

**Re-establishment of the Family Eumedonidae Dana, 1853 (Crustacea: Brachyura)**

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On the basis of a re-examination of all available data concerning the systematic position and status of the genus *Eumedonus* and allied genera it is concluded that these taxa form a separate family within the superfamily Xanthoidea (*sensu* Guinot, 1978). The family is characterized not only by particular morphological features but by the symbiotic mode of life of its members.

KEYWORDS: Eumedonidae, Revision, Brachyura, Symbiosis.

**Introduction**

The subject of the present revision is a small group of brachyuran crabs variously classified as the subfamily Eumedoninae of either the families Parthenopidae or Pilumnidae, as a separate family, the Eumedonidae, or even as the superfamily Eumedonoidea. We address the problem of whether the earlier classification is correct, and suggest changes on the basis of new knowledge. This revision focuses on the alleged relationships of the eumedonine crabs with the parthenopids or with the pilumnids as a key to the solution of the problem. Accordingly, each of these taxa is critically compared. This comparison includes all criteria used by previous authors as well as newer criteria given by Guinot (1978, 1979).

*Historical review*

The first eumedonine crab to be described was *Eumedonus niger* H. Milne Edwards (1834) which was included in the tribe 'Parthénopeins'. Dana (1853) subsequently included this genus, together with the genera *Ceratocarcinus* White, *Harrovia* Adams and White, and *Gonatonotus* White in his newly described family Eumedonidae, placing it in the legion 'Parthenopinea' or Maiioidea 'Cancriidica'. Neumann (1878), however, relegated these genera to the subfamily Eumedoninae, included within the family Parthenopidae. Miers (1879b, 1886) followed this classification. Ortmann (1893, 1894), however, concluded that these genera required a familial rank and so resurrected the family Eumedonidae. Nevertheless, all subsequent authors, including Alcock (1895), Klunzinger (1906), Borradaile (1907), Rathbun (1910, 1925), Flipse

(1930), Gordon (1934), Stephensen (1945), Balss (1957), Serène *et al.* (1958) [in a revision of the group], Serène (1968), Serène and Romimohtarto (1963), Glaessner (1969), Sakai (1965, 1976), and Takeda (1973), continued to consider eumedonines as a subfamily of the Parthenopidae. An exception is Estampador (1937, 1959), who listed them again as a separate family. Tirmizi and Serène (1971), however, suggested that the eumedonines belong to the Xanthidae, and Ng (1938), in his revision of the pilumnid crabs included the Eumedoninae in the Pilumnidae (see also Ng and Rodríguez, 1986). Guinot (1978) considered the relationships of the group as an open question but later lists them as the superfamily Eumedonoidea (Guinot, 1985).

In addition, the genera *Calmania* Laurie and *Dentoxanthus* Stephensen have been included in the Eumedoninae. Although *Calmania prima* was described by Laurie (1906) and placed in the Xanthidae, authors such as Balss (1922, 1957) and Gordon (1934) placed it in the Eumedoninae. *Dentoxanthus* was described from a single female and included in the Xanthidae but in an uncertain subfamily (Stephensen, 1945). Balss, in his comment by letter (see Stephensen, 1945, p. 163–164), pointed out the unique characteristics as well as the difficulties in the classification of this genus. Thereafter, Holthuis (see Serène *et al.*, 1958, p. 139) drew attention to some 'eumedonine' characteristics in the genus. Another female specimen was later described by Tirmizi and Serène (1971) and thereafter two male specimens by Tirmizi and Kazmi (1982). The latter authors included *Dentoxanthus* in the Eumedoninae and considered it to be close to the genus *Harrovia*.

A re-examination of the literature on the eumedonines shows that most of the published information is confined primarily to descriptions of genera and species and that the discussion of their systematic positions and relationships are scant. Some useful information on their morphology has been given by Gordon (1934), Serène *et al.* (1958), Guinot (1964), Serène and Rominohtarto (1963), Sakai (1976), and Tirmizi and Kazmi (1982). Until recently (Castro, 1978; Van Dover *et al.*, 1986) the larvae for any eumedonine genus was unknown.

#### *Relationships to the Family Parthenopidae*

Eumedonines share with the parthenopids several morphological characteristics. Common features include:

1. The body shape is of an 'oxyrhynchous' type. The anterolateral margins of the carapace converge and the front usually projects into a pseudorostrum.
2. The orbits are small, circular, and well defined, with the inner orbital hiatus filled by the basal antennal article and, in some genera, also with the following article.
3. The eyestalks are usually short and thick and can be retracted into the orbits.
4. The antennules are more or less obliquely folded in antennular fossae.
5. The antennae are not fused with the front or the epistome. The first antennal article (urinal) is very small and in contact with the epistome; the basal (second = 2+3) is the largest, whereas the following articles are more slender. The flagellum is slender and short.
6. The epistome is short, wide, not overlapped by the third maxillipeds, and produced forward in the middle.
7. The buccal cavern is usually quadrangular and completely covered by the third maxillipeds. The palp of the latter is articulated at the anterointernal angle of the merus.
8. The chelipeds are not pressed tightly against the anterolateral margin of the

carapace and are rarely asymmetrical. They may be extended laterally or held transversely in front of the carapace. The fingers are much shorter than the palm and curved abruptly on the hand at an angle toward the side of the fixed finger at its dactylo-propodal articulation. The ischio-meral articulation is fused, but it has a distinct suture.

