NOTES AND BIBLIOGRAPHY ON THE LARVAE OF XANTHID CRABS, WITH A KEY TO THE KNOWN XANTHID ZOEAS OF THE WESTERN ATLANTIC AND GULF OF MEXICO

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NOTES AND BIBLIOGRAPHY ON THE LARVAE OF XANTHID CRABS, WITH A KEY TO THE KNOWN XANTHID ZOEAS[1] OF THE WESTERN ATLANTIC AND GULF OF MEXICO

Joel W. Martin

ABSTRACT

The known xanthid crab zoeas can be assigned to six groups, based primarily upon morphology of the antennal exopod. A brief description of each group is given, and a table listing all known zoeas in each group is presented. The abbreviated number of zoeal stages in some xanthid species seems not attributable solely to restricted environments; however, no alternative reason for abbreviated development in xanthids is known. A key is given for identification of 22 xanthid zoeas in the western Atlantic and Gulf of Mexico for which descriptions are available, and a bibliography of all known descriptions of xanthid larvae is included.

The first published mention of a larval stage belonging to the brachyuran family Xanthidae MacLeay, 1838, is a short communication by J. Vaughn Thompson (1836). In this paper, Thompson noted that the larval stages of the genus *Eriphia* Latreille, 1817 and other brachyuran genera corresponded to the genus *Zoea* of earlier workers. Since that time, the larvae of crabs of the family Xanthidae (*sensu lato,* not *sensu* Guinot, 1978) have received a considerable amount of attention. Gurney (1939) listed 25 publications in the succeeding 103 years which mentioned a total of 20 genera of xanthids for which at least one larval stage was known. Many of the early workers cited by Gurney (1939, 1942) gave only brief descriptions of the larvae, often without illustrations, and few identified the parental crabs to species level. Wear (1970) listed an additional 23 references containing descriptions of the larvae of 31 xanthid species. In a recent review of brachyuran zoeal morphology, Rice (1980) listed another 18 species (one of which was assigned to genus only, *Tetralia* sp.) in which the larvae are now known. Not mentioned by Rice are the accounts of larvae of *Platyxanthus crenulatus* (A. Milne Edwards, 1879) by Menú-Marque (1970), *Leptodius exeratus* [sic] (H. Milne Edwards, 1864) by Tufail and Hashmi (1964), and the descriptions of larvae belonging to 12 xanthid species from the Indian Ocean by Hashmi (1970a; b; c). In addition, several accounts of xanthid larvae have been published since Rice's (1980) review. Terada (1980, 1982) described zoeas of *Atergatis reticulatus* de Haan, 1835, *Cycloxanthops truncatus* (de Haan, 1837), *Leptodius distinguendus* (de Haan, 1835), *Leptodius exaratus* (H. Milne Edwards, 1864), and *Pilodius nigrocrinitus* Stimpson, 1858. Lim and Tan (1981) described larval development in *Pilumnus vespertilio* (Fabricius, 1798), Williamson (1982) illustrated the telson of the first zoea of *Monodaeus couchi* (Bell, 1851), and Salman (1982) redescribed the larvae of *Pilumnus hirtellus* (Linnaeus, 1761); all larvae of that species had already been described by Lebour (1928). The description of larvae belonging to *Eurytium limosum* (Say, 1818) by Kurata et al. (1981) included references for another three

[1] "Megalopa" is a Greek term, and therefore may be considered singular or plural without further modification. "Zoea" is a Latin term, the classical plural of which should be "zoeae." However, as noted by Rice (1981b), Leach originally coined the generic name *Megalopa* to mean "big eyes," thus he considered "opa" the plural form of "ops." Both Rice (1981b) and Williamson (1982) have adopted the English forms zoea (plural zoeas) and megalopa (plural megalopas) to avoid classical confusion; I have followed their suggestion herein.

species of xanthids. That paper, plus the recent descriptions of larvae belonging to two species of *Micropanope* by Andryszak and Gore (1981), and Gore et al. (1981), bring the number of xanthid species for which at least one larval stage is known to about 80 (Table 1). Thus, larvae are now known from approximately 8% of the estimated 1,000 species of xanthid crabs (Powers, 1977; Rice, 1980).

This relatively large number of described larvae allows a comparison to be made between zoeal groupings and the accepted classification of adult xanthids. Rice (1980) attempted to do exactly this, and although he was not completely successful in correlating zoeal and adult groupings, he did perform the valuable task of dividing the known xanthid larvae into distinct groups. Earlier, Guinot (1978) elevated the family Xanthidae to superfamily rank and divided the known xanthoid genera into eight families. Guinot did not make use of the described xanthid larvae in her revision; Rice (1980) stated that at present insufficient larvae have been described to allow a detailed examination for or against Guinot's scheme. Van Dover et al. (1982) discussed the significance of the larval scaphognathite in the classification of anomuran and brachyuran crustaceans, and noted that larval evidence should be considered in any resolution of the current controversy regarding classification of decapod Crustacea (Guinot, 1977; 1978; Fincham, 1980; Rice, 1980; 1981a; in press; Saint-Laurent, 1980a; b; Felgenhauer and Abele, in press; Burkenroad, 1981). Because the family Xanthidae is such an enormous and probably heterogeneous assemblage, it is imperative that all lines of evidence be examined before attempting to subdivide or reorder this family. The present paper is an attempt to categorize all known xanthid zoeas into distinct groups in hopes that this may facilitate further revisions of the family or at least elucidate questionable lineages.

Classification of Xanthid Larvae

Many earlier workers (Hyman, 1925; Lebour, 1928; Aikawa, 1929; 1933; 1937; Wear, 1970) attempted to divide the xanthid zoeas into distinguishable groups, based primarily upon morphology of the antennal exopod and spination of the telson. Hashmi's (1970a) paper on the brachyuran larvae of west Pakistan included 12 species of xanthids, and classified them on the basis of the morphology of the telson, abdomen, antenna, carapacial spines and on the size of the zoeas. Unfortunately Hashmi did not illustrate the larvae, and his figure of the brachyuran antennal types (his fig. 2) does not sufficiently discriminate among the antennal types of the Xanthidae. The xanthid species treated by Hashmi (1970a) are included in the present work; however, the placement of these species in the larval groupings proposed herein must be viewed with skepticism until complete descriptions of these larvae become available.

