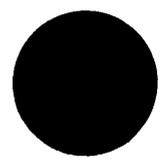


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# The eumedonid file: a case study of systematic compatibility using larval and adult characters (Crustacea: Decapoda: Brachyura)

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## Summary

Eumedonid crabs have an unusual ecology. They are a specialized group of brachyurans, which are wholly symbiotic with echinoderms. Consequently, this taxon has received much attention from carcinologists, but consensus on the familial status of these crabs has not been reached. Eumedonids have been variously regarded as a subfamily of the Parthenopidae, as pilumnids and as a distinct family. The taxonomic position of the Eumedonidae is appraised using available first zoeal and adult characters. The validity of this family status is challenged, and the present study shows that this group of crabs cannot be distinguished from the pilumnids and therefore supports the view that the eumedonids are a subfamily of the Pilumnidae.

**Key words:** First zoeal and adult characters, phylogenetics, systematics, Eumedoninae, Pilumnidae, Parthenopidae, Xanthoidea

## Introduction

The crabs assigned to the Eumedonidae Dana, 1854, are unusual within the Brachyura in that all known members are obligate symbionts on echinoderms. The variety in carapace and pereopodal form has resulted in a multitude of classifications for its various genera. At one time or another, the genera now recognized in the Eumedonidae have been referred to the Majidae, Parthenopidae, Xanthidae, Pilumnidae, Trapeziidae, Portunidae and even the Pinnotheridae! Most of the genera assigned to the eumedonids have

been regarded as a distinct group. Until the early 1970s, most workers followed Balss (1957) and recognized this group as a subfamily of the Parthenopidae. However, in the late 1960s doubts were beginning to be raised against this accepted position. The general consensus was that the eumedonids should not be assigned to the Parthenopidae — it is a monophyletic taxon and allied to the Pilumnidae — but its systematic rank was far from certain. Past systematic studies have included eumedonid larval and adult characters.

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### Larval systematics

Larval stages for only a few of the 32 described eumedonid species (see Table 1) are known and all these have been reported relatively recently. Castro (1978) was the first to rear eumedonid larvae (*Echinoecus pentagonus*) in the laboratory and the zoeal stages, together with the megalop, were described by Van Dover et al. (1986). Subsequently, the zoeal and megalop phases of *Zebrida adamsii* (by Mori et al., 1991) have been described and the first stage zoea of *Harrovia longipes* (as *H. albolineata*) by Lim and Ng (1988), *H. albolineata* [*s. str.*] by Chia et al. (1993) and *Rhabdonotus pictus* by Chia and Ng (1995) were reported.

Van Dover et al. (1986) considered that the morphological and developmental characters exhibited by the larvae of *Echinoecus pentagonus* indicated that the species was not a member of the Parthenopidae. Although the zoea showed strong morphological relationships to xanthid crabs, subfamily Pilumninae, Van Dover et al. (1986) were uncertain if *Echinoecus pentagonus* were a typical representative of the eumedonids, and this made them hesitant concerning the systematic position of the taxon. Consequently, they commented that only further studies on larvae of species in the subfamily Eumedoninae will determine whether *E. pentagonus* and other eumedonine genera would eventually be reassigned either as a separate family (Eumedonidae), or as a subfamily (Eumedoninae) of the Xanthidae *sensu lato* or the Pilumnidae *sensu* Guinot (1978).

Števc̆ić et al. (1988) also reviewed larval characters and they supported the removal of *E. pentagonus* from the Parthenopidae. This was based on the number of zoeal stages and setation of the maxillary and maxillulary endopods. According to them, the eumedonids were more closely related to the Xanthoidea (*sensu* Guinot, 1978), and in particular the pilumnids. They considered that the larval stages of *E. pentagonus* were nearly identical to those of some pilumnids (e.g., *Pilumnus dasypodus* by Sandifer, 1974) in almost every appendage feature, including positioning and number of setae, telson and most abdominal somite armature. In fact, according to them, the larvae were so similar that they were difficult to separate, but Števc̆ić et al. (1988) were uncertain about the significance of these similarities and consequently they concentrated on adult characters.

### Adult systematics

Henri Milne Edwards (1834) described the first eumedonid genus and regarded *Eumedonus* as a

member of the Parthenopidae. Later, Dana (1854) established the family Eumedonidae for four genera, *Eumedonus* H. Milne Edwards, 1834, *Ceratocarcinus* Adams and White (in White, 1847), *Gonatonotus* Adams and White (in White, 1847), and *Harrovia* Adams and White, 1849, placing the taxon in a “Legio Parthenopinea”. Dana (1851, 1854), however, regarded the parthenopid crabs as part of the family Majidae. Neumann (1878) subsequently considered the eumedonids as a subfamily of the Parthenopidae and almost every subsequent worker who regarded the parthenopids as a distinct family followed his classification. This included Miers (1879a, 1879b, 1886), Alcock (1895), Rathbun (1910), Flipse (1930), Sakai (1938, 1965, 1976), Miyake (1939, 1983), Stephensen (1946), Balss (1957), Serène et al. (1958), Serène and Romimohtarto (1963), Serène (1968), Glaessner (1969), Castro (1978), Dai et al. (1986), Tirmizi and Kazmi (1988), and Dai and Yang (1991). There are exceptions. Ortmann (1893, 1894) and Estampador (1937, 1959) regarded the eumedonids as a family, but they did not elaborate on their decision, and presumably merely followed Dana (1854).

During the years following Neumann (1878), five new genera were assigned to the Eumedonidae, viz. *Echinoecus* Rathbun, 1894, *Zebridonus* Chia et al., 1995, *Permanotus* Chia and Ng, 1998, *Tauropus* Chia and Ng, 1998, and *Tiaramedon* Chia and Ng, 1998; and three genera were transferred to the family. These were *Zebrida* White, 1847 (by Henderson, 1893, originally in the Majidae), *Rhabdonotus* A. Milne Edwards, 1879 (by Johnson, 1962, originally in the Trapeziidae) and *Hapalonotus* Rathbun, 1897 (by Vandenspiegel et al., 1992; originally in the Pinnotheridae and later Xanthidae). Johnson (1962) also regarded *Caphyra archeri* Walker, 1887, which was classified in the Portunidae for a long time, as a junior synonym of the type species, *Rhabdonotus pictus* A. Milne Edwards, 1879. Several unusual genera have been referred to the Eumedonidae at one time or another, viz. *Calmania* Laurie, 1906, *Dentoxanthus* Stephensen, 1946, *Glyptocarcinus* Takeda, 1973, and *Otognathon* Ng and Števc̆ić, 1993; but all these genera have now been assigned to other families: *Calmania*, *Dentoxanthus*, and *Otognathon* to the Pilumnidae by Števc̆ić et al. (1988), Števc̆ić and Ng (1988), Ng and Števc̆ić (1993), respectively; and *Glyptocarcinus* to the Xanthidae [*s. str.*] by Ng and Chia (1994).

In an unpublished thesis, Ng (1983) suggested that on the basis of the structures of the male abdomen, gonopods and larvae, the eumedonids are pilumnids

(sensu Guinot, 1978). Much earlier, Serène (1968: 112) had noted "... that the Eumedoninae would also have to be removed from the Parthenopidae to near (or into) the Xanthidae, at least the 'pulumnoid' type of the male pleopod suggests such a move". Ng and Rodriguez (1986), Van Dover et al. (1986), Lim and Ng (1988) and Chia et al. (1993) subsequently maintained that eumedonids are part of the Pulumnidae. In the interim, Guinot (1985a) assigned the group to the Eumedonoidea. But this was primarily in order to make the taxon compatible with the superfamilial system she (see Guinot 1978) established and was not intended to have any phylogenetic significance (Guinot, pers. comm.). But Števčić et al. (1988) compared the Eumedonidae, Parthenopidae and Pulumnidae (sensu Guinot, 1978), and argued, using adult characters only, that the eumedonids should be regarded as a separate family. In recognizing the group as a distinct family, Števčić et al. (1988) also acknowledged two subfamilies, Eumedoninae Dana, 1854, and a new subfamily, Ceratocarcininae, that included nine genera and 26 species. Števčić et al. (1988) based their subfamilial separation mainly on differences in the form of the carapace, position of the antennules, structure of the chelipeds, first pair of walking legs and the identity of the host. Chia and Ng (1995) questioned the validity of their subfamilial division with regard to the genus *Rhabdonotus* and commented that this classification was probably incorrect, as the genus was apparently intermediate between the two subfamilies. Chia and Ng (1995) argued that *Rhabdonotus* species bear a close similarity in carapace form to *Echinoecus* and, because of this, both could be referred to the Eumedoninae (sensu Števčić et al., 1988). However, with regard to the position of antennule, cheliped characters, length of the first pair of walking legs and host preference, *Rhabdonotus* according to Chia and Ng (1995) was also close to *Ceratocarcinus* and *Harrovia*. Both these genera were referred to the subfamily Ceratocarcininae by Števčić et al. (1988).

Once the Eumedonidae were established by Števčić et al. (1988), the familial status of the group gained general acceptance in brachyuran literature. Ng (1998), in a key to the marine brachyuran families of the world, recognized the Eumedonidae. He used primarily the special dactylopropodal process on the ambulatory legs (formed by a rounded submedian extension of the lateral margin, which is shaped to slide beneath a projecting button on subproximal edge of the dactylus), as well as their close symbiotic relationship with echinoderms as diagnostic eumedonid features. More

authors recognized the Eumedonidae including Castro (1989), Ng and Lim (1990), Mori et al. (1991), Chia and Ng (1993), Castro et al. (1995), Chia et al. (1995), Chia and Ng (1998), Chia et al. (1999), Chia and Ng (1999, 2000), Ng and Chia (1999), and Ng and Jeng (1999). Currently the family contains 12 genera, viz. *Ceratocarcinus* Adams and White (in White, 1847) (three species), *Echinoecus* Rathbun, 1894 (three species), *Eumedonus* H. Milne Edwards, 1834 (five species), *Gonatonotus* White, 1847 (three species), *Hapalonotus* Rathbun, 1897 (monotypic), *Harrovia* Adams and White, 1849 (seven species), *Permanotus* Chia and Ng, 1998 (monotypic), *Rhabdonotus* A. Milne Edwards, 1879 (three species), *Tauropus* Chia and Ng, 1998 (monotypic), *Tiaramedon* Chia and Ng, 1998 (monotypic), *Zebrida* White, 1847 (three species), and *Zebridonus* Chia, Ng and Castro, 1995 (monotypic) (fide, Chia and Ng, 1995, 1998, 1999, 2000; Chia et al., 1993, 1995; Ng and Chia, 1999; Vandenspiegel et al., 1992), with 32 species (Table 1).

### Aims

The purpose of this present study is to examine all available first stage zoeal and adult evidence in order to reach a compatible solution to eumedonid systematics. The long-standing association of the eumedonids with the Parthenopidae will be briefly reviewed. This investigation will ascertain if the eumedonids should be regarded as a distinct family (sensu Števčić et al., 1988) or as a subfamily of the Pulumnidae (sensu Ng and Rodriguez, 1986). The first stage zoea of *Permanotus purpureus* (eumedonid) and *Rhinolambrus pelagicus* (parthenopid) are described for the first time and this information will be used to support adult evidence.

Specimens examined during this study are deposited in the Zoological Reference Collection of the Raffles Museum, National University of Singapore (ZRC), National Museum of Natural History, Washington (USNM), the Rijksmuseum van Natuurlijke Historie (RMNH), Muséum national d'Histoire Naturelle, Paris, France (MNHN), Queensland Museum, Brisbane, Australia (QM), Institut Royale des Sciences Naturelles de Belgique/Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium (IRSNB), United States National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), Zoological Museum, University of Copenhagen, Denmark (ZMUC) and The Natural History Museum, London (NHM). The abbreviations G1 and G2 are

Table 1. List of genera and species assigned to the Eumedoninae Dana, 1854, with types listed first

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*Ceratocarcinus* Adams and White (in White, 1847)

*C. longimanus* White, 1847 (= *Ceratocarcinus speciosus* Dana, 1851; *Ceratocarcinus dilatatus* A. Milne Edwards, 1872; *Ceratocarcinus intermedius* Zehntner, 1894)

*C. frontodentata* (Shen, Dai and Chen, 1982)

*C. trilobatus* (Sakai, 1938)

*Echinoecus* Rathbun, 1894 (= *Liomedon* Klunzinger, 1906; *Proechinoecus* Ward, 1934)

*E. pentagonus* (A. Milne Edward, 1879) (= *Eumedon convictor* Bouvier and Seurat, 1905; *Liomedon pentagonus* Klunzinger, 1906; *Eumedonus petiti* Gravier, 1922; *Echinoecus rathbunae* Miyake, 1939; *Echinoecus klunzingeri* Miyake, 1939)

*E. nipponicus* Miyake, 1939

*E. sculptus* (Ward, 1934)

*Eumedonus* H. Milne Edwards, 1834

*E. niger* H. Milne Edwards, 1834 (= *Gonatonotus crassimanus* Haswell, 1880; *Eumedonus villosus* Rathbun, 1918)

*E. brevirhynchus* Chia and Ng, 2000

*E. intermedius* Chia and Ng, 2000

*E. vicinus* Rathbun, 1918

*E. zebra* Alcock, 1895

*Gonatonotus* Adams and White (in White, 1847)

*G. pentagonus* White, 1847

*G. granulatus* (MacGilchrist, 1905)

*G. nasutus* Chia and Ng, 2000

*Hapalonotus* Rathbun, 1897 (= *Malacosoma* De Man, 1879, *nomen preoccupatum*)

*H. reticulatus* (De Man, 1879)

*Harrovia* Adams and White, 1849

*H. albolineata* Adams and White, 1849

*H. cognata* Chia and Ng, 1998

*H. elegans* De Man, 1887

*H. japonica* Balss, 1921

*H. longipes* Lanchester, 1900 (= *Harrovia plana* Ward, 1936)

*H. ngi* Chen and Xu, 1992 (= *Harrovia longipes* Chen and Xu, 1991, *nomen preoccupatum*)

*H. tuberculata* Haswell, 1880

*Permanotus* Chia and Ng, 1998

*P. purpureus* (Gordon, 1934) (= *Harrovia bituberculata* Shen, Dai and Chen, 1982)

*Rhabdonotus* A. Milne Edwards, 1879

*R. pictus* A. Milne Edwards, 1879 (= *Caphyra archeri* Walker, 1887)

*R. pilipes* Chia and Ng, 1995

*R. xynon* Chia and Ng, 1995

*Tauropus* Chia and Ng, 1998

*T. egeriae* (Gordon, 1947)

*Tiaramedon* Chia and Ng, 1998

*T. spinosum* (Miers, 1879)

*Zebrida* White, 1847

*Z. adamsii* White, 1847 (= *Zebrida paucidentata* Flipse, 1930)

*Z. longispina* Haswell, 1880

*Z. brevicarinata* Ng and Chia, 1999

*Zebridonus* Chia, Ng and Castro, 1995

*Z. mirabilis* Chia, Ng and Castro, 1995

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used for the male first and second pleopods, respectively.

### Materials Examined

#### Zoeal specimens

All first stage zoea used for this present study were dissected and examined.

*Harrovia albolineata* Adams and White, 1849: Singapore, coll. D. Vandenspiegel, May 1992, ZRC 2000.91 (see Lim and Ng, 1988). Number of specimens dissected = 5.

*Rhabdonotus pictus* A. Milne Edwards, 1879: Johore Shoals, Singapore, coll. Diana Chia, 29 August 1994, 20m, from host *Cyllometra manca* (Carpenter, 1888), ZRC 1995.224 (see Chia and Ng, 1995). Number of specimens dissected = 5.

*Zebrida adamsii* White, 1847: Murote Beach, Uchiumi Bay, Shikoku Island, Japan, coll. Y. Yanagisawa, 4 August 1989, 4 m, from *Toxopneustes pileolus* (Lamarck, 1816), ZRC 1991.293 (see Mori et al. 1991). Number of specimens dissected = 5.

*Permanotus purpureus* (Gordon, 1934): Padoz Tinan Reef, Madang, Singapore, coll. P. Castro from host *Comatella stelligera* (Carpenter, 1880) by SCUBA, 15 December 1993; hatched 17 December 1993; ZRC 2000.92. Number of specimens dissected = 7.

