as *Tiarina* are almost certainly from a pilumnine xanthid (Van Dover, Gore & Castro 1986), and Lebour (1934) described an unidentified xanthid zoea and megalopa. Finally, four unidentified xanthid megalopas were described by Muraoka & Shibata (1980), an unidentified xanthid fourth stage zoea and megalopa were described by Muraoka (1986), and a species formerly assigned to the Parthenopidae was tentatively transferred to the Xanthidae on the basis of its zoeal morphology (*Echinoecus pentagonus* A. Milne Edwards, 1879; see Van Dover *et al.* 1986).

Many of the works cited above and in Martin (1984) include detailed descriptions of zoeal stages only. Of those papers that include the megalopa, the majority are listed in Tables 1 and 2. Several are not included because the description is incomplete, often only a simple line drawing of the carapace. These are the works of Cano (1892), Bourdillon-Casanova (1960), Forss & Coffin (1960), Garth (1961), Hale (1931), Hood (1962), Hyman (1925), Knudsen (1960), Kurian (1956), and Lebour (1928, 1934). Some references do not appear in the Tables because the megalopa description agrees exactly with another more detailed work (e.g. Fukuda 1978, not listed for *Leptodius exaratus*). Finally, Terada's (1982) study on larvae of *Pilodius* was erroneously listed by Martin (1984) as having a description of the megalopa and is not included here.

Characters examined

The literature was surveyed and each species was examined for 28 morphological characters (see Appendix). The raw data for 14 characters are tabulated in Tables 1 and 2, organized according to the previously discussed five zoeal groupings. For example, although *Homalaspis plana* and *Platyxanthus crenulatus* were placed together in the Platyxanthidae by Guinot (1977), they are listed alphabetically with the Group III larvae (Table 2) by virtue of their zoeal characters (see Rice 1980). Characters were chosen that are commonly described and/or illustrated and that also are likely to be accurately reported. For instance, while setation of the endites of the first maxilliped was not included because the setae are dense and difficult to count or illustrate, the 'long smooth setae' of the epipod of that appendage were included, since these setae are widely spaced and relatively easy to record. Similarly, although the setation of the endopod of the maxillule was tabulated, the setose endites were not. In this manner the most accurate information was gathered. Future workers may wish to employ additional characters.

It is obvious from Tables 1 and 2 that most descriptions do not provide adequate morphological detail. The number of missing values and the number of meristic counts necessarily taken from illustrations (marked with an asterisk) seem excessive. Of the 28 characters in the Appendix, many are probably of little or no value and were not included in the tables or phenetic analysis. Characters 2 (development of the rostrum) and 28 (rounding or squaring of the telson) are subjective decisions. Indeed, evaluation of these

Table 1. Comparison of selected characters in xanthid megalopas of species that have Group I zoeas.

Species	Character no.																References
	1	4	7	12	13	14	15	16	17[c]	18[c]	19[c]	23	24	25	26	27	
Chlorodiella nigra	no	2+2	3	—	—	—	—	no	—	—	—	8	—	8	—	ab	Gohar & Al-Kholy (1957)
Cycloxanthops truncatus	no	1+3	10	54–57	13*	7–8	20–21	—	0*	0*	0*	18*	—	—	—	9*	Hong (1977)
Dyspanopeus sayi[a]	no	1+3	4	43*	4	5	12*	no*	—	—	—	—	—	10*	—	6*	Chamberlain (1961)
,, ,,	yes	—	—	—	—	—	—	yes	3	3	3	—	—	—	—	—	Kurata (unpublished)
Dyspanopeus texana[a]	yes	1+1+4	8	38–43	5–7	1–3	11–17	yes	3	3	3	15	3	13	3	8	McMahan (1967)
Etisus laevimanus	yes	1+3	8–9	47–48	7	1*	16	yes	3*	1*	3*	18	2	17	2	11	Suzuki (1978)
Eurypanopeus depressus	no	1+3	7	—	6	—	12	—	—	—	—	13	—	11	—	5–6	Costlow & Bookhout (1961b)
,, ,,	no	—	—	—	—	—	—	no	2	2	2	—	—	—	—	5–6	Kurata (unpublished)
Eurypanopeus abbreviatus	yes	1+3	10	≏38	5	—	12	yes	3	3	3	15	3	13	3	9	Negreiros-Fransozo (1984)
Eurytium limosum	yes	—	—	—	—	—	—	yes	3	3	3	—	—	—	—	8–9	Kurata, Heard & Martin (1980)
Hexapanopeus angustifrons	yes	1+2	9	46*	7*	—	13*	yes*	0*	0*	0*	—	—	—	—	—	Costlow & Bookhout (1966)
(as *Panopeus occidentalis*)	yes	—	—	—	—	—	—	yes	3	3	3	—	—	—	—	8	Kurata (unpublished)
Leptodius exaratus	yes	1+3*	9	46–47	7	—	13	yes*	0*	0*	0*	16	3	15	3	7	Fielder, Greenwood & Jones (1979)
,, ,,	yes	1+1	11	43	7	—	6	yes	0*	0*	0*	15*	3	14–17	3	10	Saba (1976)
Lophopanopeus bellus	no	1+3	8	56*	7*	3*	12*	yes	—	—	—	16	3	15	3	8	Hart (1935)
L. bellus diegensis	yes	1+1	—	≏50(44)	—	—	—	yes	—	—	—	—	—	—	—	9	Knudsen (1959a)
L. leucomanus leucomanus	no	1	—	42*	—	—	—	yes	—	—	—	16	3*	16	3*	8	Knudsen (1958)
Neopanope packardii	yes	1+3	8	34*	7*	—	11*	no*	—	—	—	11	—	11	—	6	Costlow & Bookhout (1967)
Panopeus americanus	yes	3	9–10	37	7	—	8	yes	3	3	3	14–15	3	13	2	8	Negreiros-Fransozo (1986)
Panopeus bermudensis	yes	—	7–8	40–44	5–6	—	12–13	yes	—	3	—	—	—	13	3	—	Martin, Truesdale *et al.* (1985)
Panopeus herbstii	yes	1+1+3	10	49*	7*	—	12*	yes	—	—	—	15	—	15	—	8	Costlow & Bookhout (1961a)
,, ,,	yes	—	—	—	—	—	—	yes	3	3	3	—	—	—	—	7–8	Kurata (unpublished)

Panopeus occidentalis	no	1+1+2	10–11	49–50	1,2	3[b]	6,7	yes	3	3	2	15–16	2–3	16	2–3	10	Ingle (1985)
(as *Panopeus* sp.)	yes	—	—	—	—	—	—	yes	3	3	3	—	—	—	—	7	Kurata (unpublished)
Panopeus turgidus	no	—	7–8	36	5–6	—	11	yes	—	3	—	—	—	12	2	—	Martin, Felder *et al.* (1984)
Paraxanthias taylori	no	1	—	—	—	—	—	yes	—	—	—	19	3	—	3	—	Knudsen (1959b)
Pseudomedaeus agassizii	yes	1+3	11	43*	9*	—	13*	yes	—	—	—	—	—	—	—	—	Costlow & Bookhout (1968)
Rhithropanopeus harrisii	no	4	3–4	25–28	3–4	5	18–20	—	—	—	—	9–10	—	9–10	—	5–6	Chamberlain (1962) (text only)
,, ,,	no	—	—	—	—	—	—	—	—	—	—	—	3	—	3	—	Connolly (1925)
,, ,,	no	—	—	—	—	—	—	yes	1	1	1	—	—	—	—	3–4	Kurata (unpublished)
Xantho incisus	yes	2	10–11	57–58	8–10	0	11*	yes	4	4	4	17	4	19	3	12	Ingle (1983)

Meristic counts taken from illustrations are in parentheses if they differ from text descriptions. * = taken from illustration only; — = character(s) not described; ab = appendage absent. Characters are given in Appendix, p. 100.