Rice (1980) suggested that at least four distinct xanthid groups can be distinguished on the basis of zoeal characters in all stages as follows:

Group I. Antennal exopod reduced, less than ¼ length of protopod (=spinous process), never armed with more than 2 short terminal setae, these sometimes absent (Fig. 1A); antennal protopod approximately same length as rostrum; carapace spines (dorsal, rostral, and lateral) all well developed (Fig. 1B); dorsolateral knobs always on second and third abdominal segments, never on more posterior segments (Fig. 1C); distal segment of endopod of maxillule always with 6 setae of which 2 are subterminal (Fig. 1D); endopod of maxilla always with 8 setae (Fig. 1E); basal segment of endopod of first maxilliped always with 3 setae (Fig. 1F), that of second maxilliped with a single seta (Fig. 1G); telson fork armature variable. Usually 4 zoeal stages.

Table 1. Known zoeas of xanthid crabs arranged according to six xanthid zoeal groupings shown in Figure 1. * = occurs in western Atlantic and/or Gulf of Mexico; † = questionable placement in Xanthidae; ‡ = questionable identification. Abbreviations: Abrev. = abbreviated or advanced development; AcS = accessory carapacial spines; NCS = no lateral carapacial spines

Species	Described Stages	Author
GROUP I		
Atergatis reticulatus de Haan, 1835	zoea 1–4	Terada, 1980
Cataleptodius floridanus (Gibbes, 1850)*		
(as *Leptodius floridanus*)	zoea 1	Kurata, 1970
Chlorodiella nigra (Forskäl, 1775)	zoea 1–4, megalopa	Gohar and Al-Kholy, 1957
(as *Chlorodiella niger*)	zoea 1	Gurney, 1938
(as *Chlorodius niger*)	zoea 1	Prasad and Tampi, 1957
Cycloxanthops novemdentatus (Lockington, 1877)	zoea 1–4, megalopa	Knudsen, 1960
Cycloxanthops truncatus (de Haan, 1837)	zoea 1–4	Suzuki, 1979
Cycloxanthops truncatus (de Haan, 1837)	zoea 1–4	Terada, 1980
(as *C. truntatus*)	zoea 1–4, megalopa	Hong, 1977
Cymo melanodactyla (de Haan, 1858)		
(as *C. andreossyi* var. *melanodactyla*)	zoea 1	Gurney, 1938
Etisus laevimanus Randall, 1839	zoea 1–4, megalopa	Suzuki, 1978
Etisus laevimanus Randall, 1839	zoea 1	Hashmi, 1970a
Eurypanopeus depressus (Smith, 1869)*	zoea 1–4, megalopa	Costlow and Bookhout, 1961b
Eurypanopeus depressus (Smith, 1869)*	zoea 1–4, megalopa	Kurata, 1970
Eurypanopeus depressus (Smith, 1869)*	zoea 1	Hyman, 1925
Eurypanopeus depressus (Smith, 1869)*	zoea 1	Sandifer, 1972
Eurypanopeus depressus (Smith, 1869)*	zoea 1–2	Shipp, 1977
(as *Panopaeus depressus*)	zoea 2	Birge, 1883
Eurytium limosum (Say, 1818)*	zoea 1–4, megalopa	Kurata et al., 1981
Eurytium limosum (Say, 1818)*	zoea 1–4, megalopa	Kurata, 1970
Heteractaea ceratopus (Stimpson, 1860)*	zoea 1	Gurney, 1936
Heterozius rotundifrons A. Milne Edwards, 1867†[a]	zoea 1–2, megalopa (Abrev.)	Wear, 1968
Hexapanopeus angustifrons (Benedict and Rathbun, 1891)*	zoea 1–4, megalopa	Costlow and Bookhout, 1966
Hexapanopeus angustifrons (Benedict and Rathbun, 1891)*	prezoea only	Hyman, 1925
Hexapanopeus angustifrons (Benedict and Rathbun, 1891)*	zoea 1	Sandifer, 1972
(as *Panopeus occidentalis*)	zoea 1–4, megalopa	Kurata, 1970
Leptodius crassimanus (A. Milne Edwards, 1867)	zoea 1	Hashmi, 1970a
Leptodius distinguendus (de Haan, 1835)		
(as *Macromedaeus distinguendus*)	zoea 1–4	Terada, 1980
Leptodius exaratus (H. Milne Edwards, 1834)	zoea 1	Chhapgar, 1956
Leptodius exaratus (H. Milne Edwards, 1834)	zoea 1–4, megalopa	Fielder et al., 1979

[a] Placed in the family Atelecyclidae by Balss (1957) and Rice (1980), but included in the Belliidae by Guinot (1978).

Table 1. Continued

Species	Described Stages	Author
Leptodius exaratus (H. Milne Edwards, 1834)	zoea 1–4, megalopa	Saba, 1976
Leptodius exaratus (H. Milne Edwards, 1834)	zoea 1–4	Terada, 1980
Leptodius exaratus (H. Milne Edwards, 1834)	zoea 1	Hashmi, 1970a
(as *L. exeratus*)	zoea 1–2	Tufail and Hashmi, 1964
(as *Xantho exaratus*)	zoea 1	Aikawa, 1929
Lophopanopeus bellus (Stimpson, 1860)	zoea 1–4, megalopa	Hart, 1935
Lophopanopeus bellus (Stimpson, 1860)	zoea 1, megalopa	Forss and Coffin, 1960
L. bellus diegensis Rathbun, 1930	zoea 1–4, megalopa	Knudsen, 1959a
Lophopanopeus leucomanus (Lockington, 1877) subsp. *leucomanus* Rathbun, 1930	zoea 1–4, megalopa	Knudsen, 1958
Medaeus granulosus (Haswell, 1882)	zoea 1	Hashmi, 1970a
Neopanope packardii (Kingsley, 1879)*	zoea 1–4, megalopa	Costlow and Bookhout, 1967
Neopanope sayi (Smith, 1869)*		
(as *N. texana sayi*)	zoea 1–4, megalopa	Hyman, 1925
(as *N. texana sayi*)	zoea 1–4, megalopa	Chamberlain, 1957, 1961
(as *N. texana sayi*)	zoea 1–4, megalopa	Kurata, 1970
(as *N. texana sayi*)	zoea 1	Sandifer, 1972
(as *N. texana*)	zoea 1	Hillman, 1964
(as *Panopaeus sayi*)	zoea 1–4, 2 megalopas	Birge, 1883
Neopanope texana (Stimpson, 1859)*	zoea 2	Shipp, 1977
(as *N. texana texana*)	zoea 1–4, megalopa	McMahan, 1967
Neopanope sp. (as *Panopaeus* sp.)	zoea 1	Conn, 1884
Panopeus ?africanus A. Milne Edwards, 1867 (ASM 27)	zoea 2	Rice and Williamson, 1977
Panopeus herbstii H. Milne Edwards, 1834*	zoea 1–4, megalopa	Costlow and Bookhout, 1961a
Panopeus herbstii H. Milne Edwards, 1834*	zoea 1–4, megalopa	Kurata, 1970
Panopeus herbstii H. Milne Edwards, 1834*	zoea 1	Hyman, 1925
Panopeus herbstii H. Milne Edwards, 1834*	zoea 1	Sandifer, 1972
Panopeus herbstii H. Milne Edwards, 1834*	zoea 1	Shipp, 1977
Panopeus turgidus Rathbun, 1930*	zoea 4, megalopa	Martin et al., in press
Panopeus turgidus Rathbun, 1930*	zoea 4, megalopa	Martin, 1981
Panopeus sp.*	zoea 1–4, megalopa	Kurata, 1970
Pilodius nigrocrinitus Stimpson, 1858	zoea 1–3, megalopa (Abrev.)	Terada, 1982
Pilodius spinipes (Heller, 1861) (as *Chlorodopsis spinipes*)	zoea 1	Gurney, 1938
Paraxanthias taylori (Stimpson, 1861)	zoea 1–4, megalopa	Knudsen, 1959b
Pseudomedaeus agassizii (A. Milne Edwards, 1880)* (as *Leptodius agassizii*)	zoea 1–4, megalopa	Costlow and Bookhout, 1968

