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 pereiopodal 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 (*Echinocarcinus pentagonus*) in the laboratory and the zoal stages, together with the megalop, were described by Van Dover et al. (1986). Subsequently, the zoal and megalop stages of *Zebrida adamsii* (by Mori et al., 1991) have been described and the first stage zoal of *Harrovia longipes* (as *H. albolineata*) by Lim and Ng (1988), *H. albonineata* [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 *Echinocarcinus pentagonus* indicated that the species was not a member of the Parthenopidae. Although the zoal showed strong morphological relationships to xanthid crabs, subfamily Pilumninae, Van Dover et al. (1986) were uncertain if *Echinocarcinus 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).

Števčić 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 zoal 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 Števčić 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 *Eumedon* as a member of the Parthenopidae. Later, Dana (1854) established the family Eumedonidae for four genera, *Eumedon* 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 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. *Echinocarcinus* Rathbun, 1894, *Zebridanus* Chia et al., 1995, *Permanotus* Chia and Ng, 1998, *Tauropus* Chia and Ng, 1998, and *Tiarademdon* Chia and Ng, 1998; and three genera were transferred to the family. These were *Zebridaea* 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 *Otognath* Ng and Števčić, 1993; but all these genera have now been assigned to other families: *Calmania*, *Dentoxanthus*, and *Otognath* to the Pilumnidae by Števčić et al. (1988), Števčić and Ng (1988), Ng and Števčić (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
echinoderms as diagnostic eumedonid features. More
 projecting button on subproximal edge of the dactylus),
formed by a rounded submedian extension of the
special dactylopropodal process on the ambulatory legs
recognized the Eumedonidae. He used primarily the
lateral margin, which is shaped to slide beneath a
general acceptance in brachyuran literature. Ng (1998),
et al. (1988), the familial status of the group gained
by Stevcic et al. (1988).

genera were referred to the subfamily Ceratocarcininae
Rhabdonotus
according to Chia and Ng (1995) was
in a key to the marine brachyuran families of the world,
Harrovia.
Ceratocarcinus
Both these
and
also close to
position of antennule, cheliped characters, length of the
first pair of walking legs and host preference,
both could be referred to the Eumedoninae (sensu
Stevic et al., 1988). However, with regard to the
species bear a close similarity
argued that
Rhabdonotus
in carapace form to
and, because of this,
Echinoecus
division with regard to the genus
and
Echinoecus
White, 1847 (three
(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, 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 Stevic et al., 1988) or as a subfamily of the
Pilumnidae (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
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Once the Eumedonidae were established by Stevic
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
Ceratocarcinus Adams and White (in White, 1847)
(three species), Echinoecus Rathbun, 1894 (three
species), Eumedon H. Milne Edwards, 1834 (five
species), Gonatotus 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
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Table 1. List of genera and species assigned to the Eumedoninae Dana, 1854, with types listed first