[a] Formerly *Neopanope*; see Martin & Abele (1986).

[b] Two epipods described for second maxilliped.

[c] These characters (17–19) combined for phenetic analysis; see Appendix p. 100.

Table 2. Comparison of selected characters in xanthid megalopas of zoeal Groups II, III, IV, and V.

Species	Character no.															References
	1	4	7	12	13	14	15	16	17[h]	18[h]	19[h]	23	24	25	26	27	
Group II																	
Echinoecus pentagonus[a]	yes	1+3–4	6	33–45	8–12	1	13	no	0	0	0	11–12	2–3	11–12	2–3	7	Van Dover *et al.* (1986)
Heteropanope glabra	yes	1+1+3	6(5)	45–46	7	0*	9	yes(3)	—	—	—	15	2–3	13	2–3	6	Lim *et al.* (1984)
,, ,,	yes	1+1+4	5*	45	7–8	0*	9–12	yes(3)	0*	—	—	10–12	3	10–12	3	6	Greenwood & Fielder (1984b)
Parapilumnus trispinosus	yes	1+1+4	7	35–38	5	—	10	yes(2)	0	0	0	13	3	13	2	6	Quintana (1986c)
Pilumnopeus eucratoides[c]	yes	1+1+3	6	28–32	5	—	7	no[b]	1*	—	—	10	2	11	2	4	Lim *et al.* (1986)
Pilumnus dasypodus	no	1+1+3	7–8	34–39	4–7	—	7–9	no	few	few	few	12–13	2–3	11–12	2–3	6	Sandifer (1974)
,, ,,	no	2+4(1+3)	7	36	5	—	8	no	yes[d]	yes[d]	yes[d]	13	2	11	2	5	Bookhout & Costlow (1979)
Pilumnus hirtellus	no	1+1+3	9	34–36	8	—	9	no	3*	—	—	14	3	13	3	5–7	Salman (1982)
,, ,,	no	—	—	—	—	—	—	—	—	—	—	13	—	13	—	—	Ingle (1983)
Pilumnus lumpinus[c]	yes	1+1+2	—[e]	—	12*	0	19*	no	—[e]	—[e]	—[e]	15	6	13	4	6–7	Wear (1967)
Pilumnus novaezealandiae[c]	yes	1+1+2	11*	48*	26*	17*	13*	no	0	—	—	15	4	—	—	8	Wear (1967)
Pilumnus sayi	no	—	—	—	—	—	—	no	3	3	3	12	2	9	2	6	Kurata (unpublished)
Pilumnus vespertilio[c]	no	1+4	4–5	30–34	4	0*	10(11)	no	—	—	—	13–14	2–3	13–14	2–3	7	Lim & Tan (1981)
Group III																	
Baptozius vinosus	no	1+4	14	90–93	11	13	29	no	3	3	3	25*	5*	23*	5*	13	Saba, Takeda & Nakasone (1978a)
Epixanthus dentatus[c]	no	1+1+2	12	≏50	10	2	10	no	3	3	3	22*	5*	—	4–5	10–11	Saba, Takeda & Nakasone (1978b)
Eriphia gonagra	no	4	13	63–70	18	15	29	no	0	0	0	24–25	6	22–23	5	18	Fransozo (1982)
Eriphia verrucosa	no	1+1+3	15	88	19	16	29	—	—	—	—	25–26	6	24	5	7	Lumare & Gozzo (1972)
Homalaspis plana	no	1+2+4	15	≏72	9	—	24	—	—	—	—	20–22	3	20–22	3	11	Fagetti (1970)
Monodaeus couchii	yes	1+4	8–10	49–50	1–2	4	5*	yes	4	4	2	15–16	4	18–19	4	10	Ingle (1983)
Ozius rugulosus	no	1+1+3	9(8)	≏51	6	0	15	no	2	2	2	19	—	19	—	10	Kakati & Nayak (1977)
Ozius truncatus	no	4–5	—[f]	—[g]	10*	8*	14*	yes	3	3	3	22	4*	22	—	12	Wear (1968)

Pilumnoides perlatus	no	1+1+4	11	≃60	6*	6*	13*	—	—	—	—	17–19	—	15–17	—	8	Fagetti & Campodonico (1973)
Platyxanthus crenulatus	no	1+4	14	58	10	6	20	no	—	—	—	21	4	20	4	10	Menú-Marque (1970)
Group IV																	
Menippe adina	no	1+1+2+3	11–14	70–78	22–23	9–10	18	no	5	5	5	21–22	3–4	—	—	12–14	Personal observation
Menippe mercenaria	no	—	—	—	—	—	—	—	4–5	4–5	4–5	—	—	—	—	11–12	Kurata (unpublished)
Menippe nodifrons	no	1+2+5	10–13	66	12–20	<10	18	no	5	5	5	20–21	3	20–21	3	11	Scotto (1979)
Menippe rumphii	no	1+1+2+3	9	≃65(38)	18	8	22	no	0*	—	—	20	—	18	—	12	Kakati (1977)
Group V																	
Micropanope barbadensis[c]	yes	1+5	10	45–46	7	2	8	yes	3	3	3	15*	3*	16*	2*	8	Gore, Van Dover & Wilson (1981)
Micropanope sculptipes	yes	1+3	—	—	—	—	—	yes	3	3	3	15–16	2	13–14	2	7–8	Andryszak & Gore (1981)

Meristic counts taken from illustrations are in parentheses if they differ from text descriptions. * = taken from illustration only; — = character(s) not described. Characters are given in Appendix, p. 100.

[a] Formerly of the Parthenopidae; see Van Dover *et al.* (1986).

[b] No ischial spine but large spine on merus.

[c] Abbreviated development; see Martin (1984).

[d] No number given.

[e] Wear (1968) described these as similar to *P. novaezealandiae.*

[f] Similar to fourth zoea (Wear 1968).

[g] Similar to *Heterozius rotundifrons* (Wear 1968).

[h] These characters (17–19) combined for phenetic analysis; see Appendix p. 100.

two characters differed occasionally from existing tables of xanthid megalopal characters (e.g. Andryszak & Gore 1981) that were derived from the same literature sources. Other characters are useless because they do not vary across taxa. Examples are the number of setae on the proximal segment of the mandibular palp (character 6), which is (with one exception) always 0, and the number of spines on the carapace (character 3), which is also 0 with only two clearly unrelated exceptions. However, sufficient information is available from the meristic data to suggest that certain patterns exist. Meristic counts for 14 such characters (see Appendix, p. 100) were broken down into scores of 0, 1, or 2 for use in a phenetic analysis. As an example, the number of setae on the uropod (character 27) is almost always 9 or less in species with Group I larvae, but always 10 or more in Group IV and most of Group III; this was scored as 1 and 0, respectively, for the phenetic analysis. Data for the original 28 characters are available upon request from the author.