Table 1. C(

Species	Described Stages	Author
Rhithropanopeus harrisii (Gould, 1841)*	zoea 1–4, megalopa	Connolly, 1925
Rhithropanopeus harrisii (Gould, 1841)*	zoea 1–4, megalopa	Chamberlain, 1962
Rhithropanopeus harrisii (Gould, 1841)*	zoea 1–4, megalopa	Hood, 1962
Rhithropanopeus harrisii (Gould, 1841)*	zoea 1–4, megalopa	Kurata, 1970
Rhithropanopeus harrisii (Gould, 1841)*	zoea 1–4	Shipp, 1977
Rhithropanopeus harrisii (Gould, 1841)*	zoea 1	Sandifer, 1972
R. harrisii subsp. *tridentatus* (Maitland, 1874)		
(as *Heteropanope tridentata*)	zoea 1	Tesch, 1922
Xanthodius denticulatus (White, 1847)*	zoea 1	Lebour, 1944
Xantho granulicarpus Forest, 1953		
(as *X. incisus* subsp. *granulicarpus*)	zoea 1–4	Bourdillon-Casanova, 1960
Xantho incisus incisus (Leach, 1814)		
(as *Xantho incisus*)	zoea 1–4, megalopa	Lebour, 1928
(as *Xantho incisus*)	megalopa	Kurian, 1956
Xantho poressa (Olivi, 1792)	zoea 1	Bourdillon-Casanova, 1960
(as *Xantho hydrophilus*)	zoea 1	Lebour, 1928
(as *Xantho rivulosus*)	zoea 1	Gourett, 1884
Xantho (*Lophoxanthus*) *scaberrimus* Walker, 1886		
(var. *baccalipes* Alcock, 1898)	zoea 1	Hashmi, 1970a
Xantho spp.	zoea 1–4, 2 megalopas	Hyman, 1925
Xantho sp.	zoea 1–4, 2 megalopas	Cano, 1892
Xantho sp.	zoea 1	Aikawa, 1929
Xantho sp.	zoea 1	Couch, 1844
Xantho sp.	zoea 1	Czerniawsky, 1878
Xantho sp.	zoea 1	Müller, 1862
Xantho sp.	zoea 1	Müller, 1869
Xantho sp.	zoea 1	Williamson, H. C., 1915
GROUP II		
Actumnus setifer (de Haan, 1835)	zoea 1	Aikawa, 1937
Eurycarcinus orientalis A. Milne Edwards, 1867	zoea 1	Hashmi, 1970a
Eurycarcinus orientalis A. Milne Edwards, 1867	zoea 1	Hashmi, 1970b
Heteropanope glabra Stimpson, 1858	zoea 1 (NCS)	Aikawa, 1929
Heteropanope laevis (Dana, 1852)	zoea 1	Hashmi, 1970a
Heteropanope laevis (Dana, 1852)	zoea 1	Hashmi, 1970b
Heteropilumnus ciliatus (Stimpson, 1858)	zoea 1	Takeda and Miyake, 1968