*Echinoecus pentagonus* (A. Milne Edwards, 1879): Kaneohe Bay, Oahu Island, Hawaiian Island, coll. P. Castro, 30 m, from host *Echinothrix calamaris* (Pallas, 1774) by SCUBA, September 1969, USNM 222684, NHM 1985.448, RMNH D-37053 (see Van Dover et al., 1986). Number of specimens dissected = 3.

*Tanaocheles bidentata* (Nobili, 1901): Sentosa Reef, Singapore, 21 November 1987, hatched 24 November 1987. ZRC 1998.794 (see Ng and Clark, 2000). Number of specimens dissected = 5.

*Pilumnus hirtellus* (Linnaeus, 1761): Falmouth Harbour, England, coll. R. Lincoln, 15 April 1975, hatched in NHM, 4-5 June 1975, NHM 1998: 600. Number of specimens dissected = 5.

*Rhinolambrus pelagicus* (Rüppell, 1830): Labrador, Singapore, coll. L. Tan, 30 December 1986; hatched 4 January 1987; ZRC 2000.90. Number of specimens dissected = 5.

*Pilumnus vespertilio* (Fabricius, 1793); sta. 4a, Ponduine, Southwest Inhaca, Mozambique, coll. P. Clark and J. Paula, 15 November 1997; hatched 16 November 1997, NHM 2000.413. Number of specimens dissected = 5.

*Pilodius pugil* Dana, 1852: Albion Rocks, Baie de la Petite Rivière, off Victory Road, Petite Rivière, Albion, ca. 20°12'5"S 57°23'5"E, Mauritius, coll. P. Clark, by SCUBA, 3-7m, 6 May 1995, hatched 20 May 1995, NHM 1998: 604 (see Ng and Clark 2000). Number of specimens dissected = 5.

*Eriphia smithii* MacLeay, 1838 Native Jetty, Manora Island, Karachi, Pakistan, coll. S.S. Hashmi, NHM 1986: 908. Number of specimens dissected = 5.

#### Adult specimens

Type species were selected as far as possible (indicated by an asterisk) to represent the genera used for the adult cladistic analysis, but, because of practical reasons, only part of the material examined has been listed. As far as possible, both sexes are included.

\**Ceratocarcinus longimanus* White, 1847: holotype ♂ (8.0 by 6.6 mm) (NHM 1939.9.20.7), Balambangan, Borneo, Sabah, Malaysia; 2 ♂♂, 2 ♀♀ (MNHN-B4601), New Caledonia, coll. 1903.

\**Echinoecus pentagonus* (A. Milne Edwards, 1879): holotype ♂ (8.5×7.9 mm) (MNHN), Mauritius, 3 ♂♂, 5 ♀♀ (ZRC 1997.154161), Hawaii, coll. P. Castro, 1970s.

\**Eumedon niger* H. Milne Edwards, 1834: holotype ♂ (10.9×10.5 mm) (MNHN-B646), China seas; 1 ♂ (11.0×11.5 mm), 1 ♀ (QM W18637), Northwest Shelf, Western Australia, sta. 05B02S, 19°56'7'S, 117°53'6'E, 41 m, epibenthic sledge, marine, sublittoral, coll. CSIRO, R.V. *Soela*, 26 October 1983.

\**Gonatonotus pentagonus* White, 1847: holotype ♀ (10.1×12.0 mm) (NHM 1847.21), eastern seas, Borneo, coll. Capt. Sir E. Belcher; 1 ♂ (12.5×15.3 mm) (NHM 78.11), Java seas, Indonesia, 3°21'S, 108°39'E, 22 m, coll. J.G. Jeffreys, no other data; 1 ♀ (ZRC 1984.7858), Sudong Island, Singapore, dredged, coll. D.S. Johnson, 16 March 1953.

\**Harrovia albolineata* Adams and White, 1849: lectotype ♂ (8.9×7.0 mm) (NHM 43.6), Philippine Islands, coll. H. Cuming, HMS *Samarang*, 1843/1846; 1 paralectotype ♀ (9.5 × 7.4 mm) (NHM 43.6), same data as lectotype; 10 ♂♂, 6 ♀♀ (ZRC 1992.9477.9492), Johore Shoals, Singapore, coll. P.K.L. Ng, 15 May 1992.

\**Permanotus purpureus* (Gordon, 1934): holotype ♂ (3.6×4.9 mm) (IRSNB IG9223), Sorong Door, western New Guinea (= Irian Jaya), Indonesia, 2 March 1929; 1 ♀ (ZRC 1997.201), Barracuda Point, Sipadan Island, East Malaysia, coll. D. Lane, 21 May 1992.

- \**Rhabdonotus pictus* A. Milne Edwards, 1879: neotype ♂ (6.4×6.9 mm) (ZRC 1984.7862), Johore Shoals, Singapore, coll. D.S. Johnson, 17 June 1953; 1 ♀ (6.8×7.4 mm) (ZRC 1984.7863), same data as neotype.
- \**Tauropus egeriae* (Gordon, 1947): holotype ♀ (11.2×16.6 mm) (NHM 93.11.3.79), Macclesfield Bank, 82m, coll. Bassett Smith, HMS *Egeria*.
- \**Tiaramedon spinosum* (Miers, 1879): holotype juv. (3.6×4.0 mm) (NHM 62.53), Australia sea, coll. HMS *Herald*; 1 ♂ (ZRC 1997.203), Reef crest, Padoz Tinan Reef, Madang, Papua New Guinea, 5°09'53'S, 145°48'88'E, on *Clarkcomanthus littoralis*, coll. P. Castro, 16 December 1993; 1 ♀ (ZRC 1997.204), Reef crest, Padoz Tinan Reef, Madang, Papua New Guinea, 5°09'53'S, 145°48'88'E, on *Comanthus suavia*, coll. P. Castro, 18 December 1993.
- \**Zebrida adamsii* White, 1847: holotype ♀ (14.2×12.5 mm) (NHM 1939.9.20.6), Borneo, coll. Capt. Sir E. Belcher; 1 ♂ (NHM 1907.5.22.193), Gulf of Manaar, coll. Herdman, no other data; 1 ♂, 2 ♀♀ (ZRC 1997.209311), Sri Lanka coll. H. Müller, 1990s.
- \**Zebridonus mirabilis* Chia, Ng and Castro, 1995: holotype ♂ (6.8×7.4 mm) (QM W17404), Gulf of Carpentaria, Queensland, Australia, coll. FRV *Southern Surveyor*, 45 m, 29 November 1990.
- \**Hapalonotus reticulatus* (De Man, 1879): holotype ♀ (20×24 mm) (RMNH 319), Amboina, Indonesia, coll. D.S. Hoedt, 1864; 1 ♂ (16.1×19.3 mm), 1 ♀ (20.5×24.7 mm) (ZRC 1997.170171), Hansa Bay, seagrass beds off Awar Plantation, 4°08'27'S, 144°51'22'E, 10 m, in the respiratory of a holothurian, coll. C. Massin, 13 October 1989.
- \**Pilumnus hirtellus* (Linnaeus, 1761): 2 ♂♂ (largest 13.0×9.1 mm), 1 ovig. ♀ (12.2×8.5 mm) (ZRC), Iles Chausey, Atlantic coast, France, coll. A. Crosnier et al., 29 August 1992.
- \**Rhizopa gracilipes* Stimpson, 1858: neotype ♂ (9.7×7.0 mm) (ZMUC), Sound of Koh Chang, Gulf of Thailand, 35 fms depth, leg. Th. Mortensen, between 24 December 1899 and 6 January 1900; 1 ♂, 1 ♀ (NHM 1930.3.29.45), same data as neotype.
- \**Bathypilumnus sinensis* (Gordon, 1930): 3 ♂♂ (largest 27.8×21.3 mm), 2 ♀♀ (larger 22.2×16.5 mm) (ZRC 1984.55695573), South China Sea, ca. 150 miles off Singapore, coll. H. Huat, 28 August 1983.
- \**Dentoxanthus iranicus* Stephensen, 1946: 1 ♂ (23.7×18.7 mm) (ZRC 1999.1104), Pakistan, from fish port, coll. N. Tirmizi, no date.
- \**Galene bispinosa* (Herbst, 1793): 3 ♂♂ (largest 59.8×43.4 mm), 1 ♀ (43.0×32.7 mm) (ZRC 1996.1918), Tuas, Singapore, coll. W.M. Lee, 4 September 1985.
- \**Halimede fragifer* De Haan, 1835: 1 ♂ (25.8×21.4 mm), 1 ovig. ♀ (27.6×22.2 mm) (ZRC 1998.477), Tashi port, Ilan County, Taiwan, coll. P.K.L. Ng, 31 March 1998.
- \**Calmania prima* Laurie, 1906: 1 ♂ (7.4×8.2 mm), 1 ♀ (7.6×7.8 mm) (ZRC 1999.63), Japan, no other data.
- \**Tanaocheles stenochilus* Kropp, 1984: holotype ♂ (6.2×4.5 mm) (USNM 210636), 1 ♀ (7.3×5.6 mm) (USNM 210637), Apra harbour, Western Shoals, Guam, Mariana Islands, on *Leptoseria gardineri*, 27 m, coll. V. Tyndzik, 23 July 1981.
- \**Daldorfia horrida* (Linnaeus, 1758): 1 ♂ (128.0×91.0 mm), 1 ♀ (113.2×86 mm) (ZRC 1999.1028), Longtong port, Ilan County, Taiwan, coll. S.H. Wu and P.K.L. Ng, May 1999.
- \**Rhinolambrus longimanus* (Linnaeus, 1764): 3 ♂♂ (largest 34.7×30.6 mm), 6 ♀♀ (largest, ovig., 40.3×34.5 mm) (ZRC 1984.206214), Horsburg Lighthouse, South China Sea, coll. H. Huat, 26 November 1982.
- \**Cryptopodia fornicata* (Fabricius, 1781): 1 ♂ (51.5×31.5 mm), 1 ♀ (45.0×29.0 mm) (ZRC 1965.511134), off Singapore, leg. N.S. Shark, October 1927.
- \**Mimilambrus wileyi* Williams, 1979: holotype ♂ (26.0×24.3 mm) (USNM 172222), ManofWar Bay, Tobago Island, West Indies, coll. M.L. Wiley et al., 14 April 1978; 1 ♀ (35.0×29.8 mm) (ZRC 1987.510), Venezuela, coll. G. Kremmer and M. Bevilacava, 4 March 1984.
- \**Carpilius maculatus* (Linnaeus, 1758): 1 ♂ (85.4×62.7 mm) (ZRC 1965.11.9.2), Pulau Pisang, Malacca Straits, coll. January 1934; 1 ♀ ovig. (87.0×63.0 mm) (ZRC 1999.209), Pichai fish port, Andaman Sea, coll. S. Chaitiamvong, December 1998.
- \**Myomenippe hardwickii* (Gray, 1831): 1 ♂ (87.5×61.4 mm) (ZRC 1999.225), near Sentosa Island, Singapore, coll. C.M. Yang, 2 December 1985; 3 ♀♀ (largest 75.4×52.4 mm) (ZRC 1999.336), Pulau Seringat, Singapore, coll. S. H. Tan et al., 24 July 1997.
- \**Pilodius pubescens* (Dana, 1852): 1 ♂ (11.5×7.6 mm) (ZRC 1965.11.11.136), Northwest Island, Capricorn Group, Queensland, Australia, coll. M. Ward, July 1929.
- \**Eriphia verrucosa* (Forskål, 1775): 1 ♂ (32.5×44.2 mm), 1 ♀ (18.1×27.1 mm) (NHM 1974.504), El Haauciria, shore collection, Project Mermaid, Tunisia, coll. P. Clark, 31 August 1974; 1 ♂ (20.9×29.9 mm), 1 ♀ (35.0×50.3 mm) (RMNH 11511), Havenvan, Barcelona, Spain, ca. 0.1 m, coll. Kademuur, 19–22 September 1957.

## Methods

### Examination of specimens

#### Zoea

The present study did not use any existing eumedonid larvae descriptions. All first-stage zoeal material used was dissected and examined in order to ensure that comparisons and analyses were completely accurate. The first-stage zoeas were not stained. Appendages were dissected under a Wild M5 binocular microscope with a  $\times 2$  supplementary lens and mounted in polyvinyl lactophenol. Cover slips were sealed with clear nail varnish and the appendages were drawn using an Olympus BH-2 microscope equipped with Nomarski interference contrast and attached *camera lucida*. The long plumose natatory setae of the first and second maxilliped and the antennular aesthetascs are drawn truncated. The sequence of the zoeal description (see Clark et al., 1998) is based on the malacostracan somite plan and described from anterior to posterior. Setal armature on appendages is described from proximal to distal segments and in order of endopod to exopod.

#### Adults

Museum specimens preserved in alcohol were borrowed from a number of institutes. Terminology follows Ng (1998).

### Phylogenetics

The software package PAUP (version 3.1.1; Swofford, 1993) was used to analyze first-stage zoeal and adult data. *Eriphia smithii* and *Myomenippe hardwickii* were assumed to be the outgroup for the adult data sets and only *E. smithii* for the zoea. The plesiomorphic character state was coded by 0.

Members of the family Eriphiidae are generally considered to be among the most ancient of the xanthoid lines and, together with the Carpiliidae, contain the most ancient known fossil species (see Glaessner, 1969). Studies on their morphology have also shown that these two families are the most plesiomorphic in the Xanthoidea (Guinot, 1977, 1978). These plesiomorphic characters include the form of the carapace (transversely hexagonal), transversely folding antennules, broad and subquadrate basal antennal segment, presence of prominent endostomial ridges, male abdomen (relatively broad and all segments freely movable), simple male first pleopod (tubular, almost straight and not ornamented with long spines or complex setae) and elongate male second pleopod (subequal in length or longer than first pleopod).

### Zoeal characters

A data matrix (see Appendix 1) was prepared for phylogenetic analysis, being comprised of 12 characters and 11 taxa. These taxa included the first stage zoeas of five eumedonids (*Harrovia albolineata*, *Rhabdonotus pictus*, *Zebrida adamsii*, *Permanotus purpureus* and *Echinoecus pentagonus*); three pilumnids (*Pilumnus hirtellus*, *Pilumnus vespertilio* and *Tanaocheles bidentata*); a xanthid (*Pilodius pugil*); one parthenopid (*Rhinolambrus pelagicus*) and the eriphiid *Eriphia smithii*. A description of the zoeal characters used for the analysis is listed in Appendix 3.

### Adult characters

A cladistic analysis of the 12 “eumedonid” genera as well as eight genera of Pilumnidae, four genera of Parthenopidae, one genus of Carpiliidae and two genera of Eriphiidae was conducted using 57 adult characters. One species of Eriphiidae, *Myomenippe hardwickii*, was identified as the outgroup. See Appendix 2 for the data matrix and Appendix 4 for the description of adult characters.

### Zoeal analysis

PAUP with the branch and bound search settings was used to analyze the zoeal data set. Characters 2, 10–12, were unordered and characters 1, 3–9 were polarized irreversible up.

### Adult analysis

PAUP with the heuristic search settings was used to analyze the adult data set and all characters were unordered.

## Results

### Zoea I descriptions

*Rhinolambrus pelagicus* (Rüppell, 1830) (Figs. 1a–d, 2a–c, 3a,b, 4a,b).

Carapace (Fig. 1a): dorsal spine long, curved and smooth, nearly twice as long as rostral spine; rostral spine much shorter than dorsal spine, fractionally longer than protopod of antenna and smooth; lateral spines relatively long, smooth and straight; 1 pair of posterodorsal setae; ventral margin without setae; eyes sessile.

Antennule (Fig. 1a, b): uniramous, endopod absent; exopod unsegmented with 2 broad and 1 slender terminal aesthetascs plus 1 terminal setae.