<table>
<thead>
<tr>
<th>Genus</th>
<th>Species Information</th>
</tr>
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<tbody>
<tr>
<td>Ceratocarcinus</td>
<td>Adams and White (in White, 1847)</td>
</tr>
<tr>
<td>C. longimanus</td>
<td>White, 1847 (= Ceratocarcinus speciosus Dana, 1851; Ceratocarcinus dilatatus A. Milne Edwards, 1872; Ceratocarcinus intermedius Zehntner, 1894)</td>
</tr>
<tr>
<td>C. frontodentata</td>
<td>(Shen, Dai and Chen, 1982)</td>
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<tr>
<td>C. trilobatus</td>
<td>Sakai, 1938</td>
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<tr>
<td>Echinoecus</td>
<td>Rathbun, 1894 (= Liomedon Klunzinger, 1906; Proechinoecus Ward, 1934)</td>
</tr>
<tr>
<td>E. pentagonus</td>
<td>(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)</td>
</tr>
<tr>
<td>E. nipponicus</td>
<td>Miyake, 1939</td>
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<tr>
<td>E. sculptus</td>
<td>Ward, 1934</td>
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<tr>
<td>Eumedonus</td>
<td>H. Milne Edwards, 1834</td>
</tr>
<tr>
<td>E. niger</td>
<td>H. Milne Edwards, 1834 (= Gonatonotus crassimanus Haswell, 1880; Eumedon villosus Rathbun, 1918)</td>
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<tr>
<td>E. brevirhynchus</td>
<td>Chia and Ng, 2000</td>
</tr>
<tr>
<td>E. intermedius</td>
<td>Chia and Ng, 2000</td>
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<tr>
<td>E. vicinus</td>
<td>Rathbun, 1918</td>
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<tr>
<td>E. zebra</td>
<td>Alcock, 1895</td>
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<tr>
<td>Gonatonotus</td>
<td>Adams and White (in White, 1847)</td>
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<tr>
<td>G. pentagonus</td>
<td>White, 1847</td>
</tr>
<tr>
<td>G. granulosus</td>
<td>(MacGilchrist, 1905)</td>
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<tr>
<td>G. nasutus</td>
<td>Chia and Ng, 2000</td>
</tr>
<tr>
<td>Hapalonotus</td>
<td>Rathbun, 1897 (= Malacosoma De Man, 1879, nomen preoccupatum)</td>
</tr>
<tr>
<td>H. reticulatus</td>
<td>(De Man, 1879)</td>
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<tr>
<td>Harrovia</td>
<td>Adams and White, 1849</td>
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<tr>
<td>H. albolineata</td>
<td>Adams and White, 1849</td>
</tr>
<tr>
<td>H. cognata</td>
<td>Chia and Ng, 1998</td>
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<tr>
<td>H. elegans</td>
<td>De Man, 1887</td>
</tr>
<tr>
<td>H. japonica</td>
<td>Balss, 1921</td>
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<tr>
<td>H. longipes</td>
<td>Lanchester, 1900 (= Harrovia plana Ward, 1936)</td>
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<tr>
<td>H. ngi</td>
<td>Chen and Xu, 1992 (= Harrovia longipes Chen and Xu, 1991, nomen preoccupatum)</td>
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<tr>
<td>H. tuberculata</td>
<td>Haswell, 1880</td>
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<tr>
<td>Permanotus</td>
<td>Chia and Ng, 1998</td>
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<tr>
<td>P. purpureus</td>
<td>(Gordon, 1934) (= Harrovia bituberculata Shen, Dai and Chen, 1982)</td>
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<tr>
<td>Rhabdonotus</td>
<td>A. Milne Edwards, 1879</td>
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<tr>
<td>R. pictus</td>
<td>A. Milne Edwards, 1879 (= Caphyra archeri Walker, 1887)</td>
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<td>R. pilipes</td>
<td>Chia and Ng, 1995</td>
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<td>R. xynon</td>
<td>Chia and Ng, 1995</td>
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<tr>
<td>Tauropus</td>
<td>Chia and Ng, 1998</td>
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<tr>
<td>T. egeriae</td>
<td>(Gordon, 1947)</td>
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<tr>
<td>Tiaramedon</td>
<td>Chia and Ng, 1998</td>
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<tr>
<td>T. spinosum</td>
<td>(Miers, 1879)</td>
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<tr>
<td>Zebrida</td>
<td>White, 1847</td>
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<tr>
<td>Z. adamsii</td>
<td>White, 1847 (= Zebrida paucidentata Flipse, 1930)</td>
</tr>
<tr>
<td>Z. longispina</td>
<td>Haswell, 1880</td>
</tr>
<tr>
<td>Z. brevicarinata</td>
<td>Ng and Chia, 1999</td>
</tr>
<tr>
<td>Zebridonus</td>
<td>Chia, Ng and Castro, 1995</td>
</tr>
<tr>
<td>Z. mirabilis</td>
<td>Chia, Ng and Castro, 1995</td>
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</tbody>
</table>
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.


*Rhabdonotus pictus* A. Milne Edwards, 1879: Johore Shoals, Singapore, coll. Diana Chia, 29 August 1994, 20 m, 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.


*Pilumnus vespertilio* (Fabricius, 1793); sta. 4a, Pondouine, 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, 3-7 m, 6 May 1995, hatched 20 May 1995, NHM 1998: 604 (see Ng and Clark 2000). 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.


*Eumedonus 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.


*Harrovia albolineata* Adams and White, 1849: paraleuctotype ♂ (9.5 × 7.4 mm) (NHM 43.6), Philippine Islands, coll. H. Cuming, HMS *Samarang*, 18431846; 1 paraleuctotype ♀ (9.5 × 7.4 mm) (NHM 43.6), same data as lectotype; 10 ♂♂, 2 ♀♀ (ZRC 1992.9477.9492), Johore Shoals, Singapore, dredged, coll. P.K.L. Ng, 15 May 1992.