Because megalopal characters were sought that might differentiate between previously recognized zoeal groups, the methodology is obviously somewhat flawed in that it involves a degree of circularity and a subjective decision of which characters to employ. Certain taxa, for which over half of the scored characters are missing from the Tables, were deleted from the analysis. Two species, *Eurypanopeus abbreviatus* and *Eriphia gonagra*, came to my attention too late to be included. The resulting data matrix, consisting of 43 taxa and 16 characters (three of which were combined, so that a total of 14 characters was used; see Appendix p. 100), was analysed for phenetic relationships by UPGMA (unweighted pair-group method using arithmetic averages) employing Euclidean distance and using the MINT computer package (Rohlf 1971). Specimens examined with scanning electron microscopy (SEM) were prepared following guidelines given by Felgenhauer (1987) but with 100% ethanol instead of amyl acetate used as the transitional fluid.

Results

Descriptions

The following descriptions are arranged according to the zoeal groupings of Rice (1980) and Martin (1984). It should not be assumed that the megalopas are readily divided into the same groups as the zoeas.

Group I megalopas (Figs 2, 3)

Carapace usually quadrate, with or without acute anterolateral projections (16 species with, 13 without), usually without produced acute rostrum, and without spines (except Hong's (1977) description of *Cycloxanthops truncatus*, in which the spine figured is in the same location as a commonly occurring mid-dorsal bump, and probably corresponds to the dorsal carapace spine of the zoea. This spine sometimes persists in megalopas that die during the moult from fourth zoea; Hong's (1977) megalopa may be showing this abnormality.) Ventral ramus of antennule with 4 setae, 3 terminal and 1 subterminal; rarely with fewer terminal setae, occasionally with additional subterminal dorsal seta. Antenna with 7 to 11 (rarely 12) total segments. Mandibular palp 2-segmented (sometimes described with 3 segments, apparently a misinterpretation of segmentation by the author), no setae on proximal segment(s) (except for *Eurypanopeus abbreviatus* with 1 seta) and 3 to 11 (usually 7 to 10) stout spines or setae on distal segment. Maxillule usually with 2 or 3 setae, one of which is basal, on proximal segment of endopod, and 2 to 6 (most commonly 4 or 6, arranged 2+2 or 2+2+2) setae on distal segment of endopod. Maxilla with 0, 1 or 2 non-plumose setae on endopod, or 6 to 8 setae in clumps of 2 to 3. Bilobed basal endite of maxilla with 4 to 9 setae on proximal lobe and 5 to 10 (12 in *Dyspanopeus texana*) setae on distal lobe. Scaphognathite fringed with 25 (*Rhithropanopeus*) to 58 (*Xantho incisus*) setae, usually 35 to 50. Epipods of maxillipeds 1 to 3 variable, with 1 to 13 (usually 4 to 7), 0 to 8 (usually 5 or fewer), and 6 to 21 (usually 11 to 13) long smooth setae, respectively. Basal distally-protruding enlargement of epipod of first maxilliped usually with only one such seta. Cheliped usually with strong recurved hook on ischium (most exceptions are from illustrations, so possibly this feature was overlooked; Kurata (unpublished) noted the spine does not exist in *Eurypanopeus depressus*, although Negreiros-Fransozo (1984) records it for *E. abbreviatus*). Spination of dactylus of periopods rarely documented; where described or illustrated, usually with 3 spines on ventral border, rarely 1 (*Rhithropanopeus harrisii*), 2 (*Eurypanopeus depressus*) or 4 (*Xantho incisus*). Dactylus of fifth pereiopod usually devoid of spines (with only *Panopeus occidentalis* and *P. americanus* with 1 and 3 spines, respectively) and usually with 3 long serrate setae (rarely 0 to 2). Spination of ischium of pereiopods 2–5 documented for too few species to allow generalizations. First and third pleopods with 11 (rarely fewer) to 19 setae on distal segment of exopod and 2 to 3 hooks on endopod (4 in *Xantho incisus*). Uropods with 5 to 10 setae, rarely fewer (3 to 4 in *Rhithropanopeus harrisii*) or more (11 in *Etisus laevimanus*, 12 in *Xantho incisus*). Telson variable in form, nearly circular or sharply truncate on posterior border.

Group II megalopas (Fig. 4)

Carapace as described for Group I, with or without sharp anterolateral projections and usually without produced rostrum; small sharp carapace spines appear only in *Pilumnus novaezealandiae* on anterolateral dorsal surface. Ventral ramus of antennule usually with 5 or more setae, 1 or 2 subterminal. Antenna with 9 to 15 (usually 10) total segments. Mandibular palp

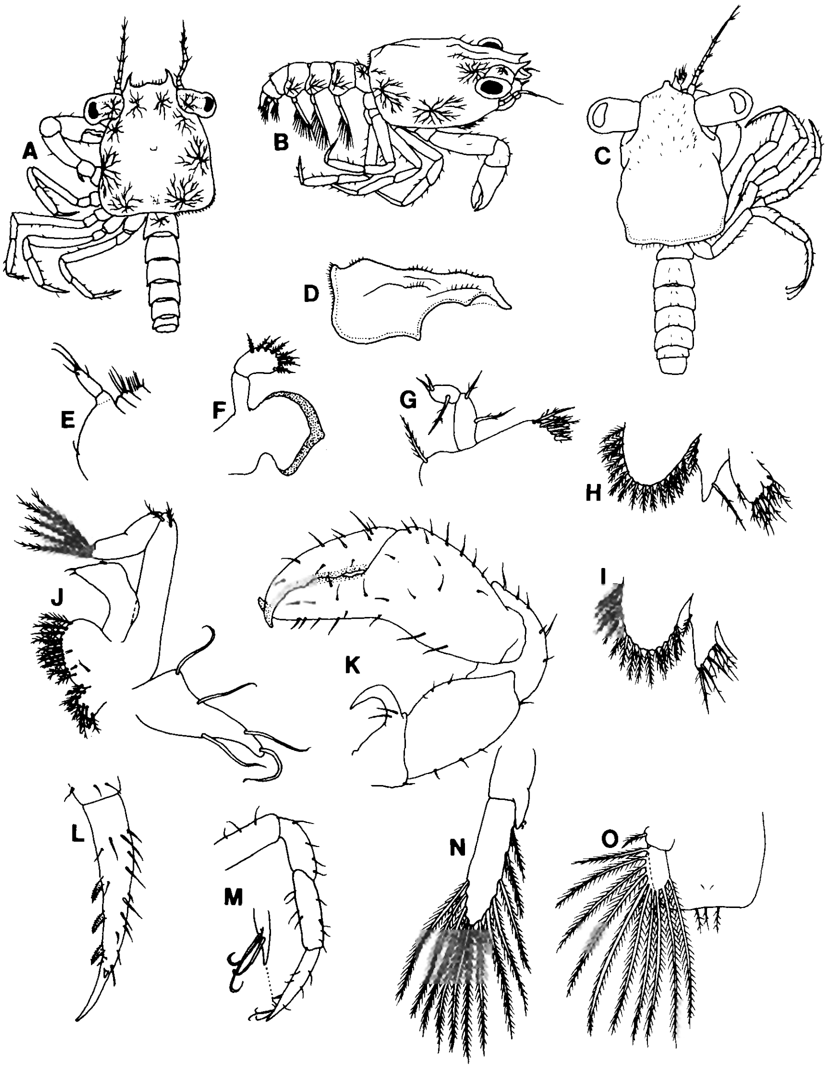

Fig. 2. Selected megalopal characters of xanthid species with Group I zoea larvae. A, B, dorsal and lateral view, *Hexapanopeus angustifrons*; C, D, dorsal and lateral view of carapace, *Panopeus occidentalis*; E, ventral ramus of antennule, *P. occidentalis*; F, mandible, *P. bermudensis*; G, endopod of maxillule, *P. bermudensis*; H, endopod of maxilla (with single non-plumose seta), *P. bermudensis*; I, endopod of maxilla (with 3+2+3 setal arrangement), *P. turgidus*; J, first maxilliped, *P. bermudensis*; K, cheliped, *P. bermudensis*; L, dactylus of third pereiopod, *P. turgidus*; M, dactylus of fifth periopod, *P. occidentalis*; N, third pleopod, *P. turgidus*; O, uropod and margin of telson, *P. occidentalis*. A and B from Costlow & Bookhout (1966); C, D, E, M and O from Ingle (1985); all other figures from Martin, Felder *et al.* (1984). Not drawn to scale.