Antenna (Fig. 1a, c, d): protopodal process spinulate, fractionally shorter in length to rostral spine;

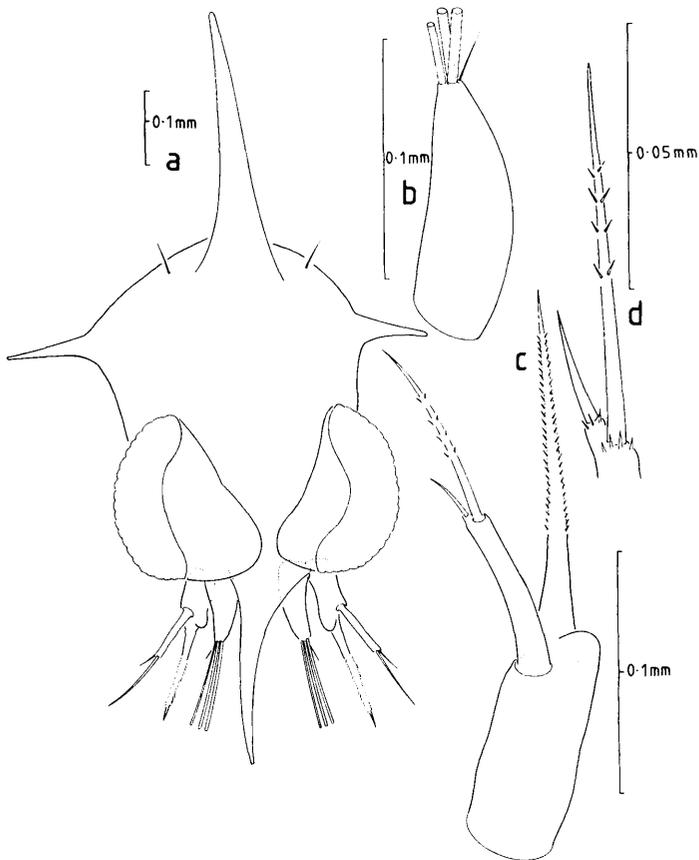


Fig. 1. *Rhinolambrus pelagicus* (Rüppell, 1830): first stage zoea, a. anterior view of carapace, b. antennule, c. antenna, d. antennary exopod setation.

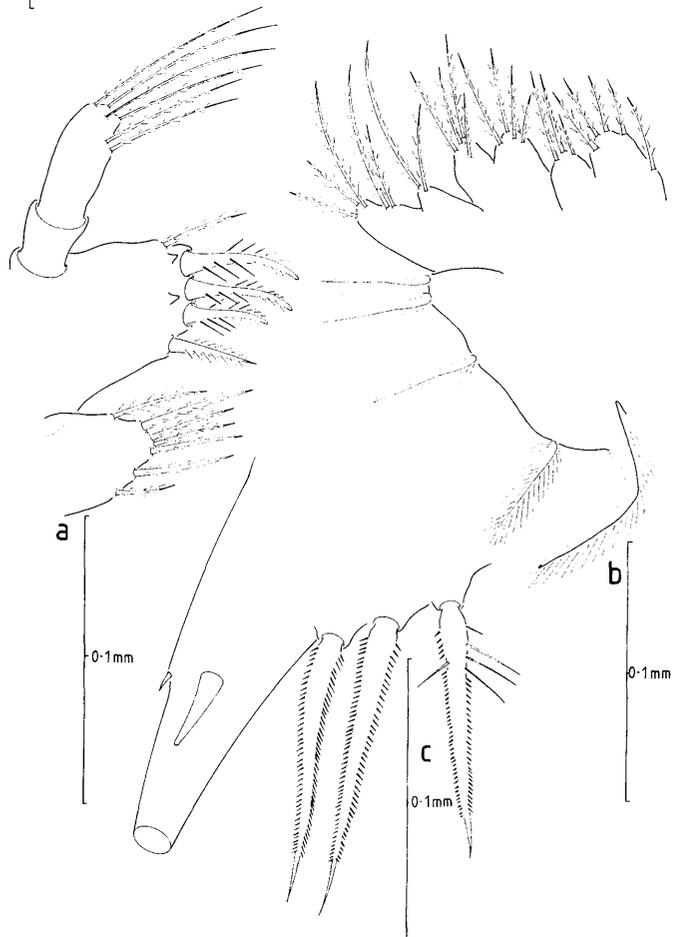


Fig. 2. *Rhinolambrus pelagicus* (Rüppell, 1830): first stage zoea, a. maxillule, b. maxilla, c. telson.

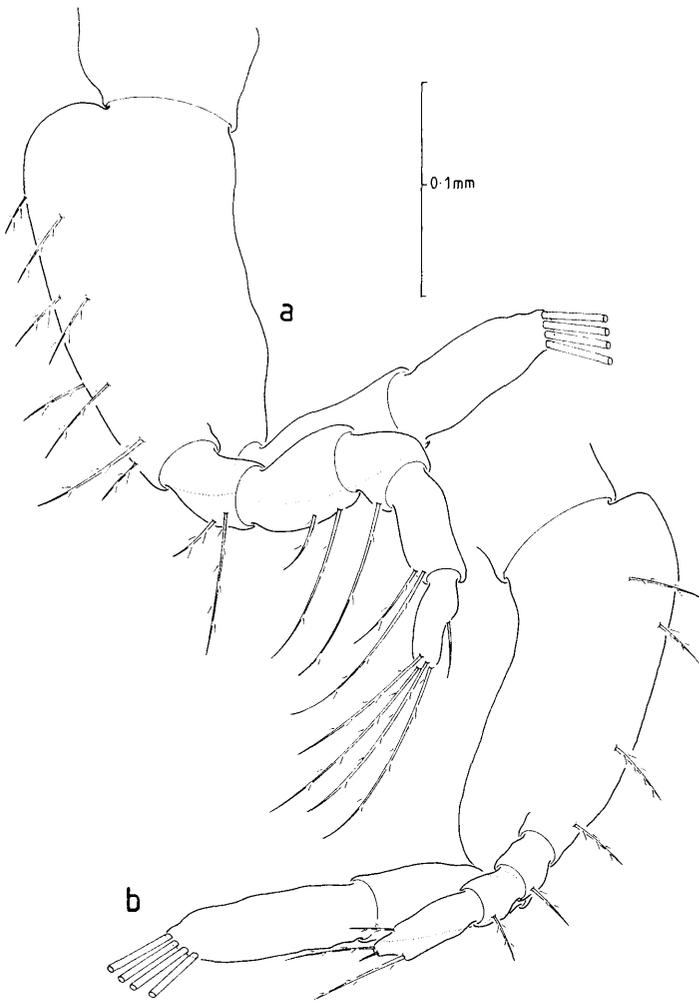


Fig. 3. *Rhinolambrus pelagicus* (Rüppell, 1830): first stage zoea, a. first maxilliped, b. second maxilliped.

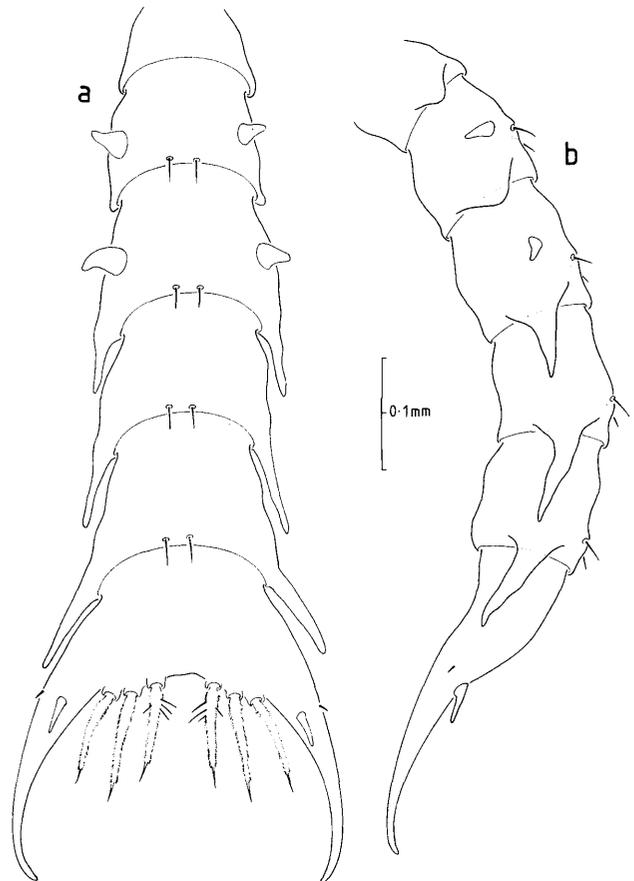


Fig. 4. *Rhinolambrus pelagicus* (Rüppell, 1830): first stage zoea, abdomen, a. dorsal view, b. lateral view.

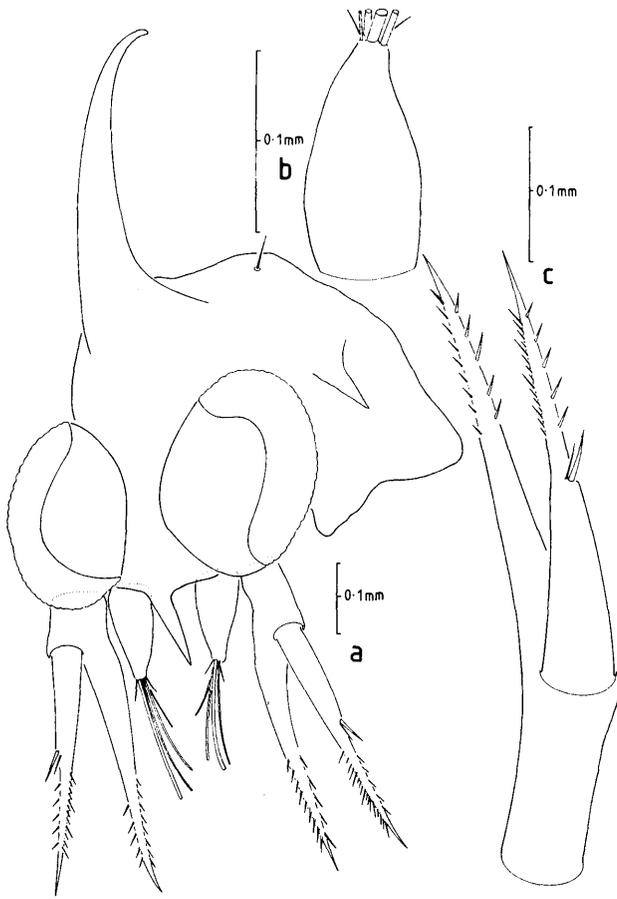


Fig. 5. *Permanotus purpureus* (Gordon, 1934): first stage zoea, a. anterior view of carapace, b. antennule, c. antenna.

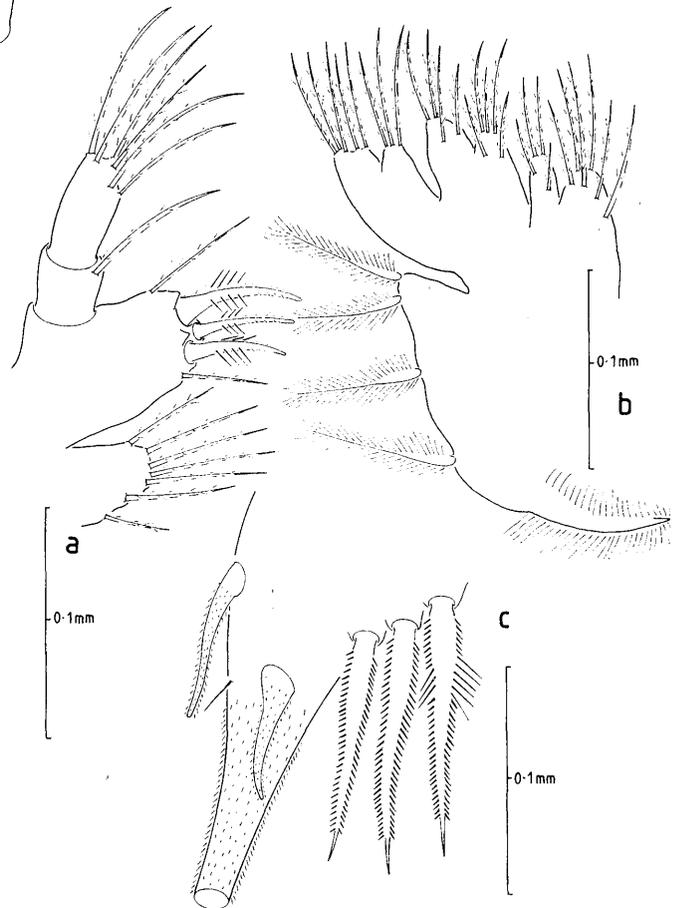


Fig. 6. *Permanotus purpureus* (Gordon, 1934): first stage zoea, a. maxillule, b. maxilla, c. telson.

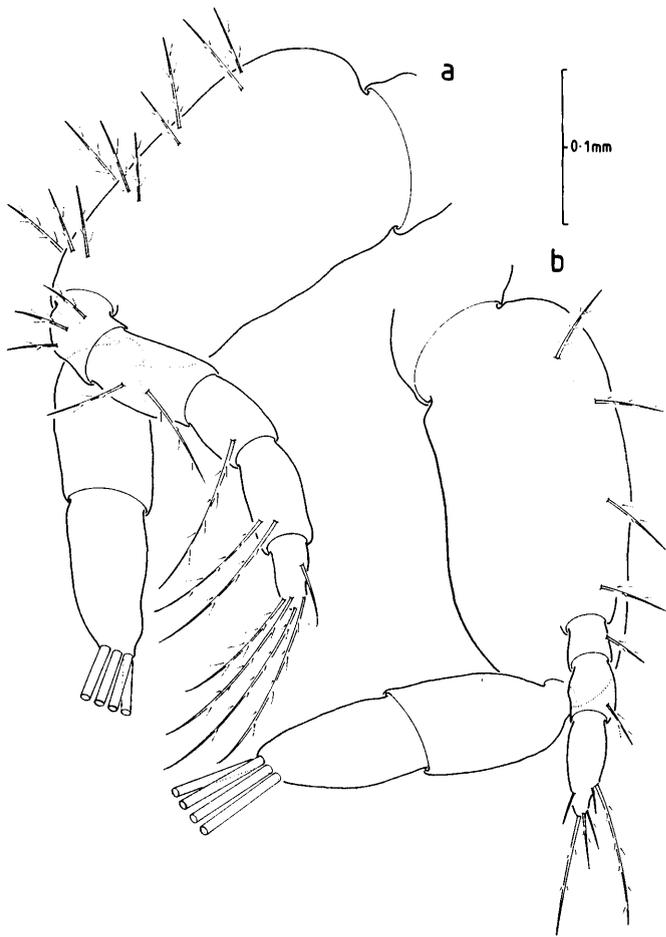


Fig. 7. *Permanotus purpureus* (Gordon, 1934): first stage zoea, a. first maxilliped, b. second maxilliped.

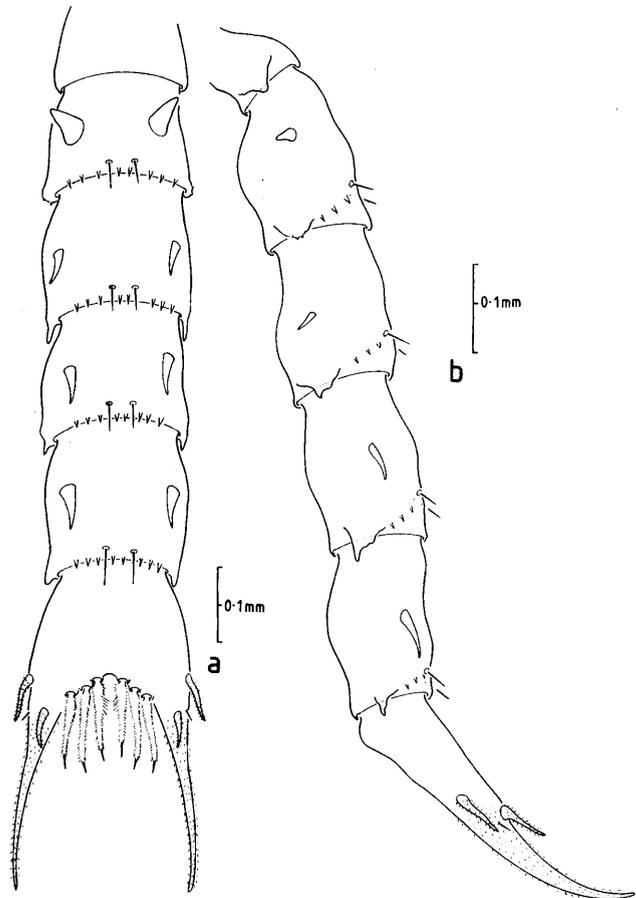


Fig. 8. *Permanotus purpureus* (Gordon, 1934): first stage zoea, abdomen, a. dorsal view, b. lateral view.

endopod bud present; exopod approximately have the length of the protopod, unsegmented with 2 unequal terminal setae each with basal spines.