*Permanotus purpureus* (Gordon, 1934): holotype ♂ (3.6×4.9 mm) (IRSNB 199223), 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.

Tauropus egeriae (Gordon, 1947): holotype ♂ (11.2×16.6 mm) (NHM 93.11.3.79), Macclesfield Bank, 82m, coll. Bassett Smith, HMS Egeria.


Zebrinus 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 cf cf (larger 13.0×9.1 mm), 1 ovig. ♀ (12.2×8.5 mm) (ZRC), lies 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 1984.556695573), 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.

Caimania 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 Leptoseris gardineri, 27 m, coll. V. Tyndzik, 23 July 1981.

Daldorfia horrida (Liitmsieus, 1758): 1 cf (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.


Pilodius pubescens (Dana, 1852): 1 ♂ (11.5×7.6 mm) (ZRC 1965.11.136), 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), Havennon, 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 ×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 antennulary 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 analysis

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 Tanocheles 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 analysis

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

Results

Zoea 1 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.
Maxillula (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 posteroventral
processes and 3–5 with extended posteroventral 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, unseg­
mented, distally spinulate with 1 long and 1 smaller
medial setae unequal in length.
Mandible: endopod palp absent.
Maxillula (Fig. 6a): coxal endite with 7 setae; basal
endite with 5 terminal setal processes and 2 small
tooth; endopod 2-segmented, proximal segment with 1
seta; distal segment with 6 (2 subterminal + 4 terminal)
setae; exopod seta absent.
Maxillula (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 posteroventral
processes and 3–5 with short posteroventral spinous
processes; somite 1 without setae; somites 2–5 with 1
dorsal setae; somites 2–5 with 1 pair of posteroventral 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**

**Zoeal tree description**

The zoeal 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,
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, Zebridonius, 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 Stevčić et al. (1988).

Parthenopid adults

The systematics of the Parthenopidae MacLeay, 1838 is confused, and this has affected 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 Stevčić 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. Chelifeds 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, 11, respectively) for E. pentagonus. They also describe minute dentition along the posterodorsal margin of
Table 2. Comparison between the characters of first-stage zoeas of *Permanotus purpureus* (Gordon, 1934) [eumedonid] and those of a typical parthenopid *Rhinolambrus pelagicus* (Ruppell, 1830), as described in this present study

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

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 Halimédiens") 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 Števčič 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, pereiopods, 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 Stevčić 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**

Števčić 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. Števčić et al. (1988) considered that, because there was no agreement as to which larval features are pleiomorphic 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), Števčić 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 zoal cladogram (see Fig. 9) which has a basal dichotomy separating Eriphia smithii, Rhinolambrus pelagicus and Pilodus 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 zoal 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 antennulary 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 vesperitilo. 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 antennary 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.

Števčić 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 vespertilio*) 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 zoae 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 Števčić 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 Ceratocarcininae). 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 (Števčić 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), Števčić and Gore (1981), Ng and Rodriguez (1986) and Števčić 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 zeas 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).

Acknowledgements

Diana Chia completed most of the alpha taxonomic work on eumedonines, Tan Swee Hee is now studying the parthenopids and Oliver Chia helped with the adult datasets for the cladistic analysis. To them and for their kind help, the authors are most grateful. Diana Chia and Peter Castro were a great help to us because their intrepid collecting obtained many important species and larvae. Didier Vandenspiegel was most kind in helping us get specimens of *Hapalonotus*. PKLN is also very grateful to Daniele Guinot and Peter Davie for reading early versions of his draft manuscript on the Pilumnidae and their many useful suggestions, from which many of the present ideas are drawn. Discussions with Zdravko Števčić on the composition of the Eumedoninae and Pilumnidae have also helped facilitate development of many of the ideas presented in this paper.

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### APPENDIX 1

**Zoeal data matrix**

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### APPENDIX 2

**Adult character matrix**

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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 was coded as 0 = absent, 1 = present.

3. Antennule: the number of terminal setae; the number of terminal antennulary 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 sub-terminal. 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 zoea 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


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 lobeiform, 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 number of teeth 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 maxillipede**: Almost all xarthoids 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 maxillipede**: Eriphiids have relatively broad exopods (plesiomorphic). This character state was coded as: broad (0) or narrow (1).

22. **Length of exopod of third maxillipede**: 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 maxillipede**: 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 subspatul-
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 sub-rectangular (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 opposed 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).