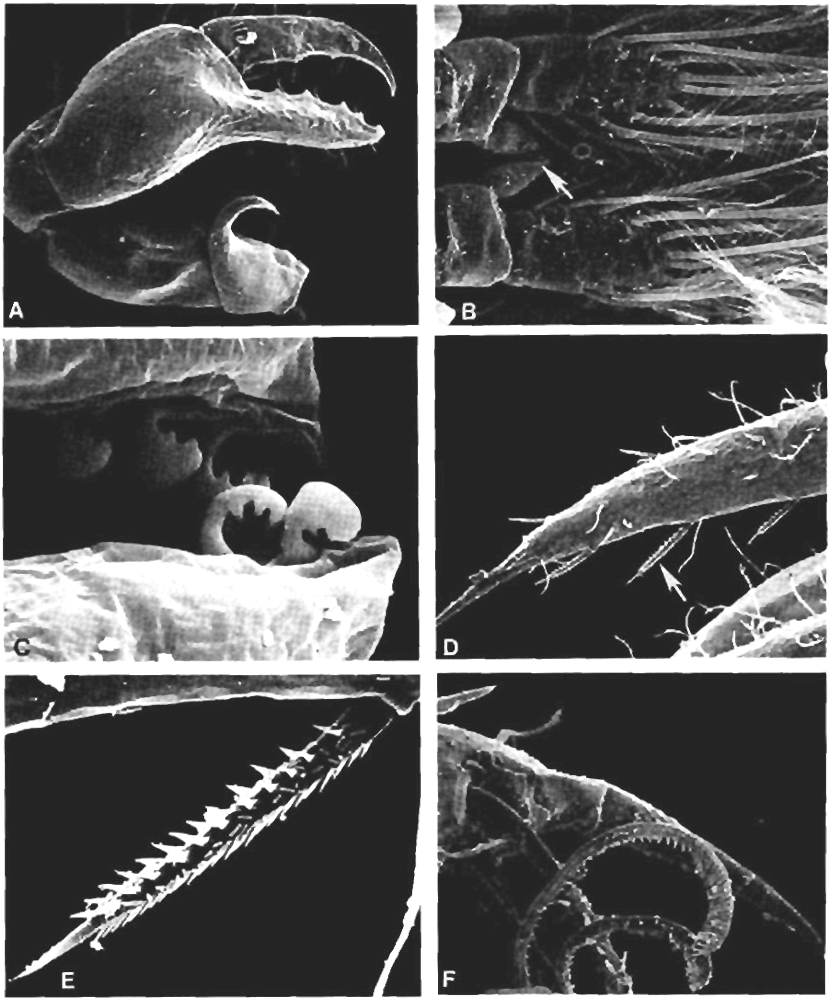

Fig. 3. Scanning electron microscopy of selected xanthid megalopal characters. A, cheliped with strong ischial spine (×85); B, fourth pair of pleopods showing endopods and natatory setae (×225); C, hook-like setae of endopods indicated by arrow in B (×3250); D, dactylus of third pereiopod showing three stout serrate spines on ventral border (×200); E, higher magnification of seta indicated by arrow in D (×1150); F, tip of dactylus of fifth pereiopod showing three long serrate setae (×900). All figures are of species of *Panopeus*.

similar to above description, with 9 to 15 spines or setae on distal segment. Endopod of maxillule with 1 or 2 setae on proximal segment (4 in *Pilumnus novaezealandiae*) and 2 to 6 setae on distal segment, at least 1 subterminal. Setation of endopod and basal endites of maxilla as described for Group I. Scaphognathite fringed with 28 to 48 (usually 30 to 45) plumose setae. Setation of first to third maxillipedal epipods 4 to 12 (but 26 in *Pilumnus novaezealandiae*), 0 or 1 (17 in *P. novaezealandiae*), and 7 to 13 (19 in *P. novaezealandiae*). Basal protrusion of epipod of first maxilliped with 1 long seta. Cheliped either without large recurved ischial spine, or with more than one; condition seen in Group I larvae (single large recurved spine) not found. Spination of ventral border of dactylus of pereiopods 2 to 5 varies from 0 to 3. Fifth pereiopod with 0 to 3 long serrate setae, most commonly 0 or 1 rather than 3 as in Group I. Where documented, ischial segments of pereiopods 2 to 5 bear spines, with *Echinoecus pentagonus* the only exception. First pleopod with 10 to 15 (usually 13 to 15) setae on exopod and usually 2 to 3 hooks on endopod (4 in *Pilumnus novaezealandiae*, 6 in *P. lumpinus*). Third pleopod with 10 to 14 (usually 11 to 13, but 9 in *Pilumnus sayi*) setae on exopod, and 2 to 3 hooks on endopod (4 in *P. lumpinus*). Uropods with 5 to 8 setae (4 in *Pilumnopeus eucratoides*). Telson variable.

Group III megalopas (Fig. 5)

Carapace without sharp anterolateral projections (except *Monodaeus couchii*), rostrum never acute and produced. Range of antennule setation and antenna segmentation as for Group II. Proximal segment of mandibular palp always devoid of setae, as in Groups I and II, but distal segment with 8 to 15 (usually >10) spines or setae. Range of setation of maxillule as for Group II. Maxilla with no non-plumose setae on endopod (except *Pilumnoides perlatus*, with 3+3+3 setae), with 6 to 11 plus 9 to 12 setae on proximal and distal lobes of basal endite, respectively. Scaphognathite with from 'about 50' (*Epixanthus dentatus*, *Monodaeus couchii*) to over 90 (*Baptozius vinosus*) fringing plumose setae. Setation of maxillipedal epipods variable; first maxilliped with from 1 or 2 (*Monodaeus couchii*) to 19 (*Eriphia verrucosa*) long smooth setae, second maxilliped with 0 to 16 setae (with the same two species having extreme values), third maxilliped with 5 (*Monodaeus couchii*) to 29 (*Baptozius vinosus*) setae. Basal protrusion of epipod of first maxilliped with 1 to 5 long setae. Ischial cheliped spines described for only two species, *Monodaeus couchii* and *Ozius truncatus*. Dactylus of pereiopods 2 to 4 with 2 to 4 spines. Fifth pereiopod with 0 to 2 spines and 2 to 3 long serrate setae (apparently 4 in Lumare & Gozzo's (1972) figure of *Eriphia verrucosa*). First pleopod with 15 to 26 (usually 21 or more) setae on distal segment of exopod and 3 to 6 hooks on endopod. Third pleopod with 15 to 24 (usually 19 or more) setae on exopod and 4 to 5