Mandible: endopod palp absent.

Maxillule (Fig. 2a): coxal endite with 7 setae; basal endite with 5 setal processes and 2 small teeth; endopod 2-segmented, proximal segment without setae; distal segment with 6 (2 subterminal, 4 terminal) setae; exopod seta absent.

Maxilla (Fig. 2b): coxal endite bilobed with 5+3 setae; basal endite bilobed with 4+4 setae; endopod bilobed, with 2+5 (2 subterminal and 3 terminal) setae; exopod (scaphognathite) margin with 4 setae and 1 long distal stout process.

First maxilliped (Fig. 3a): coxa without setae; basis with 8 setae arranged 2,2,2,2; endopod 5-segmented with 2,2,1,2,5 (1 subterminal and 4 terminal) setae respectively; exopod 2-segmented, distal segment with four long terminal plumose natatory setae.

Second maxilliped (Fig. 3b): coxa without setae; basis with 4 setae; endopod three-segmented, with 1,1,4 (2 subterminal and 2 terminal) setae, respectively; exopod 2-segmented, distal segment with four long terminal plumose natatory setae.

Third maxilliped: absent.

Pereiopods: absent.

Abdomen (Fig. 4a, b): 5 somites; somite 2 with 1 pair of dorsolateral processes directed anteriorly; somite 3 with 1 pair of dorsolateral processes directed ventrally; somites 1–2 with rounded posterolateral processes and 3–5 with extended posterolateral spinous processes; somite 1 without setae; somites 2–5 with 1 pair of posterodorsal setae; pleopod buds absent.

Telson (Figs. 2c, 4a, b): each fork long, not spinulate, gradually curved distally; 1 minute lateral spine; 1 large dorsal medial spine; posterior margin with 3 pairs of stout spinulate setae.

*Permanotus purpureus* (Gordon, 1934) (Figs. 5a–c, 6a–c, 7a,b, 8a,b)

Carapace (Fig. 5a): dorsal spine smooth, curved distally, approximately six times as long as rostral spine; rostral spine smooth, much shorter than dorsal and antennal protopod; lateral spines short and unarmed; 1 pair of posterodorsal setae; ventral margin without setae, eyes sessile.

Antennule (Fig. 5a, b): uniramous, endopod absent; exopod unsegmented with 4 terminal aesthetascs, (1 broad and long, 2 shorter and slender, 1 thin) plus 2 terminal setae of unequal length.

Antenna (Fig. 5a, c): protopod distally spinulate, longer in length than rostral spine but approximately

equal in length to exopod; endopod absent; exopod approximately equal in length to protopod, unsegmented, distally spinulate with 1 long and 1 smaller medial setae unequal in length.

Mandible: endopod palp absent.

Maxillule (Fig. 6a): coxal endite with 7 setae; basal endite with 5 terminal setal processes and 2 small teeth; endopod 2-segmented, proximal segment with 1 seta; distal segment with 6 (2 subterminal + 4 terminal) setae; exopod seta absent.

Maxilla (Fig. 6b): coxal endite bilobed with 6+4 setae; basal endite bilobed with 5+4 setae; endopod bilobed with 3+5 (2 subterminal + 3 terminal) setae; exopod (scaphognathite) margin with 4 setae and 1 long distal stout process.

First maxilliped (Fig. 7a): coxa without setae; basis with 10 setae arranged 2,2,3,3; endopod 5-segmented with 3,2,1,2,5 (1 subterminal and 4 terminal) setae respectively; exopod 2-segmented, distal segment with 4 long terminal plumose natatory setae.

Second maxilliped (Fig. 7b): coxa without setae; basis with 4 setae; endopod 3-segmented, with 1,1,6 (3 subterminal and 3 terminal) setae respectively; exopod 2-segmented, distal segment with 4 long terminal plumose natatory setae.

Third maxilliped: absent.

Pereiopods: absent.

Abdomen (Fig. 8a, b): 5 somites; somite 2 with a pair of dorsolateral processes directed anteriorly; somites 3–5 with a pair of dorsolateral processes directed ventrally; somites 1–2 with rounded posterolateral processes and 3–5 with short posterolateral spinous processes; somite 1 without dorsal setae; somites 2–5 with 1 pair of posterodorsal setae; posterior margin of somites 2–4 spinulate; pleopod buds absent.

Telson (Figs. 6c, 8a, b): each telson fork long, spinulate and gradually curved distally; 1 long and 1 small lateral spine; dorsal medial spine present; posterior margin with 3 pairs of stout spinulate setae.

### **Phylogenetic analysis**

#### *Zoal tree description*

The zoal analysis produced one tree (see Fig. 9) which had a consistency index = 0.700, tree length = 20, homoplasy index = 0.300, retention index = 0.829, a rescaled consistency index = 0.580, *f* value 58 and the *f*-ratio was 0.1883.

#### *Adult tree description*

The adult analysis produced two trees, both had a consistency index = 0.420, tree length = 162,

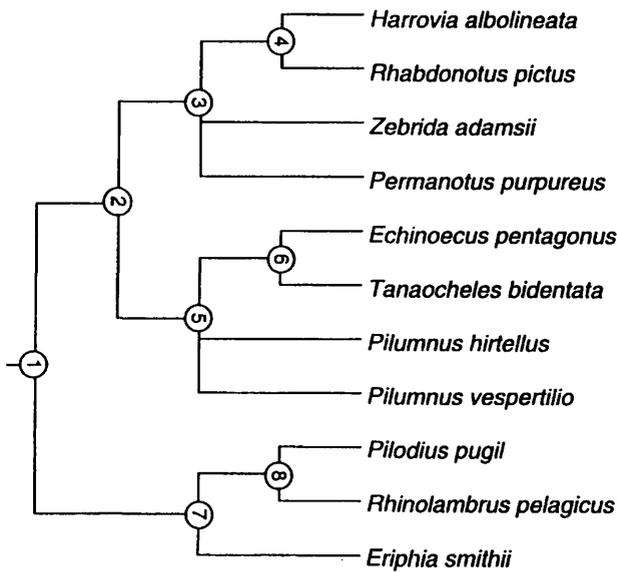


Fig. 9. Cladogram of first-stage zoeal analysis.

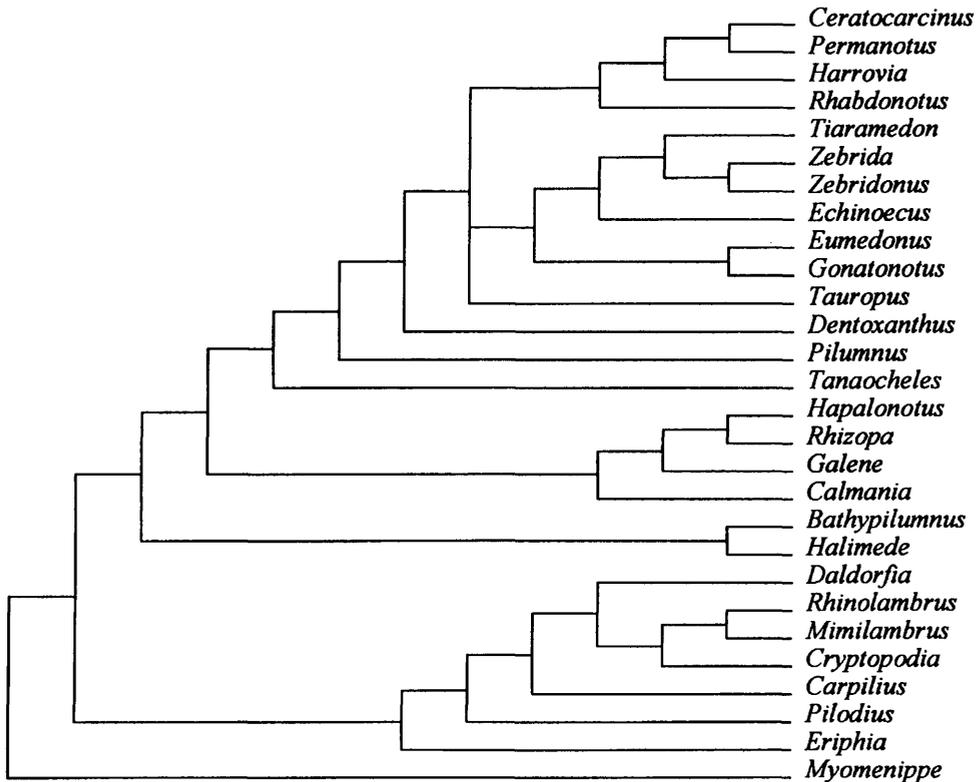


Fig. 10. Cladogram of adult analysis.

homoplasy index = 0.580, retention index = 0.618, rescaled consistency index = 0.259, *f*-value = 2156 and the *f*-ratio 0.5180. The analysis produced two trees which differ only in position of *Tauropus*. In the first tree, *Tauropus* forms the sister group to the clade containing *Ceratocarcinus*, *Permanotus*, *Harrovia*,

*Rhabdonotus*, *Tiaramedon*, *Zebrida*, *Zebridonus*, *Echinoecus*, *Eumedonius*, *Gonatonotus*. In the second tree, *Tauropus* forms an unresolved polytomy with the afore-mentioned clade. From these two trees a strict consensus tree (see Fig. 10) was calculated. The strict consensus tree had a consistency index = 0.420, tree

length = 162, homoplasy index = 0.580, retention index = 0.618, rescaled consistency index = 0.259, *f* value = 2156 and the *f*-ratio 0.5180.

## Discussion

### *Parthenopidae*

#### *Parthenopid zoeas*

Knowledge of parthenopid larvae is considered to be poor (Rice, 1980) and currently, zoeas for only *Platylambrus serrata* (by Yang, 1971), *Parthenope massena* and *Heterocrypta maltzami* (both by Thiriot, 1973), and *Platylambrus validus* (by Kurata and Matsuda, 1980; Terada, 1985b) are described. The first stage zoea of *Rhinolambrus pelagicus* is reported here for the first time. Table 2 compares the first-stage zoea morphology of *Permanotus purpureus*, as a representative of the eumedonids and the parthenopid *Rhinolambrus pelagicus*. There are 13 character incongruences listed between these two taxa which confirm that the eumedonids should not be assigned to the Parthenopidae, as previously suggested by Van Dover et al. (1986) and Števc̆ić et al. (1988).

#### *Parthenopid adults*

The systematics of the Parthenopidae MacLeay, 1838 is confused, and this has effected the position of the eumedonids. Initially the parthenopids were regarded as a subfamily of the Majidae. But the family status of the parthenopids has not been in question in the modern era, and Števc̆ić and Gore (1981) have recently reviewed this taxon. Miers (1879a) divided the family into two subfamilies, Parthenopinae and Eumedoninae, a system followed by most workers including Flipse (1930) and Balss (1957). Guinot (1978) had argued that the Parthenopidae, as she redefined it, did not include the Eumedoninae, and four unnamed groups could be discerned. Ng and Rodriguez (1986) also stated that eumedonines were not parthenopids, and considered that the four groups of Guinot (1977, 1978) had merit and formally named them. Ng et al. (2001) recognized three Indo-West Pacific subfamilies of Parthenopidae for convenience, viz., Parthenopinae, Cryptopodiinae and Daldorfiinae, and they too excluded the eumedonids from the family (see also Guinot and Bouchard, 1998). The Parthenopidae can be defined as follows: carapace triangular to almost round; surfaces often heavily tuberculated or eroded; front and frontal region narrow to very narrow. Chelipeds often very long; merus and chela often prismatic in cross section. Male abdominal segments

3–5 always immovable, sometimes completely fused, although sutures may be weak to distinct. G1 stout to very stout, relatively simple, without complex folds, sometimes with strong spines and G2 of varying lengths.

### *Pilumnidae*

#### *Pilumnid zoeas*

The understanding of the Pilumnidae has progressed beyond traditional adult morphological features; zoeal characters are being used to provide important familial information concerning xanthoid systematics (see Ng and Clark, 2000). Pilumnid larval characters were reviewed by Rice (1980) and Martin (1984), and both considered antennal morphology as diagnostic with the exopod possessing two medial unequal setae. Recently Ng and Clark (2000, Table 6) suggested additional characters that, used in combination with the antennal exopod setation, could also be used to define the pilumnids. These included antennule setation and spinulation of telson. This present study suggests another pilumnid character, the presence of spinules on the posterior margin of abdominal somites two to five. Illustrations of this character by Ng and Clark (2000) of *Pilumnus hirtellus* (see their Fig. 23) and *Tanaocheles bidentata* (see their Fig. 27) are inaccurate with regard to the somite spinulation. Re-examination of the abdominal somites showed the spinulation on the posterior margin of somite 2 for *P. hirtellus* to be present and that spinulation is also present on somites 2–5 in *T. bidentata*.

Pilumnid zoea characters are remarkably conservative and can be used to discuss the pilumnid affinities of some species such as *Tanaocheles bidentata* (see Ng and Clark, 2000). In this study the larval features vindicated the adult hypotheses based on gonopodal and male abdominal characters that *T. bidentata* was a pilumnid and, not as previously suggested, a xanthid. The larval description of *Echinoecus pentagonus* (A. Milne Edwards, 1879) by Van Dover et al. (1986) is excellent. The two unequal setae are subterminally present on the exopod of antenna (Van Dover et al., 1986, Figs. 1–3C), and this is of the pilumnid type as discussed by Rice (1980) and Martin (1984). According to Ng and Clark (2000), other pilumnid characters include the antennule setation and a spinulated telson fork. These characters are illustrated by Van Dover et al. (1986, Figs. 1B, 1I, respectively) for *E. pentagonus*. They also describe minute dentition along the posterodorsal margin of

Table 2. Comparison between the characters of first-stage zoeae of *Permanotus purpureus* (Gordon, 1934) [eumedonid] and those of a typical parthenopid *Rhinolambrus pelagicus* (Rüppell, 1830), as described in this present study

Characters	<i>Permanotus purpureus</i>	<i>Rhinolambrus pelagicus</i>
ANTENNULE		
Number of terminal aesthetascs and setae	4 + 2, respectively	3 + 1, respectively
ANTENNA		
2 setae on exopod	Subterminal	Terminal
MAXILLULE		
Seta on proximal endopod segment	Present	Absent
MAXILLA		
Setation of coxal endite	6 + 4	5 + 3
Setation of basial endite	5 + 4	4 + 4
Setation of endopod	3 + 5	2 + 5
FIRST MAXILLIPED		
Setae on basis	10 arranged 2,2,3,3	8 arranged 2,2,2,2
Setae on 1st endopod segment	3	2
SECOND MAXILLIPED		
Setae on distal endopod segment	6 (3 subterminal and 3 terminal)	4 (2 subterminal and 2 terminal)
ABDOMEN		
Spinulation of posterior somites (2–5) margin	Present	Absent
lateral processes on somites 4 and 5	Present	Absent
TELSON		
Fork	Spinulate	Not spinulate
Number of lateral spines	2	1

abdominal somites 3–5, and this margin is illustrated for the fifth somite (Van Dover et al., 1986, Fig. 11). On further examination of *E. pentagonus* material this study found spinulation of the posterodorsal margin of abdominal somite 2. The spinulation of the posterodorsal margin of somites 2–5 can be considered as diagnostic of pilumnids.

#### *Pilumnid adults*

The family Pilumnidae was established by Samouelle (1819) for the genus *Pilumnus* and its allies. Although it was long regarded as a subfamily of the Xanthidae MacLeay, 1838 *s. lato* (see Balss, 1933a, 1957), recent work has indicated that it is sufficiently distinct to warrant recognition as a family separate from the Xanthidae *s. str.* (Guinot, 1977, 1978). Guinot (1969, 1971, 1978) also suggested that the subfamily Rhizopinae Stimpson, 1858, normally placed in the Goneplacidae, had what she called “pilumnien” lineage. She also implied that genera like *Halimede*, *Galene* and *Parapanope* (in her “Rameau Halimédien”) were closely affiliated to the true pilumnids but did not formally transfer them to the Pilumnidae (see also Guinot, 1969, 1971, 1985b). In a list, Guinot (1985a) did not include the eumedonids in the Pilumnidae but instead she afforded them superfamilial status.