Table 1. Continued

Species	Described Stages	Author
Lobopilumnus agassizii (Stimpson, 1871)*		
var. *bermudensis* Rathbun, 1930	zoea 1	Lebour, 1950
Pilumnopeus indica (de Man, 1887)		
(as *Pilumnopeus indicus*)	zoea 1 (NCS)	Takeda and Miyake, 1968
Pilumnopeus serratifrons (Kinahan, 1856)		
(as *Heteropanope* (*Pilumnopeus*) *serratifrons*)	zoea 1	Wear, 1968
Pilumnus dasypodus Kingsley, 1879*	zoea 1–4, megalopa	Sandifer, 1974
Pilumnus dasypodus Kingsley, 1879*	zoea 1–4, megalopa	Bookhout and Costlow, 1979
Pilumnus hirtellus (Linnaeus, 1761)	zoea 1–4, megalopa	Bourdillon-Casanova, 1960
Pilumnus hirtellus (Linnaeus, 1761)	zoea 1–4, megalopa	Lebour, 1928
Pilumnus hirtellus (Linnaeus, 1761)	zoea 1–4, megalopa	Salman, 1982
Pilumnus hirtellus (Linnaeus, 1761)	zoea 1	Boraschi, 1921
Pilumnus hirtellus (Linnaeus, 1761)	zoea 1	Williamson, H. C., 1915
Pilumnus holosericus Rathbun, 1898*		
(as *Pilumnus* sp.)	zoea 1	Kurata, 1970
Pilumnus ?inermis A. Milne Edwards and Bouvier, 1894 (ASM 25)	zoea 3	Rice and Williamson, 1977
Pilumnus longicornis Hilgendorf, 1878	zoea 1	Prasad and Tampi, 1957
Pilumnus longicornis Hilgendorf, 1878	zoea 1	Hashmi, 1970a
Pilumnus lumpinus Bennett, 1964	zoea 1, megalopa (Abrev.)	Wear, 1967
Pilumnus minutus de Haan, 1835	zoea 1	Aikawa, 1929
Pilumnus sayi Rathbun, 1897*	zoea 1–4, megalopa	Bookhout and Costlow, 1979
Pilumnus sayi Rathbun, 1897*	zoea 1–4, megalopa	Kurata, 1970
Pilumnus spinifer H. Milne Edwards, 1834	zoea 1	Gourett, 1884
Pilumnus vespertilio (Fabricius, 1798)	zoea 1	Aikawa, 1929
Pilumnus vespertilio (Fabricius, 1798)	zoea 1–3	Hashmi, 1970c
Pilumnus vespertilio (Fabricius, 1798)	zoea 1–3, megalopa (Abrev.)	Lim and Tan, 1981
Pilumnus sp.	zoea 1	Williamson, H. C., 1915
Pilumnus sp.	zoea 1	Mayer, 1877
Pilumnus sp.	zoea 1	Couch, 1844
Pilumnus spp.	zoea 1–4, 2 megalopas	Cano, 1892
Pilumnus spp.	zoea 1–4, 2 megalopas	Hyman, 1925
?*Pilumnus* sp.* (as *Panopeus bermudensis*)	zoea 1	Lebour, 1944
Xanthodius parvulus (Fabricius, 1793)‡		
(as *Leptodius parvulus*)	zoea 1	Lebour, 1944

Table 1. Continued

Species	Described Stages	Author
GROUP III		
ASM 26 (Menippinae or (more likely) Trapeziinae)	zoea 3–4 (AcS)	Rice and Williamson, 1977
Baptozius venosus (H. Milne Edwards, 1898)	zoea 1–4, megalopa	Saba et al., 1978a
Epixanthus dentatus (White, 1847)	zoea 1–2, megalopa (Abrev.)	Saba et al., 1978b
Eriphia spinifrons (Herbst, 1785)	zoea 1–3	Bourdillon-Casanova, 1960
Eriphia spinifrons (Herbst, 1785)	zoea 1	Paolucci, 1910
Eriphia spinifrons (Herbst, 1785)	zoea 1	Boraschi, 1921
Eriphia spinifrons (Herbst, 1785)	zoea 1, 3–4	Hyman, 1925
Eriphia verrucosa (Forskäl, 1775)	zoea 1–4, megalopa	Lumare and Gozzo, 1972
Eriphia laevimana smithii MacLeay, 1838‡	zoea 1	Hashmi, 1970a
Eriphia laevimana smithii MacLeay, 1838‡	zoea 1	Hashmi, 1970b
Eriphia sp.	zoea 1	Rathke, 1837
Eriphia sp.	zoea 1	Cano, 1892
Homalaspis plana (A. Milne Edwards, 1834)†[b]	zoea 1	Fagetti-Guiata, 1960
Homalaspis plana (A. Milne Edwards, 1834)†[b]	zoea 1–4, megalopa	Fagetti, 1970
Ozius rugulosus Stimpson, 1858 (as *O. rugulosus rugulosus*)	zoea 1–4, megalopa	Kakati and Nayak, 1977
Ozius truncatus H. Milne Edwards, 1834	zoea 1–4, megalopa	Wear, 1968
Paramedaeus noelensis (Ward, 1934)	zoea 1–4	Suzuki, 1979
Pilumnoides perlatus (Poeppig, 1836)	zoea 1–5, megalopa	Fagetti and Campodonico, 1973
Platyxanthus crenulatus (A. Milne Edwards, 1879)†[b]	zoea 1–4, megalopa	Menú-Marque, 1970
Tetralia glaberrima (Herbst, 1790)	zoea 1–2 (AcS)	Gurney, 1938
Tetralia glaberrima (Herbst, 1790)	zoea 1–3 (AcS)	Al-Kholy, 1963a
Tetralia sp.	zoea 3 (AcS)	George and John, 1975
Tetralia sp.	zoea 1, 3 (AcS)	Frontier, 1963
Trapezia cymodoce (Herbst, 1801)	zoea 1	Gurney, 1938
Trapezia guttata Ruppell, 1830	zoea 1	Gurney, 1938
Trapezia maculata (MacLeay, 1838)	zoea 1	Al-Kholy, 1963b
Trapezia sp.	zoea 1	Bate, 1879
Trapezia sp.	zoea 1	Hyman, 1925
unidentified "Xanthide G.M."	zoea 1–2	Bourdillon-Casanova, 1960

[b] Transferred to the family Platyxanthidae by Guinot (1977).

Table 1. Continued

Species	Described Stages	Author
GROUP IV		
Menippe mercenaria (Say, 1818)*	zoea 1	Hyman, 1925
Menippe mercenaria (Say, 1818)*	zoea 1–5, megalopa	Kurata, 1970
Menippe mercenaria (Say, 1818)*	zoea 1–5(6)	Porter, 1960
Menippe nodifrons Stimpson, 1859*	zoea 1–5(6), megalopa	Scotto, 1979
Menippe rumphii (Fabricius, 1798)	zoea 1	Prasad and Tampi, 1957
Menippe rumphii (Fabricius, 1798)	zoea 1–5, megalopa	Kakati, 1977
Sphaerozius nitidus Stimpson, 1858	zoea 1	Aikawa, 1933
GROUP V		
Micropanope barbadensis (Rathbun, 1921)*	zoea 1–3(4), megalopa (Abrev.)	Gore et al., 1981
Micropanope sculptipes Stimpson, 1871*	zoea 1–4, megalopa	Andryszak and Gore, 1981
GROUP VI		
Panopeus bermudensis Benedict and Rathbun, 1891*	zoea 4, megalopa (NCS)	Martin, 1981
Panopeus bermudensis Benedict and Rathbun, 1891*	zoea 4, megalopa (NCS)	Martin et al., in press
INCERTAE ZOEAS		
Monodaeus couchi (Bell, 1851)	zoea 1 (telson only)	Williamson, D. I., 1982
Pilumnus novaezealandiae Filhol, 1886†	(4 prezoeas), megalopa (Abrev.)	Wear, 1967
Pilumnus vestitus Haswell, 1882†	megalopa only (Abrev.)	Hale, 1931
Z44 (? possibly xanthoid)	zoea 2	Andryszak, 1979
Z18 (? possibly xanthoid)	zoea 2	Andryszak, 1979
Eriphia caribboea† (synonymy unknown)	zoea 1 (not illustrated)	Thompson, 1836
Quadrella nitida Smith, 1869	megalopa only	Garth, 1961
Ozius rugulosus Stimpson, 1858	zoea 1	Chhapgar, 1956
Ozius rugulosus Stimpson, 1858	zoea 1	Hashmi, 1970a
NRS 46†	zoea 3 (NCS)	Williamson, D. I., 1970
EM 19†	zoea 3	Williamson, D. I., 1967
Platypodia cristata (A. Milne Edwards, 1865)	zoea 1	Hashmi, 1970a