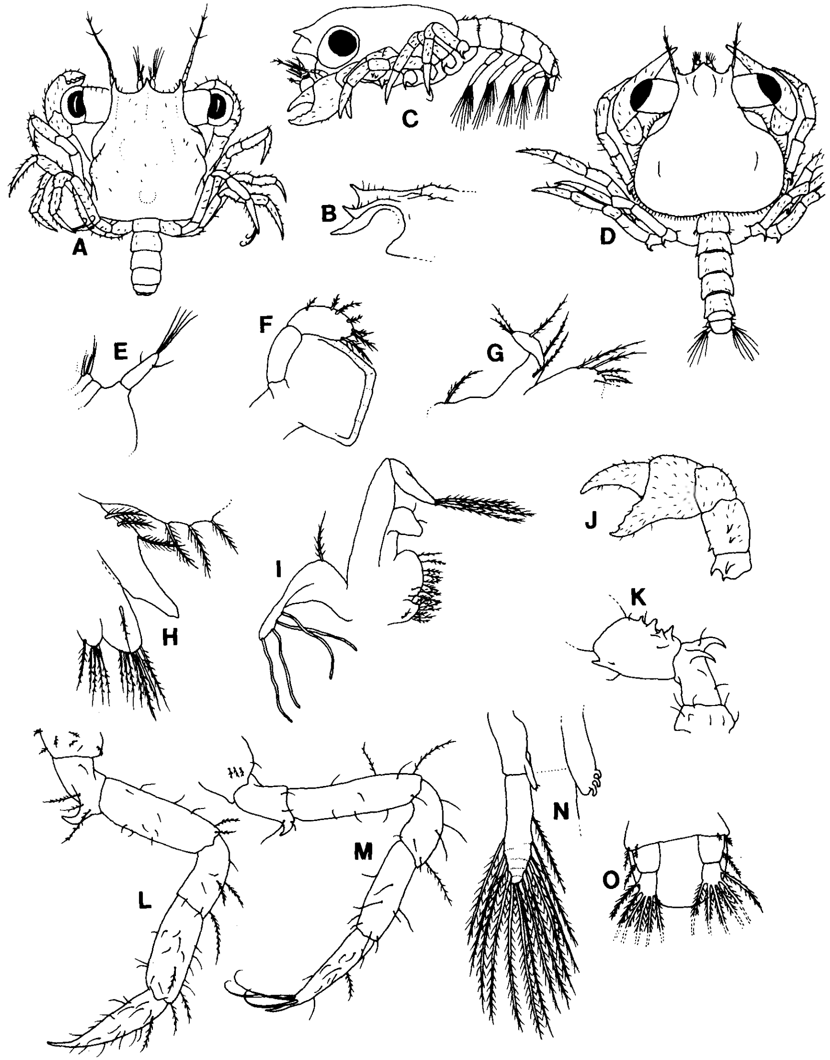

Fig. 4. Selected megalopal characters of xanthid species with Group II zoea larvae. A, B, dorsal and lateral view of carapace, *Parapilumnus trispinosus*; C, D, lateral and dorsal view, *Heteropanope glabra*; E, ventral ramus of antennule, F, mandible, G, endopod of maxillule, H, endopod of maxilla lacking non-plumose setae, I, first maxilliped, *P. trispinosus*; J, cheliped of *H. glabra*; K, proximal segments of cheliped of *P. trispinosus*; L, third pereiopod of *P. trispinosus*; M, fifth pereiopod of *P. trispinosus*; N, first pleopod (with enlarged endopod), *P. trispinosus*; O, uropods and telson, *P. trispinosus*. C, D and J from Greenwood & Fielder (1984b); all others from Quintana (1986c). Not drawn to scale.

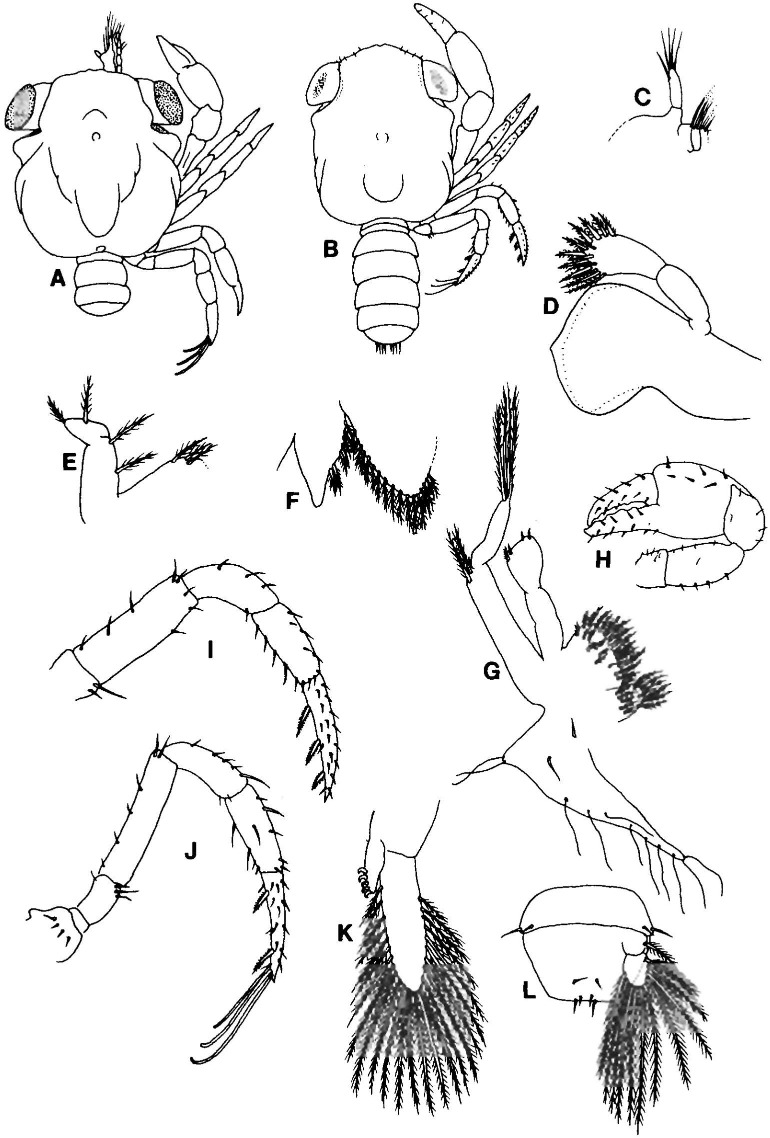

Fig. 5. Selected megalopal characters of xanthid species with Group III zoea larvae. A, dorsal view, *Epixanthus dentatus*; B, dorsal view, *Baptozius vinosus*; C, ventral ramus of antennule, *B. vinosus*; D, mandible, *B. vinosus*; E, endopod of maxillule, *E. dentatus*; F, endopod of maxilla (with no non-plumose setae), *B. vinosus*; G, first maxilliped, *B. vinosus*; H, cheliped, *B. vinosus*; I, third pereiopod, *B. vinosus*; J, fifth pereiopod, *B. vinosus*; K, first pleopod, *B. vinosus*; L, uropod and telson, *E. dentatus*. A, E and L from Saba *et al.* (1978b); all others from Saba *et al.* (1978a).

hooks on endopod. Uropods with 10 to 13 setae, rarely 7 (*Eriphia verrucosa*) or 8 (*Pilumnoides perlatus*). Telson variable.