However, Ng (1983) had different ideas and provisionally recognized nine Pilumnidae groups — *Pilumnus*, *Rhizopa*, *Parapanope*, *Calmania*, *Galene*, *Halimede*, *Bathypilumnus*, and *Dentoxanthus* — but included *Eumedonus*. Ng and Rodriguez (1986) and Števčić and Ng (1988) suggested that eumedonids are pilumnids based on adult characters but did not indicate the systematic rank or their position within the Pilumnidae. Lim and Ng (1988) regarded eumedonids as a subfamily of the Pilumnidae.

The definition of the presently recognized Pilumnidae has changed drastically since Samouelle (1819). The idea that members of the family share the basic “*Pilumnus*” form (that of a “xanthoid” crab with a very setose carapace and appendages, and well developed, but not complete, endostomial ridges) is obsolete. The diagnostic characters of the G1 (very slender and sinuous, with the distal part simple, without folds, long setae or long spines) and G2 (very short and sigmoidal), first used by Balss (1933a), has proven to be invaluable in distinguishing the Pilumnidae. Gordon (1931), Guinot (1969, 1978), Griffin (1970) and Ng and Tan (1984) have also shown that pilumnids can also have very slender but straight G1s (as in *Halimede*, *Galene* and *Bathypilumnus*) instead. The fact that all the male abdominal segments are movable and never fused at any stage of their life is

also a key character (see also Ng, 1998; Ng and Tan, 1984; Ng and Davie, 1991; Davie, 1988, 1989a, 1989b; Takeda and Ng, 1997). According to Ng (1998), pilumnid affinities can be discerned when the above mentioned characters are used as a suite.

In summary, the Pilumnidae, as redefined here and excluding the eumedonids for the time being, can be defined as follows: carapace of varying shapes but typically with “xanthoid” form. Third maxillipeds quadrate to subquadrate; endostomial ridges usually well developed. Male and female abdomens with all somites being freely movable, never fused to any degree. Male gonopores coxal to coxosternal. G1 very slender, simple, straight to sinuous, without prominent folds, strong spines or other complex structures; G2 very short, sigmoidal, distal segment very short, forming distinct cup-like structure.

The current study would suggest that there are no obvious adult characters that distinguish the eumedonids from the Pilumnidae as currently understood. In the general form, the eumedonid epistome, mouthparts, anterior thoracic sternum, pereopods, male abdomen and gonopods are indistinguishable from those of typical pilumnids. The only character which distinguishes eumedonids from typical pilumnids is the special dactylopropodal process on the ambulatory legs of the eumedonids (see Števc̆ić et al., 1988; Ng, 1998). The value of this character at the familial level, however, is suspect. Ng and Clark (2000) transferred *Tanaocheles stenochilus* Kropp, 1984 (originally classified in the Trapeziidae) and *T. bidentata* (Nobili, 1901) (originally classified in the Xanthidae *s. str.*), which have the special dactylopropodal process, into a new subfamily within the Pilumnidae. In any case the value of this character in a natural classification is doubtful as it is probably associated with the group’s symbiotic habits. In fact, many other unrelated symbiotic crabs in the Trapeziidae and Domeciinae (Xanthidae) as well as the free-living Etisinae (Xanthidae) also possess such structures (see Serène, 1984). The presence of a special dactylopropodal process on the ambulatory legs is thus, at best, a subfamilial character.

### Phylogenetic analysis

#### Zoeal analysis

Števc̆ić et al. (1988) commented that the similarities between *Echinoecus pentagonus* and *Pilumnus dasypodus* posed some interesting and vexing questions. They considered that if larval characters

were conservative, as was traditionally held, then the xanthid features of *Echinoecus* suggested that this genus is non-parthenopid. But, they continued, until larvae of other eumedonid genera became known, it was not certain whether these characters could be a consequence of convergent evolutionary trends and/or whether the eumedonine and the pilumnid crabs shared a common ancestor. Števc̆ić et al. (1988) considered that, because there was no agreement as to which larval features are plesiomorphic or apomorphic, this part of the systematic discussion could go no further.

This present study scored the plesiomorphic and apomorphic conditions for 12 character states (see Appendix 1) from 11 taxa in order to help resolve eumedonid systematics and the phylogenetic analysis produced a tree which is illustrated in Fig. 9.

As suggested by Van Dover et al. (1986), Števc̆ić et al. (1988) and Table 2 of this study, *E. pentagonus* is not related to the parthenopids which are represented in this data set by *Rhinolambrus pelagicus*. This is supported by the zoeal cladogram (see Fig. 9) which has a basal dichotomy separating *Eriphia smithii*, *Rhinolambrus pelagicus* and *Pilodius pugil* (node 1–7) from the three pilumnids and five eumedonids (node 1–2). Three apomorphies appear to define the lineage (node 1–7); the loss of a terminal seta on the antennule, the absence of somite spinulation on the posterodorsal margin of somites 2–5 and the absence of spinulation on the telson forks.

Using zoeal characters, the recent establishment of the eumedonids as a separate family is now challenged. From the larval cladogram (Fig. 9), the three pilumnids and five eumedonids appear to form a monophyletic group defined by lineage node 1–2 and apomorphic character 4, the presence of subterminal setae on the antennary exopod. The three pilumnids and five eumedonids all possess the pilumnid type of antenna as defined by Rice (1980), Martin (1984) and Ng and Clark (2000). There are two sister groups in the pilumnid taxon; one group is comprised of *Harrovia albolineata*, *Rhabdonotus pictus*, *Zebrida adamsii*, and *Permanotus purpureus* and the other *Echinoecus pentagonus*, *Tanaocheles bidentata*, *Pilumnus hirtellus* and *Pilumnus vespertilo*. The first group is defined by the branch node 2–3 and character 1, the length of the rostral spine being approximately equal to the midpoint of the antennal protopod. The second group is defined by the branch node 2–5 and characters 8 and 9, the loss of lateral processes on abdominal somites 4 and 5, respectively. This second monophyletic group is worth further comment. Recently Ng and Clark (2000) removed *Tanaocheles bidentata* from the xanthid

subfamily Chlorodiinae as represented by *Pilodius pugil*, and assigned it to the Pilumnidae. The zoeal cladogram (Fig. 9) supports their study. Moreover, the cautious suggestion by Van Dover et al. (1986), that *Echinoecus pentagonus* may not be a typical representative of the “eumedonids” that made them hesitant with regard to the systematic position of this taxon, appears to be supported by this present study. The inclusion of *E. pentagonus* with *H. albolineata*, *R. pictus*, *Z. adamsii* and *P. purpureus* would make the “eumedonids” a paraphyletic group. However, the inclusion of *E. pentagonus* in the second group may suggest a convergent colonization of echinoderm habitats.

Števc̆ić et al. (1988) posed the interesting question as to whether the eumedonid genera and the pilumnid crabs shared a common ancestor. The zoeal analysis of this study indicates that eumedonids, represented by *H. albolineata*, *R. pictus*, *Z. adamsii* and *P. purpureus*, and the pilumnids (*Pilumnus hirtellus* and *Pilumnus vespertilo*) had a common ancestor. Therefore, the zoeal analysis supports the view that the eumedonids as represented by *H. albolineata*, *R. pictus*, *Z. adamsii* and *P. purpureus* are a subfamily of the Pilumnidae within the Xanthoidea.

#### Adult analysis

This analysis shows that all the eumedonid genera cluster within the Pilumnidae. It also suggests that the “eumedonids” are not monophyletic, and that the genus *Hapalonotus* is not closely affiliated with the other eumedonids. A similar cladistic analysis of the first zoeas of known eumedonids, as well as pilumnid and parthenopid larvae for which fresh material was available, was also performed (Fig. 10). This analysis basically supports the adult cladogram, with the eumedonid zoeal characters clustering with the pilumnids and the parthenopids belonging to a separate clade.

As noted earlier, the validity of the two subfamilies of Eumedonidae recognized by Števc̆ić et al. (1988), Eumedoninae and Ceratocarcininae, were questioned by Chia and Ng (1995) with regard to the genus *Rhabdonotus*. In addition, two other recently established genera, *Permanotus* and *Tauropus*, have a suite of features which is intermediate between the two subfamilies (Chia and Ng, 1998). *Permanotus* has a similar carapace form to that of *Gonatonotus* (supposedly belonging to the Eumedoninae), but in all other aspects it is closer to *Ceratocarcinus* and *Harrovia* (supposedly belonging to the Cerato-

carcininae). As for *Tauropus*, it also has a similar cheliped and ambulatory leg form to *Gonatonotus*, but in other aspects, especially its carapace, it more closely resembles *Permanotus*, *Ceratocarcinus* and *Harrovia*. In view of these intermediate genera which bridge the supposed differences between the two subfamilies, Ceratocarcininae (Števc̆ić et al., 1988) should be synonymized with Eumedoninae *s. str.* The adult cladistic analysis (Fig. 10) supports this synonymy. In fact, the only adult morphological character which effectively splits the “Eumedonidae” into two groups seems to be the proportions of the first ambulatory leg. In one group, the first ambulatory merus and dactylus are distinctly longer than those of other legs. This group includes *Harrovia*, *Ceratocarcinus*, *Permanotus*, *Rhabdonotus* and *Tiaramedon*, all of which are crinoid symbionts. In the second group, the first ambulatory merus and dactylus are not much longer than those of other legs and includes *Eumedonus*, *Gonatonotus*, *Zebrida*, *Tauropus*, *Zebridonus* and *Hapalonotus*; of which the first three are echinoid symbionts and the last lives with holothuroids. The value of this character, however, is not certain, and the second group is probably not a monophyletic taxon.

To summarize the adult analysis, the present study fully supports the studies by Guinot (1977, 1978), Števc̆ić and Gore (1981), Ng and Rodriguez (1986) and Števc̆ić et al. (1988), which indicate that the eumedonines are not related to the Parthenopidae (Fig. 10). There are no arguments for retaining the Eumedonidae as a distinct family, other than the fact that all its members are symbionts on echinoderms. This is a purely ecological adaptation and cannot be used as a systematic character. As such, it is more logical to subjugate the group under the family Pilumnidae and merely regard it as a subfamily.

#### Conclusions

Although the zoeal (Appendix 1) and adult (Appendix 2) data matrices differ considerably in size with regard to taxa and characters analyzed, there is basic support and compatibility from both that the eumedonids are not related to the Parthenopidae. This current study presents evidence to support the relationship between the pilumnids and eumedonids, and considers them to be a monophyletic group. However, the eumedonids as presently defined may not be a monophyletic group, and this anomaly may be resolved when the zoeas of *Eumedonus*, *Gonatonotus*, *Ceratocarcinus*, *Tiaramedon*, *Hapalonotus*, *Tauropus* and *Zebridonus* are known. Until the subfamilial

structure of the Pilumnidae is revised, the eumedonids should be regarded as a subfamily, Eumedoninae Dana, 1854 within the Pilumnidae Samouelle, 1819 (sensu Guinot, 1978).

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### References

- Adams, A. and White, A., Crustacea. The Zoology of the voyage of HMS *Samarang* under the command of Captain Sir Edward Belcher during the years 1843–1846. In: A. Adams, (ed.), Part II, London, 1849, pp. viii + 33–66. [For dates see Sherborn (1922) cxi].
- Alcock, A., The Brachyura Oxyrhyncha. Materials for a carcinological fauna of India, No. 1. J. Asiat. Soc. Beng., 64 (1895) 157–291.
- Balss, H., Diagnosen neuer Decapoden aus den Sammlungen der Deutschen Tiefsee-Expedition und der japanischen Ausbeute Dolfleins und Haberers. Zool. Anz., 52 (1921) 175–178.
- Balss, H., Beitrage zur Kenntnis der Gattungen *Pilumnus* (Crustacea Dekapoda) und verwandter Gattungen. Capita zool., 4 (1933a) 1–47.
- Balss, H., Ueber einige systematisch interessante indo-pazifische Dekapoden. Mitt. zool. Mus. Berl., 19 (1933b) 84–97.
- Balss, H., Decapoda, VIII: Systematik. In: H.G. Bronns, Klassen und Ordnungen des Tierreichs, Vol. 7, Akademische Verlagsgesellschaft, Leipzig, 1957, pp. 1131–1199.
- Bouvier, E.-L. and Seurat, G., Zoologie.-*Eumedon convictor*, Crabe commensal d'un Oursin. C. r. hebdom. Séanc. Acad. Sci., Paris, 140 (1905) 629–631.
- Carpenter, P.H., On the genus *Solanocarcinus*, Goldfuss, and its relations to recent Comatulæ. J. Linn. Soc., Lond. (Zoology), 15 (1880) 187–217.
- Carpenter, P.H., Report on the Crinoidea collected during the voyage of H.M.S. *Challenger* during the years 1873–76. Part II — The Comatulæ. In: Report on the Scientific Results of the Voyage of H.M.S. *Challenger* during the years 1873–1876 under the command of Captain George S. Nares, N.R., F.R.S. and the late Captain Frank Tourle Thomson, R.N. prepared under the Superintendence of the late Sir C. Wyville Thomson, Knt., F.R.S. andc. Regius Professor of Natural history in the University of Edinburgh of the civilian scientific staff on board and now of John Murray one of the naturalists of the Expedition. Zoology, Published by Order of Her Majesty's Government. London, Edinburgh and Dublin, HMSO, 26, 1888, pp. ix + 1–399.
- Castro, P., Settlement and habitat selection in the larvae of *Echinoecus pentagonus* (A. Milne Edwards), a brachyuran crab symbiotic with sea urchins. J. exp. mar. Biol. Ecol., 34 (1978) 259–270.
- Castro, P., Range extensions and new host records of eumedonid crabs of the genus *Harrovia* Adams and White, 1848 (Decapoda, Brachyura, Eumedonidae). Crustaceana, 57 (1989) 97–100.
- Castro, P., Chia, D.G.B. and Ng, P.K.L., On the taxonomic status of *Ceratocarcinus longimanus* White, 1847 (Crustacea: Decapoda: Brachyura: Eumedonidae), a crab symbiotic with comatulid crinoids. Raffles Bull. Zool., 43 (1995) 239–250.
- Chen, H.-L. and Xu, Z.-X., Study on the crabs of the Nansha Islands, China. Studies on the Marine Organisms of the Nansha Islands and Surrounding Seas, 3 (1991) 48–106.
- Chen, H.-L. and Xu, Z.-X., *Harrovia ngi*, a replacement name for *Harrovia longipes* Chen and Xu 1991, preoccupied by *Harrovia longipes* Lanchester, 1900 (Crustacea: Decapoda: Brachyura: Eumedonidae). Raffles Bull. Zool., 40 (1992) 265–266.
- Chia, D.G.B., Castro P. and Ng, P.K.L., Revision of the genus *Echinoecus* (Decapoda: Brachyura: Eumedonidae), crabs symbiotic with sea urchins. J. Crust. Biol., 19 (1999) 809–824.
- Chia, D.G.B. and Ng, P.K.L., New records of three rare Brachyuran crabs from Singapore seas (Crustacea, Decapoda: Parthenopidae, Xanthidae and Pilumnidae). Raffles Bull. Zool., 41 (1993) 159–167.
- Chia, D.G.B. and Ng, P.K.L., A revision of the genus