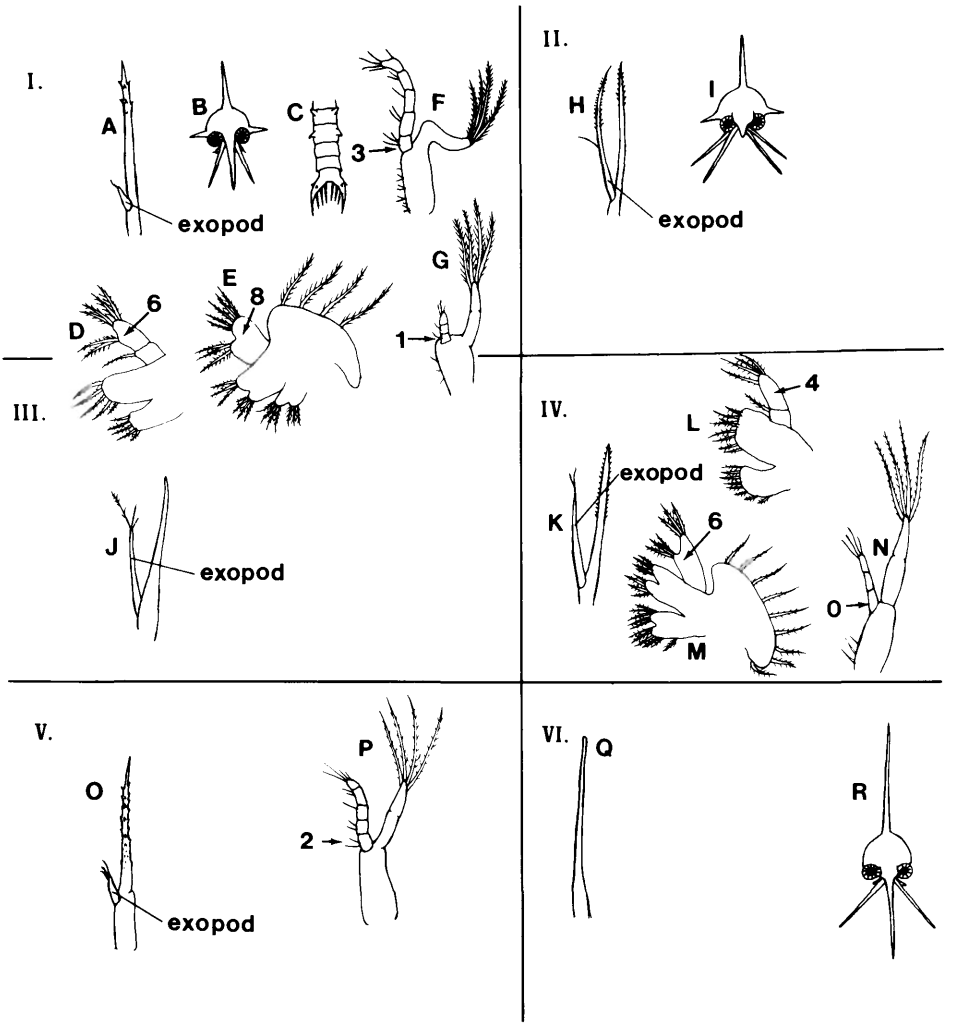

Figure 1. The six groupings of xanthid zoeas. A, antenna; B, carapace; C, abdomen; D, maxillule; E, maxilla; F, maxilliped 1; G, maxilliped 2 (Group I). H, antenna; I, carapace (Group II). J, antenna; D, E, and G as above (Group III). K, antenna; L, maxillule; M, maxilla; N, maxilliped 2 (Group IV). O, antenna; P, maxilliped 1 (Group V). Q, antenna; R, carapace (Group VI). Arabic numbers refer to setation of indicated segment.

GROUP II. Antennal exopod acutely tipped, about equal in length to or slightly longer than protopod, armed with small spinules distally and with prominent outer seta about halfway along its length (Fig. 1H); antennal protopod usually longer than rostrum (Fig. 1I). Other characters variable. Usually 4 zoeal stages.

GROUP III. Antennal exopod robust, about ½ length of protopod, armed with 3 unequal terminal setae (Fig. 1J). Some characters shared with Group I (setation of endopod of maxillule and maxilla 1–6 and 3 + 5, respectively; basal segment of endopod of second maxilliped with 1 seta). Other characters variable. Usually 4 zoeal stages.

GROUP IV. Antennal exopod about same length as Group III, but tapering

toward tip and bearing only 2 unequal setae (Fig. 1K); endopod of maxillule with only 4 setae on distal segment (Fig. 1L) (compared with 6 in all other xanthids); endopod of maxilla with 2 groups of 3 setae (Fig. 1M) (rather than a total of 8 setae in other xanthids); proximal segment of endopod of second maxilliped unarmed (Fig. 1N) (always with a single seta in other xanthids). Other characters variable. Usually 5 (rather than 4) zoeal stages.

Gore et al. (1981) proposed a fifth xanthid zoeal group to accommodate the larvae of "*Micropanope*" *barbadensis* (Rathbun, 1921), a species currently without an assigned genus following the revision of the genus *Micropanope* by Guinot (1967). This fifth zoeal group was actually an addition to Aikawa's (1929) four zoeal groups, based primarily on antennal characters, rather than to the four xanthid zoeal groups of Rice (1980). The zoea of *M. barbadensis* has an antennal exopod that is 1/7 to 1/4 the length of the protopod (spinous process), typical of Rice's Group I zoeas, but there are 3 terminal setae on the exopod, and only 2 setae (rather than 3) on the basal segment of the endopod of the first maxilliped. Thus, *Micropanope barbadensis* is deserving of a separate larval group:

GROUP V. Antennal exopod as in Group I but tipped with 3 short terminal setae (Fig. 1O); basal segment of endopod of first maxilliped with 2 (rather than 3) setae (Fig. 1P). Other characters as in Group I.