Group IV megalopas (Fig. 6)

No megalopas described for *Sphaerozius*; all information derived from species of *Menippe*. Carapace without anterolateral projections, acute rostrum, or any spination. Ventral ramus of antennule with 7 or 8 setae, of which 3 or 5 terminal. Antenna with 8 to 12 total segments. Mandibular palp with 9 to 14 setae on distal segment. Endopod of maxillule with 1 seta on proximal segment and 4 setae, in two groups of 2, on distal segment. Maxillary endopod with no long non-plumose setae on proximal border. Basal endite of maxilla with 8 to 13 setae on proximal lobe and 9 to 15 setae on distal lobe. Scaphognathite fringed with 65 to 78 setae. (Although only 38 setae are illustrated for *M. rumphii*, Kakati (1977) stated 'about 65' in text.) Epipods of first to third maxillipeds with 18 to 23, 8 to 10, and 18 to 22 long smooth setae, respectively. Basal protrusion of first maxilliped epipod with 3 long smooth setae. No large recurved ischial spine on cheliped. Dactylus of pereiopods 2 to 4 with 4 or 5 stout spines, non-serrate only in *M. nodifrons* and none illustrated for *M. rumphii*. Fifth pereiopod with 0 to 4 (*M. adina*) spines on dactylus and 3 long serrate setae; 4 setae reported from a megalopa of *M. nodifrons* that moulted from a sixth rather than a fifth zoeal stage (Scotto 1979). Ambulatory pereiopods with ischial spines in *M. mercenaria* only. Pleopod 1 with 20 to 22 setae on distal segment of exopod and 3 or 4 hooks on endopod; pleopod 3 with 18 to 21 setae and 3 hooks. Uropods more setose than in any other group, with 11 to 14 setae on distal segment. Telson variable.

Group V megalopas

Megalopas of *Micropanope sculptipes* and *M. barbadensis* (currently without an assigned genus following revision of *Micropanope* by Guinot 1967) not significantly different from Group I megalopas. Both species with acute anterolateral projections on carapace, acute and produced rostrum, and strong ischial spines on cheliped. Mouthpart setation, known only for *M. sculptipes*, similar to Groups I and II but reduced compared with Groups III and IV. Pereiopods 2 to 4 with 3 serrate spines on dactylus; pereiopod 5 with 0 or 1 spine and 2 or 3 long serrate setae. Both species with ischial spines on some of pereiopods 2 through 5. Setation of pleopods and uropods as for Groups I and II. Telson distally squared.

Phenetic analysis

The results of the phenetic analysis are seen in Fig. 7. Megalopas of species with Group III and IV zoeas are, with only one exception, grouped together and separated from all other species at the 0.88 phenon line (see Sneath &

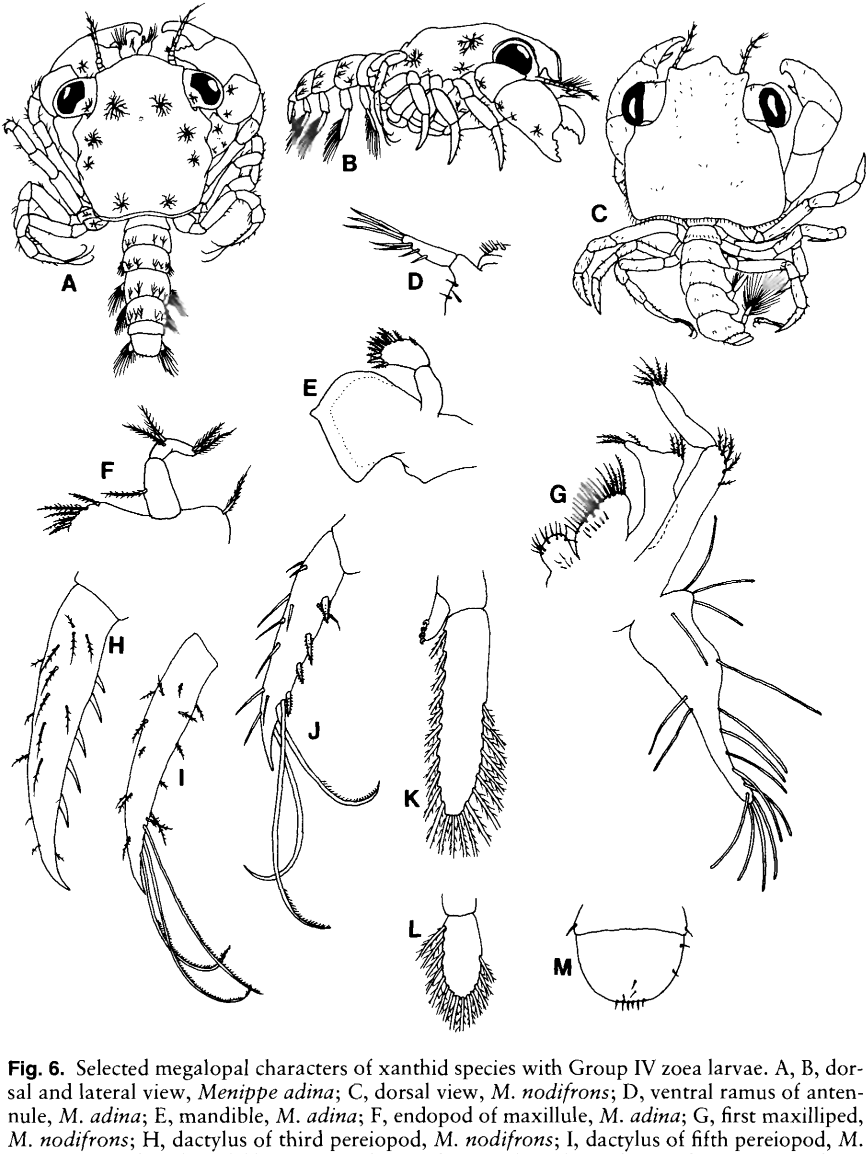

Fig. 6. Selected megalopal characters of xanthid species with Group IV zoea larvae. A, B, dorsal and lateral view, *Menippe adina*; C, dorsal view, *M. nodifrons*; D, ventral ramus of antennule, *M. adina*; E, mandible, *M. adina*; F, endopod of maxillule, *M. adina*; G, first maxilliped, *M. nodifrons*; H, dactylus of third pereiopod, *M. nodifrons*; I, dactylus of fifth pereiopod, *M. nodifrons*; J, dactylus of fifth pereiopod, *M. adina*; K, first pleopod, *M. adina*; L, uropod, *M. adina*; M, telson, *M. adina*. C, G, H and I from Scotto (1979); all others are original.