- Rhabdonotus* A. Milne Edwards, 1879, with descriptions of two new species and the first zoeal stage of *R. pictus* A. Milne Edwards, 1879 (Brachyura: Eumedonidae). Crust. Res., 24 (1995) 104–127.
- Chia, D.G.B. and Ng, P.K.L., A revision of *Ceratocarcinus* White, 1847, and *Harrovia* Adams and White, 1849 (Crustacea: Decapoda: Brachyura: Eumedonidae), two genera of crabs symbiotic with crinoids. Raffles Bull. Zool., 46 (1998) 493–563.
- Chia, D.G.B. and Ng, P.K.L., A note on the sea cucumber crab, *Hapalonotus reticulatus* (Crustacea: Brachyura: Eumedonidae). J. S. Asian Nat. Hist., Colombo, 4 (1999) 65–70.
- Chia, D.G.B. and Ng, P.K.L., A revision of *Eumedonus* H. Milne Edwards, 1834 and *Gonatonotus* White, 1847 (Crustacea: Decapoda: Brachyura: Eumedonidae), two genera of crabs symbiotic with sea urchins. J. Nat., Hist., 34 (2000) 15–56.
- Chia, D.G.B., Ng P.K.L. and Castro P., On a new genus and species of eumedonid crab from the Gulf of Carpentaria, northern Australia (Crustacea: Decapoda: Brachyura: Eumedonidae). J. Nat. Hist., 29 (1995) 1189–1195.
- Chia, D.G.B., Ng P.K.L. and Vandenspiegel D., The identities of two crinoid symbionts, *Harrovia albolineata* Adams and White, 1849, and *H. longipes* Lanchester, 1900 (Decapoda, Brachyura, Eumedonidae). Crustaceana, 64 (1993) 259–280.
- Clark, P.F. and Webber, W.R., A redescription of *Macrocheira kaempferi* Temminck, 1836) zoeas with a discussion of the classification of the Majoidea Samouelle, 1819 (Crustacea: Brachyura). J. Nat. Hist., 25 (1991) 1259–1279.
- Clark, P.F., Calazans, D.K. and Pohle, G.W., Accuracy and standardisation of brachyuran larval descriptions. Invert. Reprod. Develop., 33 (1998) 127–144.
- Clark, P.F., Interpreting patterns in chaetotaxy and segmentation associated with abbreviated brachyuran zoeal development. Invert. Reprod. Develop., in press??.
- Dai, A., Yang S., Song Y. and Chen G., Crabs of the China Seas. Beijing, China Ocean Press, 1986, pp. 17 + 642 [in Chinese].
- Dai, A. and Yang S., Crabs of the China Seas. Berlin, China Ocean Press, Beijing and Springer Verlag, 1991, pp. 21 + 608.
- Dana, J.D., 1. *Conspectus Crustaceorum quæ in Orbis Terrarum circumnavigatione, Carolo Wilkes e Classe Reipublicæ Fæderatæ Duce, lexit et descripsit* J.D. Dana. — Pars VI. \* Scientific Intelligence, III. Zoology. Amer. J. Sci. Arts, Second Ser., 11 (1851) 268–274.
- Dana, J.D., *Conspectus Crustaceorum, andc. Conspectus of the Crustacea of the Exploring Expedition under Capt. Wilkes, U.S.N. I. CRUSTACEA CANCROIDEA*, Proc. Acad. Nat. Sci., Phila., 6 (1852), 73–86 [meeting of May 1852]. [Reprint: Crustacea Cancroidea and Corystoidea. *Conspectus Crustaceorum, andc. Conspectus of the Crustacea of the Exploring Expedition under Capt. Wilkes, U.S.N. including the Crustacea Cancroidea and Corystoidea.* ibid.].
- Dana, J.D., Crustacea, Part II. in United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the Command of Charles Wilkes, U.S.N. Philadelphia, C. Sherman, [1853] 14, 1854, pp. 686–1618. [For date of publication see Haskell, 1942, p. 79].
- Davie, P.J.F., The genus *Lophopilumnus* (Crustacea: Brachyura: Pilumnidae): the rediscovery of *L. cristipes* (Calman, 1900) and the description of a new species. Beagle, 5 (1988) 77–85.
- Davie, P.J.F., Two new genera of the family Pilumnidae (Crustacea: Decapoda: Brachyura) from Queensland, Australia. J. Nat. Hist., 23 (1989a) 1353–1365.
- Davie, P.J.F., A reappraisal of *Heteropanope* Stimpson, and *Pilumnopeus* A. Milne Edwards (Crustacea: Decapoda: Pilumnidae) with descriptions of new species and new genera. Mem. Qd Mus., 27 (1989b) 129–156.
- Duncan, F.D., On the Dates of Publication of the Society's 'Proceedings,' 1859–1926. With an Appendix containing the dates of Publication of 'Proceedings,' 1830–1858, compiled by the late F.H. Waterhouse, and the late Henry Peavot, originally published in P.Z.S. 1893, 1913. Proc. Zool. Soc. Lond., Ser. A, 1937 (1937) 71–83.
- Estampador, E.P., A check list of Philippine crustacean decapods. Philipp. J. Sci., 62 (1937) 465–559.
- Estampador, E.P., Revised check list of Philippine crustacean decapods. Nat. Appl. Sci. Bull., Manila, Philippines, 17 (1959) 1–127.
- Fabricius, J.C., *Entomologia Systematica Emendata et Aucta Secundum Classes, Ordines, Genera, Species, Adjectis Synonymis, Locis, Observationibus, Descriptionibus.* Hafniae. 1793, 2, viii + 519.
- Flipse, H.J., Oxyrrhyncha [sic]: Parthenopidae. Die Decapoda Brachyura der Siboga Expedition, VI. Siboga Expeditie, 39c<sup>2</sup> (1930) 1–96. [University of Amsterdam edition has an added introduction in Dutch and a different pagination.]
- Forskål, P. *Descriptiones Animalium Avium, Amphibiorum, Piscium, Insectorum, Vermium; quæ in Itinere orientali observavit. Petrus Forskål. Post Mortem Auctoris editit* Carsten Niebuhr. *Adjuncta est materia Medica Kahirina.* Haunia, Heineck et Faber, 1775, pp. 1–9, i–xxxiv, 1–164, 1 map. Glaessner, M.F., Decapoda. In: R.C. Moore (ed.), Treatise on invertebrate paleontology, Part R, Arthropod 4. Connecticut and New York, Geological Society of America and University of Kansas, Vol. 2, 1969, pp. 399–533.
- Gordon, I., Seven new species of Brachyura from the coasts of China. Ann. Mag. Nat. Hist., 6 (1930) 519–525.
- Gordon, I., Brachyura from the coast of China. J. Linn Soc. Lond., Zool., 37 (1931) 525–558.
- Gordon, I., Crustacea Brachyura, in Résultats scientifiques du Voyage aux Indes Orientales Néerlandaises de LL. AA. RR. le Prince et la Princesse Léopold de Belgique. Mém. Mus. R. Hist. Nat. Belg., Bruxelles, 3 (1934) 1–78.
- Gordon, I., Description of a new species of crab from Macclesfield (Parthenopidae, Eumedoninae). Proc. Linn. Soc. Lond., 159 (1947) 111–113.
- Gravier, C., Sur un nouveau Crabe (*Eumedonus petiti* nov.

- sp.) commensal d'um oursin de Tuléar (Madagascar). Bull. Mus. Hist. nat., Paris, 28 (1922) 484–486.
- Griffin, D.J.G., The status of *Pilumnus terraereginae* Haswell (Crustacea, Decapoda, Xanthidae) and a giant new *Pilumnus* from Queensland waters. Mem. Qld. Mus., 15 (1970) 323–330.
- Guinot, D., Sur divers Xanthidae, notamment sur *Actaea* de Haan et *Paractaea* gen. nov. XI (Crustacea Decapoda Brachyura). Cah. pacif., 13 (1969) 222–267.
- Guinot, D., Recherches préliminaires sur les groupements naturels chez les Crustacés Décapodes Brachyours. VIII. Synthèse et bibliographie. Bull. Mus. Hist. nat., Paris, 42 (1971) 1063–1090.
- Guinot, D., Données nouvelles sur la morphologie, la phylogénèse et la taxonomie des Crustacés Décapodes Brachyours. Thèse de Doctorat d'État ès Sciences, Université Pierre et Marie Curie, 2 vols., 1977, pp. ixv, 1486, xvi–xxiv.
- Guinot, D., Principes d'une classification évolutive des Crustacés Décapodes brachyours. Bull. biol. Fr. Belg., nouvelle série, 112 (1978) 211–292.
- Guinot, D., Données nouvelles sur la morphologie, la phylogénèse et la taxonomie des Crustacés Décapodes Brachyours. Mém. Mus. natn. Hist. nat., série A (zoologie), 112 (1979) 13–54.
- Guinot, D., Crustacea (chapter restricted to Brachyuran Decapod Crustacea). In: G. Richard (ed.), Fauna and Flora. A First Compendium of French Polynesian Seadwellers, Vol. 1, French Polynesian Coral Reefs, Fifth International Coral Reef Congress, Tahiti, 1985a, pp. 446–455.
- Guinot, D., Révision du genre *Parapanope* De Man, 1895 (Crustacea Decapoda Brachyura), avec description de trois espèces nouvelles. Bull. Mus. Hist. nat., Paris, 7 (1985b) 692–696.
- Guinot, D. and Bouchard J.M., Evolution of the abdominal holding systems of brachyuran crabs (Crustacea, Decapoda, Brachyura). Zoosystema, 20 (1998) 613–694.
- Gray, J.E., Description of a new genus, and some undescribed species of Crustacea. In: Gray, J.E., The Zoological Miscellany. To be continued occasionally. London, Treuttel, Wurtz, 1831, pp. 39–40.
- de Haan, W., Crustacea. *Fauna Japonica, sive Descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis superiorum, qui summum in India Batava imperium tenent, suscepto, annis 1823–1830 collegit, notis, observationibus et adumbrationibus illustravit* P.F. de Siebold. Conjunctis studiis C.J. Temminck et H. Schlegel pro *Vertebratis atque W. de Haan pro Invertebratis elaborata Regis auctoris edita*. In: P.F. von Siebold, Leiden, Lugduni-Batavorum, Vol. I, 1835, pp. 25–64, pls 9–15, 17, C, D. (For dates see Sherborn and Jentink, 1895; Holthuis, 1953 and Holthuis and T. Sakai, 1970).
- Haswell, W.A., On the Australian Brachyura Oxyrhyncha. Proc. Linn. Soc. NSW, 4 (1880) 431–458.
- Henderson, J.R., A contribution to Indian carcinology. Trans. Linn. Soc. Lond., 5 (1893) 325–458.
- Herbst, J.F.W. Versuch einer Naturgeschichte der Krabben und Krebse, nebst einer systematischen Beschreibung ihrer verschiedenen Arten. Berlin und Stralsund, Gottlieb, August und Lange, Vol. 2, 1793, pp. 79–146. (For dates of publication see Rathbun, 1897, 157.)
- Holthuis, L.B., On the dates of publication of W. De Haan's volume on the Crustacea of P.F. Von Siebold's "Fauna Japonica". J. Soc. Bibliophy nat. Hist., 3 (1953) 36–47.
- Holthuis, L.B. and Sakai T., Ph.F. Von Siebold and Fauna Japonica. A history of early Japanese Zoology. Tokyo, Academic Press of Japan, 1970, pp. i–xviii + part I, pp. 1–132, (in English) + part II, pp. 207–323 (in Japanese) + plates I–XXXII.
- Johnson, D.S., Commensalism and semi-parasitism amongst decapod Crustacea in Singapore waters. Proc., First Regional Symposium, Scientific Knowledge Tropical Parasites, Singapore, University of Singapore, 1962, pp. 282–288.
- Klunzinger, C.B., Die Spitz- und Spitzmundkrabben (Oxyrhyncha und Oxytomata) des Roten Meeres. Stuttgart, Ferdinand Enke, 1906, pp. vii + 1–88.
- Kropp, R.K., *Tanaocheles stenochilus*, a new genus and species of crab from Guam, Mariana Islands (Brachyura: Xanthidae). Proc. Biol. Soc. Wash., 97 (1984) 744–747.
- Kurata, H. and Matsuda, T., Larval stages of a parthenopid crab, *Parthenope validus*, reared in the laboratory and variation of egg size among crabs. Bull. Nansei reg. Fish. Res. Lab., 12 (1980) 31–42.
- Laurie, R.D., Report of the Brachyura collected by Professor Herdman, at Ceylon, in 1902. In: W.A. Herdman (ed.), Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar, Part 5, Supplementary Reports, No. 40, 1906, pp. 349–432.
- Lamarck, J.B.P.A., [Monet, chevalier de] Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels, enfin, l'exposition des principaux fondamentaux de la zoologie. Paris, Quai des Augustins, Vol. 2, 1816, pp. ii + 568.
- Lanchester, W.F., On a collection of Crustaceans made at Singapore and Malacca. Part 1. Crustacea Brachyura. Proc. zool. Soc. Lond., 1900 (1900) 717–770.
- Lim, G.S.Y. and Ng, P.K.L., The first zoeal stage of *Harrovia albolineata* Adams and White, 1848 (Crustacea: Brachyura: Pilumnidae), with a note on eumedonine systematics. J. Nat. Hist., 22 (1988) 217–223.
- Linnaeus, C., *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis Synonymis, Locis*, 10th ed., *Holmiae*, 1758, pp. iii + 1–824.
- Linnaeus, C., *Fauna Suecica sistens Animalia Suecicae Regni; Mammalia, Aves, Amphibia, Pisces, Insecta, Vermes. Distributa per Classes et Ordines, Genera and Species, cum Differentiis Specierum, Synonymis Auctorum, Nominibus Incolarum, Locis Natalium,*