The larvae of *Micropanope sculptipes* Stimpson, 1871, the type species of the genus, were described by Andryszak and Gore (1981) and fall into this same category, as the zoeas have a reduced antennal exopod with 1 terminal spine and 3 terminal setae, and only 2 setae on the proximal segment of the first maxilliped.

Martin et al. (in press) described the fourth zoea of *Panopeus bermudensis* Benedict and Rathbun, 1891 and *Panopeus turgidus* Rathbun, 1930. The zoea of *Panopeus bermudensis* is very unlike the first zoea described by Lebour (1944) as the same species; it is suggested that Lebour's identification of the parent was incorrect. The zoea of *Panopeus bermudensis* described by Martin et al. (in press) (but not the zoea identified as *P. bermudensis* by Lebour) is typical of Rice's Group I xanthid zoeas, with the important exception that it lacks any carapacial spines. As all other members of the Group I xanthid zoeas have lateral carapace spines, *P. bermudensis* may be deserving of a separate larval xanthid group:

GROUP VI. Antennal exopod absent (Fig. 1Q) (as in some Group I zoeas); carapace without lateral spines (Fig. 1R). Other characters as in Group I (presumably, as only the 4th zoea is known).

These six groups presently accommodate all the known xanthid zoeas. Rice (1980) acknowledged that his four zoeal groups did not correspond with Balss's (1957) division of the Xanthidae into four subfamilies. The addition of the xanthid zoeal Groups V and VI to Rice's scheme does nothing to clarify the status of Balss's subfamilies, nor do these groupings lend additional support to Guinot's (1978) incomplete revision of the xanthids. There are, however, some phylogenetic implications that are of interest. Although Guinot (1967) removed *Micropanope barbadensis* from the genus *Micropanope*, the extremely similar larvae of *M. barbadensis* and *M. sculptipes* (the type species) perhaps suggest that these species may be congeners if larval characters validly reflect phylogenetic relationships. As noted by Martin et al. (in press), the unusual zoea of *Panopeus bermudensis* is reason to question the present generic placement of this species as well. I also believe that Lebour's (1944) description of the zoea of *Xanthodius parvulus* (as *Leptodius parvulus*) is in fact not a *Xanthodius* but a member of the Pilumninae

(=Pilumnidae *sensu* Guinot). The fact that the zoea of *Xanthodius denticulatus* (White, 1847) is a Group I zoea (Lebour, 1944) plus the fact that, as noted above, Lebour probably misidentified another pilumnine species as *Panopeus bermudensis* lend support to this suggestion.

Megalopas of western Atlantic xanthids were reviewed by Andryszak and Gore (1981), and Salman (1982) reviewed the megalopas of 23 xanthid species, but did not specify which species he examined. Megalopal characters used by Salman to distinguish between the subfamilies (of Balss, 1957) Xanthinae, Pilumninae, and Menippinae are variable and inconsistent. One character, presence or absence of frontal spines, may serve to separate the Xanthinae from the other two subfamilies examined by Salman, but serious attempts to phyletically reorder the xanthids on the basis of megalopal characters will have to await more detailed studies such as that of Rice (1981b) on the megalopas of podotremen crabs.

Many of the early descriptions of xanthid zoeas did not include the setation of the appendages and it is therefore difficult to positively assign these zoeas to any of the six groups. However, carapace morphology and the structure of the antennal exopod allow their probable placement. According to the classificatory scheme of Glaessner (1969), the superfamily Xanthoidea contains the families Xanthidae MacLeay, 1838, Potamidae Ortmann, 1896, Geryonidae Colosi, 1924, Goneplacidae MacLeay, 1838, Pinnotheridae de Haan, 1833, Grapsidae MacLeay, 1838, and Gecarcinidae MacLeay, 1838. The family Xanthidae is not further subdivided. As Glaessner's work is based upon extensive paleontological evidence as well as morphology of extant forms, and because larval evidence for further subdivision of the xanthids is lacking (see Rice, 1980), I follow this scheme in the present study. Although Wear (1970) and Gurney (1939, 1942) included members of the family Geryonidae in their bibliographies of xanthid larvae, I have excluded them from this discussion pending further revision of the geryonids. An excellent summary of geryonid larvae was provided by Ingle (1979) and Rice (1980). The xanthid genera and species listed herein (Table 1) are arranged alphabetically under each of the six zoeal groupings.

Number of Zoeal Stages in Xanthid Crabs

Wear (1970) noted that the number of zoeal stages in the Xanthidae was firmly established as four, although he was aware of two exceptions. However, as noted by Rice (1980), Kurata et al. (1981), and Andryszak and Gore (1981), several xanthids have an abbreviated or advanced larval development (see Gore, 1979 for definitions), and members of the genus *Menippe* have five and occasionally six zoeal stages (Porter, 1960; Scotto, 1979). It is now known that there are xanthid species with 5, 6, 3, 2, and 0 zoeal stages (Table 1). The usual suggestion to account for abbreviated or advanced larval development in xanthid crabs is that those species with less than four zoeal stages occupy somewhat restricted estuarine habitats (Rice, 1980; Kurata et al., 1981; Scotto, 1979); Wear (1967) noted that "partial or complete abbreviation of the planktonic phase and retention of larvae would assist with retaining the stock within a restricted locality or ecological niche." Taken alone, this explanation is untenable; several species of xanthids [e.g., *Rhithropanopeus harrisii* (Gould, 1841) and *Eurypanopeus depressus* (Smith, 1869)] occur in low salinity estuarine environments but have four zoeal stages. In fact, one of the xanthids with extremely advanced development (the eggs hatch as megalopas) is *Pilumnus vestitus* Haswell, 1882, a species typical of shallow water coral reef areas of normal salinity (Hale, 1931). Andryszak and Gore (1981) stated that factors other than environment may have an effect on the number of