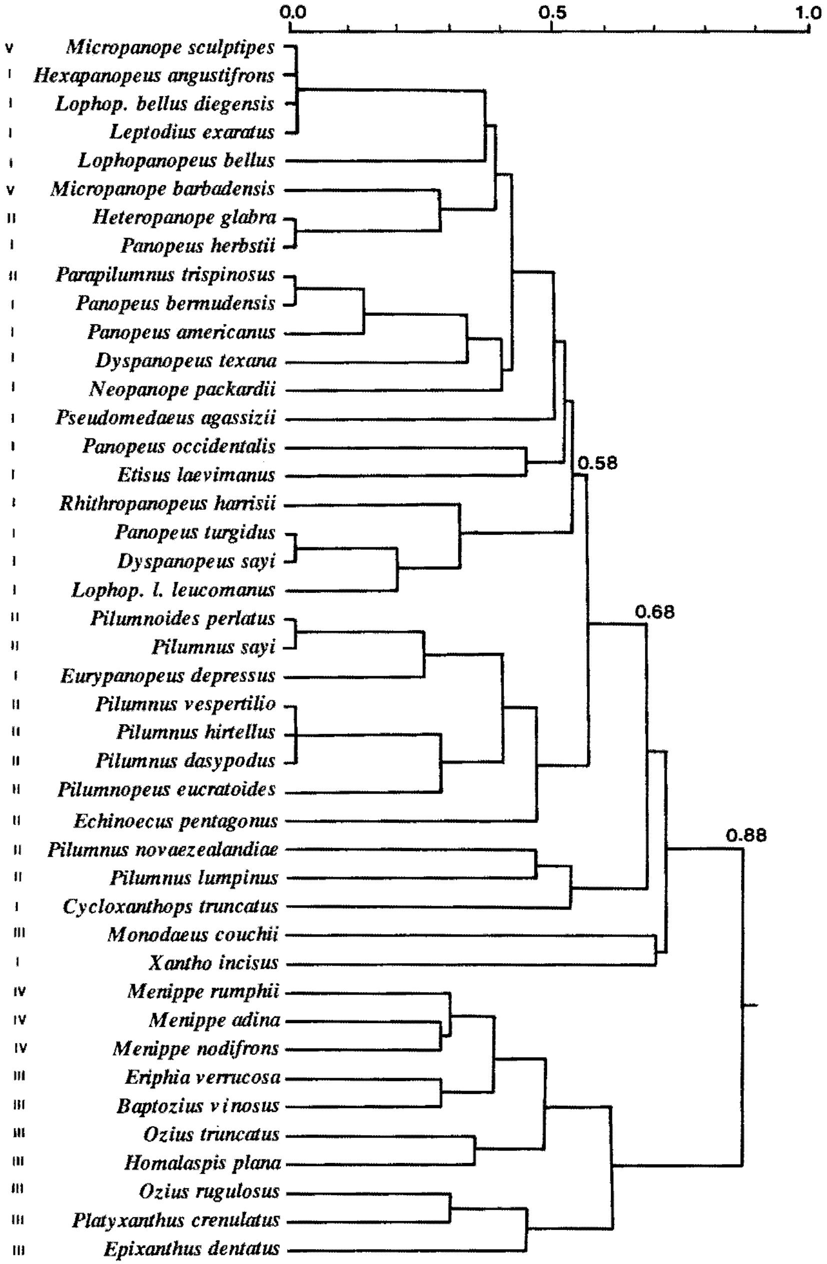

Fig. 7. Phenetic relationships of 43 xanthid species based on 14 characters of the megalopa. Roman numerals to the left of species names indicate groupings of the zoea larvae (see text).

Sokal 1973). The exception is *Monodaeus couchii*, which clearly has Group III zoeal features (Ingle 1983) but by megalopal features is most similar to Groups I and II. Group IV (*Menippe*) megalopas form a distinct grouping closest to the *Baptozius*/*Eriphia* line of Group III. Megalopas with Group I zoeas (mostly Xanthinae) and Group II zoeas (mostly Pilumninae) are roughly separated from III and IV at the 0.68 level and from each other at the 0.58 level. However, *Heteropanope glabra* and *Parapilumnus trispinosus*, both species with Group II zoeas, are paired with *Panopeus herbstii* and *P. bermudensis*, respectively, of Group I. In addition, two species of *Pilumnus*, *P. novaezealandiae* and *P. lumpinus*, are paired with *Cycloxanthops truncatus* (which has Group I zoeas). All other Group I megalopas are clustered together below the 0.58 level, with the exception of *Xantho incisus*, which is most similar to *Monodaeus couchii* of Group III. Both of the latter species appear very different not only from other groups but from each other. Megalopas with Group V zoeas (i.e. *Micropanope*) cluster with Group I species.

Discussion

General morphology

From the characters examined (Appendix; Tables 1 and 2), it is not possible to formulate a general description of all xanthid megalopas. There also is no single character or group of characters that serves to separate xanthid megalopas from those of many other brachyuran families. Many characters 'typical' of xanthid megalopas, such as the strong recurved ischial spine on the cheliped, acute anterolateral projections on the carapace, lack of spines on the carapace, and number of serrate setae on the fifth pereiopod, are known for members of other families and vary within the Xanthidae. However, Tables 1 and 2 do identify material of unknown origin. For example, of the four unidentified xanthid megalopas described by Muraoka & Shibata (1980), 'Xanthid A' and 'Xanthid B' belong to Group I (Xanthinae) species. Although anterolateral projections occur in other groups, the single recurved ischial spine on the cheliped is diagnostic of Group I. The number of setae on the distal segment of the uropod (10 in 'Xanthid A', 9 in 'Xanthid B') is within the range of Group I. Both unidentified megalopas may belong to Group III, as two members have ischial cheliped spines as well, but only one Group III species (*Monodaeus couchii*) has acute anterolateral projections. (*Monodaeus couchii* differs in many characters from other Group III megalopas, and may be an exception.) Muraoka & Shibata's 'Xanthid C' most likely has Group III or IV zoeas. The smoothly rounded frontal border of the carapace, number of setae on the ventral ramus of the antennule (7), and number of setae on the distal segment of the uropod (17) are all typical for megalopas of Groups III and IV. No megalopas of Group I have so many setae on either the antennule or the uropod, and of Group II only the platyxanthid *Homalaspis plana* has a similar antennule. However, even Group IV megalopas, which have a relatively setose uropod, do not have as many setae as 'Xanthid C'. Setation of the uropod would also indicate that 'Xanthid D' is a Group III or IV species. Another unidentified xanthid megalopa, described by Muraoka (1986), has an ischial spine on the cheliped, as do Group I megalopas. But it also has 15 setae on the mandibular palp, 15 setae on the epipod of the first maxilliped, and 60 setae bordering the scaphognathite. This setation is most like Group IV megalopas. Thus, this megalopa is difficult to assign to any of the groupings here described, but it bears striking sternal spines typical of the Portuninae (see Rice & Ingle 1975) and may not belong to the Xanthidae.

Phenetic analysis and classifications

It is clear from Fig. 7, and from Tables 1 and 2, that groupings based on megalopal characters do not agree with any proposed classification of the xanthids based on adults. A weak case could be made for recognition of three of the subfamilies of Balss (1957). The Menippinae of Balss (1957) contained *Baptozius*, *Eriphia* and *Ozius*, as well as *Menippe*. These genera are clustered together in the phenogram and are clearly separated from all other species, except *Epixanthus dentatus*, *Homalaspis plana*, and *Platyxanthus crenulatus*. The Pilumninae of Balss are represented by a large cluster of species that lies between the 'Menippinae' (the lower 10 taxa in the phenogram) and a phenon line at 0.58. This grouping includes all species of pilumnine genera, but it also includes *Cycloxanthops*, *Xantho*, and *Eurypanopeus* of Balss's Xanthinae, and *Monodaeus couchii*. The remaining species collectively correspond to Balss's Xanthinae, except that *Heteropanope glabra* and *Parapilumnus trispinosus*, both pilumnines, are also included. Unfortunately, no megalopas are known for any genera included in Balss's Trapeziinae, except for a brief description of *Quadrella nitida* Smith by Garth (1961). That description is indeed unusual; Garth's figure (1961:153; reproduced in Felder *et al.* 1985:205) shows a megalopa with very long chelipeds and a strongly serrate dactylus on all ambulatory pereiopods, which are much longer in relation to the carapace than are the pereiopods of any other described xanthid megalopa. If other megalopas in genera of Balss's Trapeziinae prove similar to *Q. nitida*, it would strongly support the separation of the trapeziids from all other xanthids.

The classifications of Takeda (1976), Guinot (1978), and Serène (1984) cannot be fully evaluated because so few megalopas have been described for any given family or subfamily. For Guinot's Xanthoidea, megalopas have not been described for the Carpiliidae and Trapeziidae (with the exception of Garth (1961), as noted above), and the geryonids have not been included in the present analysis because they are probably closer to portunids than to xanthids (see Rice 1980). Megalopas of two species from Guinot's (1977) Platyxanthidae, *Platyxanthus crenulatus* and *Homalaspis plana*, are less similar to each other than each is to different species of *Ozius*. The groupings already discussed in support of the subfamilies of Balss (1957) would also support the Menippidae and possibly the Pilumnidae of Guinot, but there is no clear distinction between species in her Panopeidae and her restricted Xanthidae.