- Descriptionibus Insectorum*. Stockholmiae, 1761, pp. 1–578.
- Linnaeus, C., *Pars I. Insecta Exotica. Museum S:æ R:æ M:tis Ludovicæ Ulricæ Reginae Svecorum, Gotborum, Vandalorumque andc. andc. andc. In qui animalia rariora, exotica impremis Insecta and Conchilia defcribuntur and determinantur Prodromi inftar. Holmiae*, 1764, pp. vi + 1–462.
- MacGilchrist, A.C., An account of the new and some of the rarer decapod Crustacea obtained during the surveying seasons 1901–1904. Natural History notes from the *R.I.M.S. 'Investigator'*, Captain T.H. Heming, R.N. (retired), Commanding. *Ann. Mag. Nat. Hist.*, 15 (1905) 233–268.
- MacLeay, W.S., On the Brachyurous Decapod Crustacea. Brought from the Cape by Dr. Smith. In: A. Smith (ed.), *Illustrations of the Zoology of South Africa; consisting chiefly of figures and descriptions of the objects of natural history collected during an expedition into the interior of South Africa, in the years 1834, 1835, and 1836; fitted out by "The Cape of Good Hope Association for Exploring Central Africa:"* together with a summary of African Zoology, and an inquiry into the geographical ranges of species in that quarter of the globe, Published under the Authority of the Lords Commissioners of Her Majesty's Treasury, Invertebratae. London, Smith, Elder and Co., [1849], 1838, pp. 53–71.
- De Man, J.G., Note XIX. On some new or imperfectly known Podophalamous Crustacea of the Leyden Museum. *Notes Leyden Mus.*, (1879) 59–73.
- De Man, J.G., Report on the Podophalmous Crustacea of the Mergui Archipelago, collected for the Trustees of the Indian Museum, Calcutta, by Dr Anderson, F.R.S., Superintendent of the Museum, Part I. *J. Linn. Soc. Lond., Zoology*, 22 (1887) 1–64.
- Martin, J.W., 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. *Bull. Mar. Sci.*, 34 (1984) 220–239.
- Miers, E.J., On the classification of the maioid Crustacea or Oxyrhyncha, with a synopsis of the families, subfamilies, and genera. *J. Linn. Soc. Lond. (Zoology)*, 14 (1879a) 634–673.
- Miers, E.J., Descriptions of new or little-known species of maioid Crustacea (Oxyrhyncha) in the collection of the British Museum. *Ann. Mag. nat. Hist.*, 4 (1879b) 128.
- Miers, E.J., Report on the Brachyura collected by H.M.S. Challenger during the years 1873–76. In: Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–1876 under the command of Captain George S. Nares, N.R., F.R.S. and the late Captain Frank Tourle Thomson, R.N. prepared under the Superintendence of the late Sir C. Wyville Thomson, Knt., F.R.S. andc. Regius Professor of Natural history in the University of Edinburgh of the civilian scientific staff on board and now of John Murray one of the naturalists of the Expedition. *Zoology*, Published by Order of Her Majesty's Government. London, Edinburgh and Dublin, HMSO., 17, 1886, pp. 1 + 362.
- Milne Edwards, A., Recherches sur la faune carcinologique de la Nouvelle-Calédonie. Chapitre Premier, Groupe des Oxyrhynques. *Nouv. Arch. Mus. Hist. nat.*, Paris, 8 (1872) 229–267.
- Milne Edwards, A., Description de quelques Crustacés nouveaux. *Bull. Soc. Philomat. Paris*, 3 (1879) 103–110.
- Milne Edwards, H., Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification des ces animaux. Paris, Librairie Encyclopédique de Roret, 1, 1834, pp. xx–xv + 468 Atlas [1834, 1837, 1840]: 132, pls 114, 14 bis, 1525, 25 bis, 26–42.
- Miyake, S., Note on crabs of the genus *Echinoecus* Rathbun living commensally with echinoids (Parthenopidae, Eumedoninae). *Annotnes zool. Jap.*, 18 (1939) 83–94.
- Miyake, S., Brachyura (Crabs). Japanese crustacean decapods and stomatopods in Color, First Edition. Hoikusha, Osaka, Vol. 2, 1983, pp.viii + 277 [in Japanese].
- Mori, A., Yanagisawa, Y., Fukuda Y. and Ng, P.K.L., The complete larval development of *Zebrida adamsii* White, 1847 (Crustacea, Decapoda, Brachyura), reared in the laboratory. *J. Crust. Biol.*, 11 (1991) 292–304.
- Neumann, R., Systematische Uebersicht der Gattungen der Oxyrhynchen. Catalog der Podophthalmen Crustaceen des Heidelberger Museums. Beschreibung Einiger Neuer Arten. Leipzig, J.B. Hirschfeld, 1878, pp. 39.
- Ng, P.K.L., Aspects of the Systematics of the family Pilumnidae Samouelle, 1819 (Crustacea, Decapoda, Brachyura) and a study on evolutionary trends in the superfamily Xanthoidea (*sensu* Guinot, 1978). Unpublished B.Sc. Honours Thesis, Department of Zoology, National University of Singapore, 1983, pp. viii + 1–251.
- Ng, P.K.L., *Garthambrus*, a new genus of deep water parthenopid crabs (Crustacea: Decapoda: Brachyura) from the Indo-Pacific, with description of a new species from the Seychelles. *Zool. Meded. Leiden*, 70 (1996) 155–168.
- Ng, P.K.L., Crabs. In: FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific, Vol. 2, Cephalopods, Crustaceans, Holothurians and Sharks. K.E. Carpenter and V.H. Niem (eds.), Food and Agriculture Organisation, Rome, 1998, pp. 1045–1155.
- Ng, P.K.L. and Chia, D.G.B., The genus *Glyptocarcinus* Takeda, 1973, with descriptions of a new subfamily, two new genera and two new species from New Caledonia (Crustacea: Decapoda: Brachyura: Xanthidae). *Raffles Bull. Zool.*, 42 (1994) 701–730.
- Ng, P.K.L. and Chia, D.G.B., Revision of the genus *Zebrida* White, 1847 (Crustacea: Decapoda: Brachyura: Eumedonidae). *Bull. mar. Sci.*, 65 (1999) 481–495.
- Ng, P.K.L. and Clark, P.F., The Indo-Pacific Pilumnidae XII. On the familial placement of *Chlorodiella bidentata* (Nobili, 1901) and *Tanaocheles stenochilus* Kropp, 1984 using adult and larval characters with the establishment of a new subfamily, Tanaoachelinae (Crustacea: Decapoda: Brachyura). *J. Nat. Hist.*, 34 (2000) 207–245.
- Ng, P.K.L. and Davie, P.J.F., The Indo-Pacific Pilumnidae VII. Notes on the taxonomy of *Heteropilumnus*

- sasekumari* (Serène, 1971) and *Cryptolutea* Ward, 1936 (Crustacea: Decapoda: Brachyura). Mem. Qd Mus., 30 (1991) 517–524.
- Ng, P.K.L. and Jeng, M.S., The brachyuran crabs (Crustacea: Decapoda: Eumedonidae and Portunidae) symbiotic with echinoderms in Taiwan. Zoological Studies, Taipei, 38 (1999) 268–273.
- Ng, P.K.L. and Lim, G.S.Y., On the ecology of *Harrovia albolineata* Adams and White (Crustacea: Decapoda: Brachyura: Eumedonidae), a crab symbiotic with crinoids. Raffles Bull. Zool., 38 (1990) 257–262.
- Ng, P.K.L. and Rodriguez, G., New records of *Mimilambrus wileyi* Williams, 1979 (Crustacea: Decapoda: Brachyura), with notes on the systematics of the Mimilambridae Williams, 1879, and Parthenopidae MacLeay, 1838, sensu Guinot, 1978. Proc. Biol. Soc. Wash., 99 (1986) 88–99.
- Ng, P.K.L. and Števcíć, Z., The identity of *Dentoxanthus komodoensis* Serène, 1971 (Crustacea: Decapoda: Brachyura: Pilumnidae) with description of a new genus. Tropical Biodiversity, Jakarta, 1 (1993) 101–106.
- Ng, P.K.L. and Tan, L.W.H., The Indo-Pacific Pilumnidae I. Description of four new species of the genus *Pilumnus* Leach, 1815 and definition of a new genus, *Bathypilumnus*. J. Singapore Nat. Acad. Sci., 13 (1984) 13–19.
- Ng, P.K.L., Wang, C.H., Ho, P.H. and Shih, H.T., A checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). Taiwan Mus. J., in press.
- Nobili, G., Decapodi e Stomatopodi Eritrei del Museo Zoologico dell'Università di Napoli. Annuario R. Museo Zoologico della R. Università di Napoli, n.s., 1 (1901) 1–20.
- Ortmann, A., Abtheilung: Brachyura (Brachyura genuina Boas) II. Unterabtheilung: Cancroidea, 2. Section: Cancrinea, 1. Gruppe: *Cyclometopa*. Hierzu Tafel 17. Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen. VII. Theil. Zool. Jb. (Systematik), 7 (1893) 411–495.
- Ortmann, A., Crustaceen. In: Zoologische Forschungsreisen in Australien und dem Malayischen archipel. Mit Unterstützung des Herrn Dr. Paul Von Ritter ausgeführt in den Jahren 1891–1893 von Richard Semon. Fünfter Band: Systematik und Tiergeographie, Anatomie Wirbelloser Tier. Mit 67 Lithographischen Tafeln und 17 Abbildungen im Text. Text. Denkschr. med.-naturw. Ges. Jena, 8 (1894) 1–80.
- Pallas, P.S., *Spicilegia zoologica quibus novae imprimis et obscurae animalium species iconibus, descriptionibus atque commentariis illustrantur*. Berolini, Gottl. August. Lange. X, 1774, pp. 1–41 + index.
- Rathbun, M.J., No. XXIV.—Descriptions of new genera and species of Crabs from the West Coast of North America and the Sandwich Islands. In: Scientific Results of Exploration by the U.S. Fish Commission Albatross Proc. U.S. natn. Mus., Washington, [1893], 16 (1894) 223–260.
- Rathbun, M.J., A revision of the nomenclature of the Brachyura. Proc. Biol. Soc. Wash., 11 (1897) 153–167.
- Rathbun, M.J., V. Brachyura. The Danish Expedition to Siam 1899–1900. K. dansk. Vidensk. Selsk. Skr., 7 Række, Naturvidenskabelig og Mathematisk Afdeling, 5 (1910) 301–368.
- Rathbun, M.J., Report on the spider crabs. Report on the Spider Crabs obtained by the F.I.S. “Endeavour” on the Coasts of Queensland, New South Wales, Victoria, South Australia and Tasmania. In Fisheris. Biological Results of the Fishing Experiments carried on by the F.I.S. “Endeavour”, 1909–14. H.C. Dannevig, Commonwealth Director of Fisheries. Published by Direction of the Minister for Trade and Customs. Hon. J.A. Jensen, M.H.R. Sydney, W.E. Smith, Vol. 5, 1918, pp. 1–29.
- Rice, A.L., Crab zoal morphology and its bearing the classification of the Brachyura. Trans. zool. Soc. Lond., 35 (1980) 271–424.
- Rüppell, W.P.E.S., Beschreibung und Abbildung von 24 Arten kurzschwänzigen Krabben, als Beitrag zur Naturgeschichte des rothen Meeres. Frankfurt a.m., H.L. Bröner, 1830, pp. 1–28.
- Sakai, T., New or rare species of Brachyura, collected by the “Misago” during the zoological survey around the Izu-Peninsula. Sci. Rep. Tokyo Bunrika Daig., (B), 2 (1935) 63–88.
- Sakai, T., Studies on the crabs of Japan III. Brachygnatha, Oxyrhyncha. Tokyo Yokendo, 1938, pp. 194–364.
- Sakai, T., The Crabs of Sagami Bay. Tokyo, Maruzen, 1965, pp. xvi+206 [English text], pp. 192 [Japanese text], pp. 132 [bibliography and indices], pls. 1–100.
- Sakai, T., Crabs of Japan and the adjacent seas. Tokyo, Kodansha, 1976, Vol. 1 [English] pp. xx–ix+773; Vol. 2 [Japanese] pp. 14–61; Vol. 3 [plates] pp. 1–61, pls 1–251.
- Samouelle, G., The Entomologist's Useful Compendium, or an Introduction to the Knowledge of the British Insects. London, Thomas Boys, 1819, pp. 496.
- Sandifer, P.A., Larval stages of the crab, *Pilumnus dasypodus* Kingsley (Crustacea, Brachyura, Xanthidae) obtained in the laboratory. Bull. Mar. Sci., 24 (1974) 378–391.
- Serène, R., The Brachyura of the Indo-West Pacific region. In: Prodrum for a check list of the nonplanctonic marine fauna of South East Asia. Singapore National Academy of Science, Special Publication Number 1, 1968, pp. 33–112.
- Serène, R., and Romimohtarto, K., On some species of Eumedoninae from IndoMalayan region. Mar. Res. Indonesia, 6 (1963) 1–14.
- Serène, R. and Umali, A.F., The family Raninidae and other new and rare species of Brachyuran Decapods from the Philippines and adjacent regions. Philipp. J. Sci., 99 (1972) 21–105.
- Serène, R., Duc, T.V. and Luom, N.V., Eumedoninae du Viet Nam (Crustacea) (avec une Bibliographie de la sousfamille). Treubia, 24 (1958) 135–242.
- Serène, R., Crustacés Décapodes Brachyours de l'Océan Indien Occidental et de la Mer Rouge. Xanthoidea:

- Xanthidae et Trapeziidae. Addendum Carpiliidae et Menippidae. A. Crosnier. Faune Tropicale (ORSTOM), Vol. 24, 1984, pp. 1–400.
- Shen, C., Dai, A. and Chen, H., New and rare species of Parthenopidae (Crustacea: Brachyura) from China Sea. *Acta Zootax. Sinica*, 7 (1982) 139–149.
- Sherborn, C.D. and Jentink, J.A., On the dates of the Parts of Siebold's 'Fauna Japonica' and Giebel's 'Allgemeine Zoologie' (1st ed.), *Proc. Zool. Soc. Lond.*, 1895 (1895) 149–150.
- Sherborn, C. L., *Index animalium sive index nominum quae ab A.D. MDCCCLVIII generibus et speciebus animalium imposita sunt societatis eruditorum adiuvantibus. Sectio secunda a kalendis Ianuariis, MDCCCI usque ad finem Decembris*. London, The Trustees of the British Museum. Part I. Introduction, Bibliography and Index A–Aff, 1801–1850, 1922, pp. 1–128.
- Stephensen, K., The Brachyura of the Iranian Gulf with an appendix: The male pleopoda of the Brachyura. *Danish Sci. Invest. Iran*, [1945] 4 (1946) 57–237.
- Števcic, Z. and Ng, P.K.L., The systematic position of the genus *Dentoxanthus* Stephensen, 1945 (Crustacea Decapoda, Brachyura, Pilumnidae). *Steenstrupia*, Copenhagen, 14 (1988) 1–5.
- Števcic, Z. and Gore R.H., Are the Oxyrhyncha a natural group? *Thalassia jugosl.*, 17 (1981) 1–16.
- Števcic, Z., Castro, P. and Gore, R.H., Reestablishment of the Family Eumedonidae Dana, 1853 (Crustacea: Brachyura). *J. Nat. Hist.*, 22 (1988) 1301–1324.
- Stimpson, W., *Prodromus descriptionis animalium evertibratorum quae in Expeditione ad Oceanum Pacificum septentrionalem a Republica Federata Missa*, Cadwaladaro Ringgold et Johanne Rodgers *Ducibus, observavit et descripsit* — Part V, Crustacea Ocyropodoidea. *Proc. Acad. Nat. Sci., Phila.* [1859], 10 (1858) 93–110 [reprint idem. pp. 38–56].
- Swofford, D.L., PAUP (Phylogenetic Analysis Using Parsimony), Ver. 3.1. Laboratory of Molecular Systematics, Smithsonian Institute, Washington, DC, 1993.
- Takeda, M., A new genus and a new species of the Parthenopidae from the sea off the Ogasawara Islands (Crustacea, Brachyura). *Bull. natn. Sci. Mus. Tokyo*, 16 (1973) 31–36.
- Terada, M., Zoelal development of *Halimede fragifer* De Haan (Xanthidae, Xanthinae). *Proc. jap. Soc. syst. Zool.*, 31 (1985a) 30–37.
- Terada, M., On the larval development of *Parthenope (Platylambrus) valida* De Haan (Brachyura, Parthenopinae). *Zool. Sci.*, Tokyo, 2 (1985b) 731–737.
- Thiriou, A., Stades larvaires de Parthenopidae méditerranéens: *Heterocrypta maltzani* Miers et *Parthenope massena* (H. Milne Edwards). *Cah. Biol. Mar.*, 14 (1973) 111–134.
- Tirmizi, N.M. and Kazmi, Q.B., Crustacea: Brachyura (Dromiacea, Archaeobrachyura, Oxystomata, Oxyrhyncha). *Mar. Fauna Pakist.*, 4 (1988) 12–44.
- Vandenspiegel, D., Ovaere, A. and Massin, C., On the association between the crab *Hapalonotus reticulatus* (Crustacea, Brachyura, Eumedonidae) and the sea cucumber *Holothuria (Metriatyla) scabra* (Echinodermata, Holothuridae). *Bull. Inst. R. Sci. nat. Belg. Bull. van het Koninklijk Belgisch Instituut voor Natuurwetenschappen, Biologie*, 62 (1992) 167–177.
- Van Dover, C.L., Gore R.H. and Castro, P., *Echinoecus pentagonus* (A. Milne Edwards, 1879): larval development and systematic position (Crustacea: Brachyura: Xanthoidea nec Parthenopidea). *J. Crust. Biol.*, 6 (1986) 757–776.
- Walker, A.O., Notes on a collection of Crustacea from Singapore. *J. Linn. Soc.* 20 (1887) 107–117.
- Waterhouse, F.H., List of the Dates of Delivery of the Sheets of the 'Proceedings' of the Zoological Society of London, from the commencement in 1830 to 1859 inclusive. *In: May 2, 1893*. Sir W.H. Flower, K.C.B., LL.D., F.R.S., President, in the Chair. *Proc. zool. Soc. Lond.*, 1893 (1893) 436–440. [Reprinted in Duncan, (1937) 78–83.]
- Ward, M., Notes on a collection of crabs from Christmas Island, Indian Ocean. *Bull. Raffles Mus., Singapore*, 9 (1934) 5–28.
- Ward, M., Crustacea Brachyura from the coasts of Queensland. *Mem. Qld Mus.*, 11 (1936) 1–13.
- White, A., 3. Descriptions of new Crustacea from the Eastern Seas. *In: April 27, 1847*. William Yarrell, Esq., Vice-President, in the Chair. *Proc. zool. Soc. Lond.*, 1847 (1847a) 56–58. [For dates of publication see Waterhouse (1893) 438 and Duncan (1937) 80.]
- White, A., 3. Descriptions of new or little-known Crustacea in the Collection at the British Museum. *In: July 27*. William Yarrell, Esq., Vice-President, in the chair. *Proc. zool. Soc. Lond.*, 1847 (1847b) 118–126. [For dates of publication see Waterhouse (1893) 438 and Duncan (1937) 80.]
- Williams, A.B., A new crab family from shallow waters of the West Indies (Crustacea: Decapoda: Brachyura). *Proc. Biol. Soc. Wash.*, 92 (1972) 399–413.
- Yang, W.T., The larval and postlarval development of *Parthenope serrata* reared in the laboratory and the systematic position of the Parthenopidae (Crustacea, Brachyura). *Biol. Bull. Mar. biol. Lab. Woods Hole*, 140 (1971) 166–189.
- Zehntner, L., Crustacés de l'Archipel Malais. Voyage de MM. Bedot et Pictet dans l'Archipel Malais. *Revue suisse Zool.*, 2 (1894) 135–214.