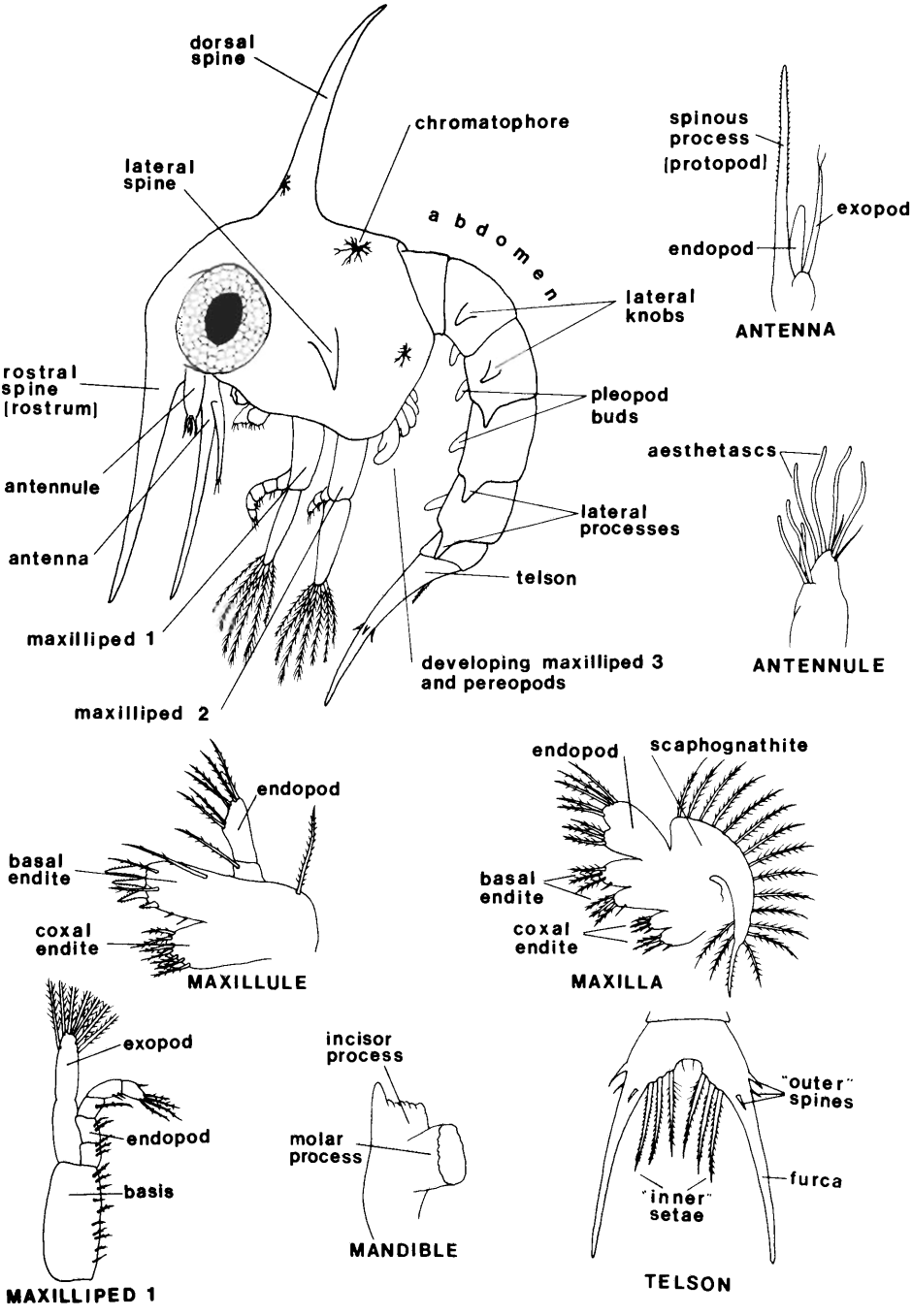

Figure 2. Schematic xanthid zoea, stage 3. Appendages not drawn to scale.

larval stages, and I am inclined to agree. The reason for abbreviated or advanced development in some xanthid species remains unknown.

Xanthid Zoeas of the Western Atlantic and Gulf of Mexico

The xanthid crab fauna of the western Atlantic and Gulf of Mexico is rich in species and genera. Powers (1977), relying primarily on literature records, listed 69 species in 33 genera from the Gulf of Mexico, although several of the species are of questionable occurrence and/or taxonomic status. The western Atlantic contains all but three of the Gulf species listed by Powers (1977), plus many additional species (Rathbun, 1930). The few larval descriptions based upon Gulf of Mexico material include *Panopeus bermudensis* and *P. turgidus* by Martin et al. (in press) and *Neopanope texana* by McMahan (1967). However, larvae have been described from xanthids which occur both in the Gulf and in other areas.

The following key incorporates all known descriptions of xanthid larvae which might occur in the western Atlantic and Gulf of Mexico. Characters used in the key are illustrated in Figure 2. The purpose of the key is to allow rapid identification of xanthid larvae to each of the six larval groups, and where possible, to species level. The couplets are based upon the xanthid zoeal characters of Rice (1980), some characters from the comparative table of zoeal characters of western Atlantic xanthids by Andryszak and Gore (1981), and upon other characters taken either from the literature or from personal observation. The key must be used with caution. Because larvae of only 22 of the more than 100 xanthid species known from the western Atlantic and Gulf are described, any couplet may apply to many undescribed forms as well as to nominate species. Also, although the characters employed are consistent for all known zoeal stages, several species are known only from the first zoea. Because zoeal morphology often changes with ontogeny, there is no guarantee that the later stages of these species will conform to the couplets designed to accommodate the known first zoeas. Zoeas may be identified to the family level with the key provided by Rice (1980), and additional xanthid zoeas may be added to the key as they are described.

Key to the Known Xanthid Zoeas of the Western Atlantic and Gulf of Mexico

1a. Antennal exopod reduced, less than or equal to ¼ length of protopod (=spinous process), or absent (Groups I, V, and VI) 9

1b. Antennal exopod more than ⅓ length of protopod, usually ½ to slightly longer than protopod 2

2a. Antennal exopod more or less equal to, or slightly longer than, protopod; armed with small spinules distally and with a prominent outer seta halfway along its length (Group II) ..... 4 (*Pilumnus, Lobopilumnus,* "*Xanthodius*")

2b. Antennal exopod about ½ to ¾ length of protopod, without a prominent outer seta halfway along length 3

3a. Antennal exopod robust, about ½ length of protopod, armed with 3 unequal terminal setae; endopod of maxillule with 6 setae on distal segment (Group III) ..... 4 *Eriphia*[2]

3b. Antennal exopod about ½ to ¾ length of protopod, tapering distally and bearing only 2 unequal setae; endopod of maxillule with only 4 setae on distal segment (Group IV) ..... 8 (*Menippe*)

4a. Lateral knobs only on abdominal segments 2 and 3 5

4b. Lateral knobs on abdominal segments 2 through 5 6

5a. Antennal protopod approximately equal in length to rostrum ..... "*Xanthodius parvulus*" *sensu* Lebour, 1944

[2] Larvae of Group III are not known from any species in the western Atlantic or Gulf of Mexico. The couplet is included here to accommodate future descriptions of Group III zoeas, and is based upon descriptions of larvae of *Eriphia* from other areas.