There is slightly more support for recognized groupings based on zoeal morphology. Because the species were organized according to zoeal groups and then examined for characters that would serve to distinguish them, this perhaps is not surprising. All megalopas of the 'Menippinae' cluster are those that have Group III zoeas, except *Menippe* itself, which has Group IV zoeas. The groupings of xanthine and pilumnine megalopas support the Group I and Group II zoeal assemblages, respectively, just as they support the subfamilies Xanthinae and Pilumninae of Balss (1957); there is close agreement between these two subfamilies of Balss and the two zoeal assemblages (Martin, Truesdale *et al.* 1985). *Echinoecus pentagonus* was suggested to be a pilumnine xanthid, rather than a parthenopid, on the basis of zoeal morphology (Van Dover *et al.* 1986), and its megalopa groups with *Pilumnus* and its allies. A review of the description of the megalopa of *Heterozius rotundifrons* by Wear (1968), a former xanthid listed in Martin (1984), showed it to be strikingly different from all other megalopas examined. The antenna is greatly reduced, the maxilla is devoid of setae on the endopod, the first and third pleopods have only eight setae, and the uropods are absent. The unusual morphology of the megalopa therefore supports the exclusion of this species from the Xanthidae on the basis of zoeal characters (Rice 1980) and adult morphology (Guinot 1976, 1978). If increased setation and spination are indicative of a plesiomorphic condition in zoeal larvae (Rice 1980), then the Pilumninae would indeed be a derived assemblage (Rice 1980) and not, as suggested by Martin, Truesdale *et al.* (1985) for the zoeas, a primitive group. However, Group IV (*Menippe*) megalopas also have very setose appendages, and this group is thought to be derived (Rice 1980).

At lower taxonomic levels, there is often little agreement between megalopal groupings and those of zoeas or adults. As an example, megalopas of *Dyspanopeus sayi* and *D. texana*, nearly indistinguishable as adults and as zoeas (Martin & Abele 1986), are very different and widely separated in the phenogram. Numerous other examples will be obvious to practising carcinologists.

The pattern that seems to be emerging from attempts to employ the megalopa as an aid to systematics and phylogeny is a disappointing one. Megalopal characters have occasionally clarified systematic problems at or below the level of genus, but at most they only reinforce pre-existing ideas of brachyuran relationships at higher taxonomic levels. This should not be taken as a dismissal of the importance of the megalopa stage in studies of systematics, or as a reason to cease examination of this interesting stage. Much of the problem probably lies with erroneous or incomplete descriptions or with misidentification of parental material. The fact that only 14 characters (three of the original 16 were combined; see Appendix p. 100), an undesirably small number, were used in the phenetic analysis points to a need for more detailed comparative studies. Indeed, it is time to echo the plea of Rice (1979) for improved standards of descriptions for this often neglected stage. But another problem is that the megalopa is subjected to selective pressures different from those acting on the planktonic zoeas and benthic adults. It is a highly specialized stage that is adapted for a specific transitional role. It should not be surprising, therefore, to see phylogenetically important information obscured by homoplasy, since the role of the megalopas of all species is essentially the same, i.e. leaving the plankton and locating suitable habitat for adult life. Numerous examples of noncongruence of larval and adult characters are found in the insect literature (e.g. Rohlf 1963).

A phenetic classification (Fig. 7) is not a reflection of evolutionary history, rather a set of hierarchical groupings based on overall similarity. The phenogram is also based on a very small number of characters, so that the addition of more characters will probably yield different results. Ideally, classifications should reflect phylogeny, i.e. they should be cladistic rather than phenetic. But previous groupings of the Xanthidae (adults and zoeas) are based on overall similarity, and character polarity is difficult to determine for megalopa stages. For example, we cannot assume that increased setation is a plesiomorphic condition. Some xanthids, such as *Baptozius vinosus* and *Eriphia verrucosa*, have more setose appendages than does the megalopa of *Raninoides benedicti* (described by Knight 1968), although raninids are generally thought to be more primitive than any of the Eubrachyura (Rice 1980, 1983). For these reasons, and until a clearer picture of character polarity emerges for the megalopa stage, a phenetic approach is justified.

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Appendix: Characters examined

Data for characters marked with an asterisk (*) appear in Tables 1 and 2; these were scored according to values in parentheses and were employed in the phenetic analysis. Characters 17, 18 and 19 were combined for the analysis so that in total only 14 characters were used.

1.* Carapace: Presence (yes) or absence (no) of acute anterolateral projections (yes = 0; no = 1).

2. Carapace: Presence or absence of an acute, produced rostrum.

3. Carapace: Presence or absence of dorsal spines.

4.* Antennule: Number and arrangement of setae on the ventral ramus (5 or more = 0; 4 or fewer = 1).

5. Antenna: Number of antennal segments, flagellum and peduncle.

6. Mandible: Number of setae on proximal segment(s) of palp.

7.* Mandible: Number of spines and setae on distal segment of palp (11 or more = 0; 10 or fewer = 1).

8. Maxillule: Number and arrangement of setae on proximal segment of endopod.

9. Maxillule: Number and arrangement of setae on distal segment of endopod.

10. Maxilla: Number and arrangement of non-plumose setae on proximal border of endopod.

11. Maxilla: Number and arrangement of setae on lobes of the basal endite.

12.* Maxilla: Number of plumose setae fringing the scaphognathite (60 or more = 0; 45 to 59 = 1; less than 45 = 2).

13.* Maxilliped 1: Number of long smooth (or minutely serrulate) setae on epipod (12 or more = 0; 11 or fewer = 1).

14.* Maxilliped 2: Number of long smooth (or minutely serrulate) setae on epipod (8 or more = 0; 7 or fewer = 1).

15.* Maxilliped 3: Number of long smooth (or minutely serrulate) setae on epipod (15 or more = 0; 14 or fewer = 1).

16.* Cheliped: Presence or absence of large recurved hook-like spine on ischium (no = 0; yes = 1).

17.* Pereiopod 2: Number of stout, usually serrate, spines on ventral border of dactylus (see character 19).

18.* Pereiopod 3: Number of stout, usually serrate, spines on ventral border of dactylus (see character 19).

19.* Pereiopod 4: Number of stout, usually serrate, spines on ventral border of dactylus. (Characters 17–19 combined into single character for phenetic analysis: 4 or more = 0; 3 or fewer = 1).

20. Pereiopod 5: Number of stout, usually serrate, spines on ventral border of dactylus.

21. Pereiopod 5: Number of long serrate setae (‘feelers’) on dactylus.

22. Pereiopods 2–5: Presence or absence of spines on the ischium of any.

23.* Pleopod 1: Number of plumose setae on distal segment of exopod (20 or more = 0; 19 or fewer = 1)

24.* Pleopod 1: Number of hook-like setae on endopod (4 or more = 0; 3 or fewer = 1)

25.* Pleopod 3: Number of plumose setae on distal segment of exopod (18 or more = 0; 17 or fewer = 1)

26.* Pleopod 3: Number of hook-like setae on endopod (4 or more = 0; 3 or fewer = 1).

27.* Uropods: Number of plumose setae on distal segment of exopod (10 or more = 0; 9 or fewer = 1).

28. Telson: Posterior border rounded or truncate and squared.