### Appendix 3

#### Description of first zoeal characters use in the phylogenetic analysis

1. **Carapace:** *length of rostral spine*; three character states; approximately equal to or just shorter than the antennal protopod (long), approximately equal to the mid-point of the protopod (medium), approximately a quarter of the antennal protopod (short). The rostral spine of the outgroup is long and this was considered to be the plesiomorphic condition, with Clark and Webber (1991) considering a reduction in length to eventual loss to be the derived condition. This character state was ordered irreversible up and the character states were coded as 0 = long, 1 = medium, 2 = short.
2. **Carapace:** *armature*; two character states were recognized, armature was either present or absent. Carapace armature was absent in the outgroup and only present in two species of the ingroup. The polarity of this character could not be determined and was left unordered for the analysis. Character state were coded as 0 = absent, 1 = present.
3. **Antennule:** *the number of terminal setae*; the number of terminal antennular setae observed was either 2 or 1. The presence of 2 terminal setae in the outgroup was considered to be the plesiomorphic condition and this character states was ordered irreversible up. Character states were coded as 0 = two present, 1 = one present.
4. **Antenna:** *exopod setation*; the setae on the antennary exopod are either terminal or subterminal. Clark and Webber (1991) considered that terminal setae on the antennary exopod to be the plesiomorphic condition in majids and this condition is present in the outgroup. Subterminal setae were considered to be the derived condition. This character state was ordered irreversible up and coded as 0 = terminal setae, 1 subterminal setae.
5. **Antenna:** *endopod*; the antennary endopod is either absent or present. According to Clark (in press), the timing of character appearance can be shown to accelerate in brachyuran species with loss of zoeal stages (abbreviated development) by reference to out sequence state assumptions. In the outgroup the endopod is absent in stage 1 zoeal and this is considered to be the plesiomorphic state. The accelerated appearance of the antennary endopod in first-stage zoea is regarded as the apomorphic condition. This character state was ordered irreversible up and coded as 0 = endopod absent, 1 endopod present.
6. **Maxilla:** *setation of proximal coxal lobe*; the number of setae on the proximal lobe of the coxa ranges from 3–6 setae. Clark and Webber (1991) considered loss of setae to be the derived condition. Six setae are present on the proximal lobe of the outgroup and this is considered to be the ancestral condition. This character state was ordered irreversible up and coded as 0 = six setae, 1 = five setae, 2 = four setae.
7. **Second maxilliped:** *subterminal setation of 3rd endopod segment*; loss of setae was considered to be the derived condition. The outgroup displayed the ancestral condition. This character state was ordered irreversible up and coded as 0 = three setae, 1 = two setae.
8. **Abdomen:** *lateral processes on somite 4*; a pair of lateral processes is either present or absent on abdominal somite 4. The presence of a pair of lateral processes was considered to be the ancestral condition and was present in the outgroup. Loss of lateral processes was regarded as the apomorphic condition. This character state was ordered irreversible up and coded as 0 = present, 1 = absent.
9. **Abdomen:** *lateral process on somite 5*; a pair of lateral processes is either present or absent on abdominal somite 5. The presence of a pair of lateral processes was considered to be the ancestral condition and was present in the outgroup. Loss of lateral processes was regarded as the apomorphic condition. This character state was ordered irreversible up and coded as 0 = present, 1 = absent.
10. **Abdomen:** *somite spinulation*; spinulation on the posterodorsal margin of somites 2–5 in first stage zoea was either present or absent. The presence of spinulation on the somite margin was absent in the outgroup, but as no polarity was given to this character it was unordered and coded as 0 = present, 1 = absent.
11. **Abdomen:** *armature of somites*; armature on the dorsal surface of somites 2–5 was either present or absent. The presence of armature on the somite margin was absent in the outgroup, but as no polarity was given to this character it was unordered and coded as 0 = present, 1 = absent.
12. **Telson:** *spinulate telson fork*; spinulation on the telson fork was either absent or present. In the outgroup, spinulation was absent from the telson fork, but the presence or absence of this character was not assigned polarity and was regarded as unordered and coded as 0 = present, 1 = absent.

### Appendix 4

#### Description of adult characters states

Taxa analyzed: “**Eumedonidae**”: 1. *Ceratocarcinus longimanus*; 2. *Harrovia albolineata*; 3. *Permanotus purpureus*; 4. *Rhabdonotus pictus*; 5. *Tiaramedon spinosum*; 6. *Tauropus egeriae*; 7. *Eumedonus niger*; 8. *Gonatonotus pentagonus*; 9. *Echinoecus pentagonus*; 10. *Zebrida adamsii*; 11. *Zebridonus mirabilis*; 12. *Hapalonotus reticulatus*; **Pilumnidae**: 13. *Pilumnus hirtellus*; 14. *Rhizopa gracilipes*; 15. *Bathypilumnus sinensis*; 16. *Dentoxanthus iranicus*; 17. *Galene bispinosa*; 18. *Halimede ochtodes*; 19. *Calmania prima*; 20. *Tanaocheles bidentata*; Parthenopidae: 21. *Daldorfia horrida*; 22. *Rhinolambrus pelagicus*; 23. *Cryptopodia fornicata*; 24. *Mimilambrus wileyi*; **Carpiliidae**: 25. *Carpilius convexus*; **Eriphiidae**: 26. *Myomenippe hardwickii*; 27. *Eriphia smithii*.

Characters: All adult characters are not ordered.

1. **Carapace shape**: The shape of the carapace is not always reliable, but certain forms can be regarded as more plesiomorphic in the Eubrachyura on the basis of the extant fossil record. The typical xanthoid facies, i.e., a transversely hexagonal shape like that found in most eriphiids is regarded as plesiomorphic here. This character state was coded as: hexagonal (0), round/ovate (1), rectangular (2) or triangular (3).
2. **Carapace proportions**: In the Eubrachyura, a broader than long carapace is regarded as plesiomorphic. This character state was coded as transverse (0), subequal (1) or longer than broad (2).
3. **Gastric spines**: A smooth gastric region without pronounced spines is regarded as plesiomorphic. This character state was and coded as: absent (0) or present (1).
4. **Pubescence on appendages**: An appendage without or with pigmented coloured setae is plesiomorphic. This character state and coded as not covered with translucent setae (0) or is (1).
5. **Front**: A medially clefted frontal margin is plesiomorphic. This character state was coded as: medially clefted (0) or entire (1).
6. **Rostrum**: A well developed rostrum or prominent is here regarded as plesiomorphic. This character state was as: distinct (0) or indistinct (1).
7. **Rostrum (frontal margin)**: Most carpiliids and eriphiids have proportionately very broad frontal margins. This character state was coded as transversely broad (0) or narrow (1).
8. **Inner supraorbital tooth**: A low tooth, which may be lobiform, is regarded as plesiomorphic. This character state was coded as: low (0), distinct (1) or undiscernible (2).
9. **Antero- and posterolateral margins**: The xanthoid form has the antero and posterolateral margins well demarcated by an angle or tooth. This character state was coded as: demarcated (0) or not (1).
10. **Anterolateral margin**: The number of teeth in eriphiids is four and is here regarded as plesiomorphic. This character state was coded as: 4 teeth (0), otherwise armed (1) or entire (2).
11. **Antero- and posterolateral margins**: The margins may be expanded (apomorphic condition) in some taxa. This character state was coded as: not clypeiform (0) or is (1).
12. **Efferent channels**: The apomorphic state is with carinated margins along the channels which help control water flow. This character state was coded as: normal (0) or carinate (1).
13. **Antennules**: Eriphiids have the antennules folding transversely or almost so. This character state was coded as: folding at less than 15° (0), 45° (1) or almost vertical (2).
14. **Second antennal segment**: A relatively squarish segment is here regarded as plesiomorphic. This character state was coded as follows: length to width ratio 1–1.9 (0), 2–3.4 (1) or 3.5 and above (2).
15. **Shape of basal antennal segment**: A relatively narrow, subcylindrical segment is typical and is regarded as plesiomorphic. This character state was coded as: narrow (0) or very broad (1).
16. **Position of basal antennal segment**: This segment is normally well separated from the anterior edge of the basal segment of the antennules. This is regarded as plesiomorphic. This character state was coded as: normal (0) or reaching to anterior edge of antennular basal segment (1).
17. **Eyes**: Normal sized eyes which are clearly visible from the dorsal view are typical and regarded here as plesiomorphic. This character state was coded as: normal/exposed (0) or small/concealed (1).
18. **Antero-external angle of merus of third maxilliped**: An auriculiform angle is regarded as apomorphic. This character state was coded as: normal (0) or auriculiform (1).
19. **Shape of merus of third maxilliped**: A squarish to subrectangular merus is considered to be the

- plesiomorphic condition, with a triangular structure (a modification for burrowing). This character state was coded as: quadrate (0) or triangular (1).
20. **Position of exopod of third maxilliped:** Almost all xanthoids have the exopod exposed and is regarded here as plesiomorphic. This character state was coded as: exposed (0) or hidden (1).
  21. **Shape of exopod of third maxilliped:** Eriphiids have relatively broad exopods (plesiomorphic). This character state was coded as: broad (0) or narrow (1).
  22. **Length of exopod of third maxilliped:** Exopods of eriphiids are typically long and reach the tip of the merus. It is here regarded as plesiomorphic. This character state was coded as: reaching tip of merus (0) or normal (1).
  23. **Sulcus on ischium of third maxilliped:** A shallow sulcus is the typical condition in eriphiids (plesiomorphic). This character state was coded as: with shallow sulcus (0), with deep sulcus (1) or none (2).
  24. **Lateral margins of male abdominal segments 3–6:** The typical eriphiid condition is a gently concave to almost straight margin and is here considered to be plesiomorphic. This character state was coded as: with lateral margins all normal (0) or deeply concave (1).
  25. **Inner angle of carpus of cheliped:** All eriphiids have a gentle to prominent tooth on the inner margin (plesiomorphic). This character state was coded as: with spine on inner angle (0) or absent (1).
  26. **Outer armature of carpus of cheliped:** Eriphiids have smooth, unarmed outer surfaces (plesiomorphic). This character state was coded as: without tooth on outer margin (0) or present (1).
  27. **Dorsal armature of carpus of cheliped:** The presence of a tooth on the dorsal margin is considered to be apomorphic. This character state was coded as: without tooth on dorsal margin (0) or present (1).
  28. **Armature of merus of cheliped:** Armed meri are here regarded as apomorphic. This character state was coded as: without spines/strong teeth (0) or armed (1).
  29. **Relative length of merus of cheliped:** A short merus is typically eriphiid and regarded as plesiomorphic. This character state was coded as: short (0) or long (1).
  30. **Carpus of cheliped:** A short carpus is considered to be plesiomorphic. This character state was coded as: short (0) or long (1).
  31. **Ratio of length of manus to fingers:** An elongated manus is regarded as apomorphic. This character state was coded as: less than 2 times length of fingers (0) or longer (1).
  32. **Margin of chela:** Eriphiids have smooth, uncrested margins (plesiomorphic). This character state was coded as: smooth (0) or distinctly crested (1).
  33. **Fingers of cheliped:** Carinate fingers are regarded as apomorphic. This character state was coded as: not carinate (0) or carinate (1).
  34. **Cutting margins of fingers:** Fingers with normal teeth are regarded as plesiomorphic. This character state was coded as: dentate (0) or denticulate (1).
  35. **Gape of fingers:** Eriphiids have the cutting edges of the fingers closing almost completely when appressed, with only scattered tufts of setae or glabrous (plesiomorphic.) This character state was coded as: normal (0) or with setose median gape (1).
  36. **Relative length of dactylus of first ambulatory leg:** A relatively long dactylus is regarded as an adaptation for mucus feeding on crinoids and considered to be an apomorphic character (see Chia and Ng, 1995, 1998). This character state was coded as: subequal in length to those of other legs (0) or distinctly longer (1).
  37. **Relative length of merus of first ambulatory leg:** A relatively long merus is regarded as apomorphic. This character state was coded as: not much longer than those of other legs (0) or distinctly elongate (1).
  38. **Merus and carpus of ambulatory legs:** Simple segments are regarded as plesiomorphic. This character state was coded as: not carinate (0) or carinate (1).
  39. **Propodus and dactylus of legs:** Subchelate structures, adapted for clinging on to echinoids, are regarded as the apomorphic condition (see Chia et al., 1995; Ng and Chia, 1999). This character state was coded as: normal (0) or subchelate (1).
  40. **Ambulatory dactylopropodal lock:** Eriphiids lack this lock, which is a specialization for clinging (see Ng and Clark, 2000) and this condition is regarded as plesiomorphic. This character state was coded as: absent (0), weak (1) or present (2).
  41. **Dactylus of last ambulatory leg:** A subspatuli-

- form dactylus is regarded as apomorphic. This character state was coded as: normal (0) or subspatuliform (1).
42. **Epistome:** A narrow epistome is believed to be apomorphic. This character state was coded as: longitudinally broad (0) or narrow (1).
  43. **Endostomial ridges:** The presence of ridges is regarded as plesiomorphic, being present in Eriphiidae. This character state was coded as: present (0) or absent (1).
  44. **Anterior thoracic sternites:** Eriphiids have relatively broad anterior thoracic sternites (here regarded as plesiomorphic). This character state was coded as: broad (0) or narrow (1).
  45. **Shape of male telson:** In eriphiids, the telson is semicircular or almost so (plesiomorphic). This character state was coded as: semicircular (0) or triangular (1).
  46. **Male abdominal shape:** Eriphiids have broadly triangular male abdomens which appear subrectangular (plesiomorphic). This character state was coded as: subrectangular (0) or triangular (1).
  47. **Position of male abdomen relative to anterior thoracic sternites:** This character state was coded as: not nearly reaching to suture between sternites 2 and 3 (0) or reach (1).
  48. **Proportions of male telson:** This character state was coded as: normal (0) or twice length of segment 6 (1).
  49. **Penis:** The coxal condition is clearly the plesiomorphic condition (*sensu* Guinot, 1978, 1979). This character state was coded as: coxal (0) or coxosternal (1).
  50. **G1 proportions:** Eriphiid G1s are invariably stout (plesiomorphic). This character state was coded as: stout (0) or slender (1).
  51. **G1 shape:** Eriphiid G1s are relatively straight (plesiomorphic). This character state was coded as: straight (0), gently sinuous (1) or very sinuous (2).
  52. **G1 base:** Eriphiid G1 bases are gently sinuous to almost straight (plesiomorphic). This character state was coded as: normal (0) or bent sharply (1).
  53. **G1 tip:** Tips of G1s are gently tapering to a tip or gently subtruncate in Eriphiidae (plesiomorphic). This character state was coded as: tapering (0) or fluted (1).
  54. **G2 shape:** This character state was coded as: elongate (0), short but not sigmoid (1) or sigmoidal (2).
  55. **Male abdominal segments:** Having all the segments freely movable is regarded as plesiomorphic. This is regardless of whether the sutures are still visible (see Ng and Chia, 1994). This character state was coded as: segments freely movable (0) or segments 3–5 fused (1).
  56. **Antennal flagellum:** A free antennal flagellum is regarded as the plesiomorphic condition. This character state was coded as: free (0) or lodged in notch in frontal margin (1).
  57. **Distal part of G1:** Eriphiids have relatively simple G1s in which the distal margins may be lined with spines of varying lengths and/or simple to slightly plumose setae (plesiomorphic) as apposed to lined with complex folds, unusually shaped tubercles (e.g., fungiform) and/or very long, very plumose setae (apomorphic). This character state was coded as: simple (0) or with elaborate folds, long setae and/or long spines (1).