5b. Antennal protopod more than 1½ times length of rostrum ..... *Pilumnus dasypodus*
6a. Telson with 1–2 outer spines on each furca 7
6b. Telson with 3 outer spines (usually 2 lateral, 1 dorsal) on each furca ..... *Pilumnus sayi, P. holosericus*
7a. Telson with 2 outer spines on each furca ..... *Lobopilumnus agassizii*
7b. Telson with 1 outer spine on each furca ..... ?*Pilumnus* sp. (Lebour's 1944 description, as *Panopeus bermudensis*)
8a. Fourth abdominal segment with a dorsolateral spine ..... *Menippe mercenaria*
8b. Fourth abdominal segment without a dorsolateral spine ..... *Menippe nodifrons*
9a. Antennal exopod present or absent: if present, with 0–2 terminal setae; basal segment of endopod of first maxilliped with 3 setae 11
9b. Antennal exopod present, with more than 2 terminal setae; basal segment of endopod of first maxilliped with 2 setae (Group V) ..... 10 (*Micropanope* (*sensu lato*))
10a. Furcae of telson each with 3 spines (dorsal, ventral, lateral) ..... *Micropanope barbadensis*
10b. Furcae of telson each with only 2 spines (dorsal and ventral) ..... *Micropanope sculptipes*
11a. Lateral carapace spines absent (Group VI) ..... *Panopeus bermudensis*
11b. Lateral carapace spines well developed (Group I) ..... 12 (*Panopeus, Eurypanopeus, Eurytium, Hexapenopeus, Neopanope, Rhithropanopeus, Pseudomedaeus, Xanthodius*)
12a. Telson lacking lateral spines, furcae smooth ..... *Hexapanopeus angustifrons*
12b. Telson with spines on furcae 13
13a. Telson with 1 dorsal spine on each furca 14
13b. Telson with at least 2 spines on each furca 19
14a. Rostral carapace spine more than 2 times carapace length; lateral processes on abdominal segment 5 much longer than those on segment 4 ..... *Rhithropanopeus harrisii*
14b. Rostral carapace spine less than or equal to 2 times carapace length; lateral processes on abdominal segment 5 not obviously longer than those on segment 4 15
15a. Antennal protopod with small spinules distally 16
15b. Antennal protopod smooth, without spinules distally 18
16a. (IF first stage zoea) 8–10 distal spinules on antennal protopod ..... *Eurypanopeus depressus*
16b. (IF first stage zoea) 3–4 distal spinule on antennal protopod ..... *Neopanope packardii*
16c. Other stages (2–4) with distal spinules on antennal protopod 17
17a. Lateral carapace spines long and slender ..... *Neopanope packardii*
17b. Lateral carapace spines short and stout ..... *Eurypanopeus depressus*
18a. Rostrum approximately 2 times carapace length ..... *Neopanope sayi*
18b. Rostrum approximately equal to carapace length ... *Neopanope packardii* (zoea 2–4), *N. texana*
19a. (IF first stage zoea) Antennal protopod with distal spinules 20
19b. (IF first stage zoea) Antennal protopod smooth, lacking distal spinules ..... *Xanthodius denticulatus*
19c. Other stages (zoea 2–4) with distal spinules on antennal protopod 24
19d. Other stages (zoea 2–4) without distal spinules on antennal protopod ..... *Eurytium limosum*
20a. Lateral knobs on abdominal segments 2 through 5 ..... *Panopeus* sp. (Kurata, 1970)[3]
20b. Lateral knobs on abdominal segments 2 and 3 only 21
21a. Distal spinules on antennal protopod 20 or more 22
21b. Distal spinules on antennal protopod 10 or less 23
22a. Lateral process of abdominal segments 3–5 extending posteriorly more than ½ length of following segment ..... *Pseudomedaeus agassizii*
22b. Lateral process of abdominal segments 3–5 not extending posteriorly to ½ length of following segment ..... *Cataleptodius floridanus*
23a. Posteriormost lateral spine on telson furcae minute, hairlike; rostral spine smooth, without distal spinules ..... *Eurytium limosum, Panopeus herbstii*[4]
23b. Posteriormost lateral spine on telson furcae thick basally, tapering toward tip; not hairlike; rostral spine with small distal spinules ..... *Heteractaea ceratopus*
24a. Short, sharp dorsally directed process on either side of rostrum ..... *Pseudomedaeus agassizii*
24b. Rostrum not bordered by short, sharp processes ..... *Panopeus herbstii, Panopeus turgidus, Panopeus* sp. (Kurata, 1970)[3]

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[3] Kurata, H. 1970. Studies on the life histories of decapod crustacea of Georgia: Part III; Larvae of decapod crustacea of Georgia. Univ. Georgia Mar. Inst. Sapelo Island. 274 pp. unpublished report.

[4] Kurata et al. (1981) noted that the first zoea of *Eurytium limosum* could be distinguished from that of *Panopeus herbstii* by the more strongly recurved tip of the dorsal carapace spine in *E. limosum*. This character is not employed in the present key.

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APPENDIX: BIBLIOGRAPHY OF THE LARVAE OF XANTHID CRABS

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Addendum

The following paper was brought to my attention while the present bibliography was in press:

Laughlin, R. A., P. J. Rodriguez and J. A. Marvel. 1983. Zoeal stages of the coral crab *Carpilius corallinus* (Herbst) (Decapoda, Xanthidae) reared in the laboratory. Crustaceana 44: 169–186.

Zoeal characters of *Carpilius corallinus* conform to those of the Group III xanthid larvae. The species occurs in the Gulf and western Atlantic and should be added to *Eriphia* in couplet 3a of the key.