9. The sternum is of moderate breadth, with sternites arranged more or less in parallel, except the last one, which is arranged radially. The sterno-abdominal cavity is present and the retaining system of the abdomen is functional. The median line is present only on one or two (last and penultimate) of the posterior sternites. The posterior part of the thoracic sternum is slightly elevated and rounded, so that the coxae of the fifth pereopods are visible from above.
10. The genital openings are coxal in males, sternal in females; the oviduct opening belongs to the concave type.
11. The first and second proximal abdominal segments are visible from above.
12. The surface of the body is never hairy (or only sparsely setose).

The morphological differences between the two groups are several. These include:

1. In eumedonines the regions of the dorsal surface of the carapace are only partially recognizable (particularly the cardiac and gastric regions), whereas in parthenopids a depression separates the branchial region from the gastric and cardiac regions. In the eumedonines (except *Rhabdonotus* A. Milne Edwards) the anterolateral and posterolateral margins of the carapace are clearly separated, usually by a spine or at least a well-marked angle. This is similar to that seen in some parthenopid genera (*Leiolambrus* A. Milne Edwards and *Heterocrypta* Stimpson).
2. The projecting front, a pseudorostrum, is present in both groups, but in parthenopids it is never notched, although it may be either sharply or bluntly pointed or even obscurely trilobed. In the eumedonines the middle of the front is notched so that it is bilobed or four-lobed in some genera, and only rarely emarginated at the tip.
3. The antennules are folded only slightly obliquely in parthenopids, whereas in eumedonines they are usually more obliquely folded in antennular cavities.
4. The basal (second = 2 + 3) antennal article usually does not reach the inner orbital margin in parthenopids; in eumedonines it reaches the inner margin and partially fills the orbital hiatus.
5. The buccal frame of eumedonines does not have any specialized features. In burying parthenopids it is sometimes slightly narrowed in front. The palp of the third maxillipeds is well developed in eumedonines, but is somewhat reduced in size in some parthenopids, where it lies more or less concealed in a groove in the merus. This groove is absent in eumedonines.
6. The chelipeds of parthenopids are disproportionately large and long in relation to the body, and characteristically extend transversely in a resting position. The chelipeds of eumedonines are of moderate size and length in relation to the cephalothorax (being relatively larger only in *Harrovia*) and when inactive they are folded beneath the anterolateral margins of the carapace. The chelipeds of parthenopids are usually triangular in cross section (with the exception of *Daldorfia* Rathbun); in eumedonines they are cylindrical in cross section. The tips of the chelae are usually directed downward in parthenopids, a situation not observed in live eumedonines.

7. The sternum is at level III B (following the terminology of Guinot, 1979) in eumedonines, whereas in parthenopids it is at level III C, that is, characterized by having all sternal sutures interrupted. The only exceptions are *Daldorfia* Rathbun and *Thyrolambrus* Rathbun, where the sternum is also at level III B (4/5 and 5/6 sternal sutures interrupted and 6/7 and 7/8 complete). The median line is complete in eumedonines, but it is incomplete or vestigial in parthenopids.
8. The abdomen is divided into seven freely articulating segments in both sexes in eumedonines; segments 3 to 5 are always fused in parthenopid males, but sutures may or may not be visible.
9. The male first pleopods of parthenopids are usually long, cylindrical, stout, more or less tapering and/or bent at the tip, sometimes bluntly truncated, and usually armed with spines, spinules, and setae. In eumedonines they belong to the *Pilumnus*-type: long, slender, and S-shaped. Its distal portion is armed with rows of bristles and the tip is obliquely curved downward and outward. The male second pleopod of parthenopids is relatively long and usually shorter than the first. Its corneous tip is spiral, elongated, and usually recurved distally. In eumedonines the gonopod tip is very minute and sigmoid; its distal end is somewhat enlarged and oblique and it is proximally armed with small spines.
10. In contrast to parthenopids, which have unspecialized pereopods, the legs of eumedonines have a very flexible dactylus, the result of a modified dactylopropodal articulation. It can be flexed to touch the propodus, thus resulting in prehensile legs. In *Zebriida* White the dactyli are subchelate. In other eumedonine genera the inner border of the propodus and dactylus is often provided with hairs and spinules. These represent adaptations facilitating attachment to the host.

*Relationships to the Family Pilumnidae (sensu Guinot, 1978)*

Morphological similarities between the eumedonine genera *Ceratocarcinus* White and *Harrovia* Adams and White (Group B of Gordon, 1934) when compared with a typical representative of the Pilumnidae (e.g. *Pilumnus spinifer* H. Milne Edwards) are of interest. The similarities between the male first pleopods of eumedonines and those of the Pilumnidae are especially intriguing. Furthermore, the larvae of the eumedonine, *Echinoecus pentagonus* (A. Milne Edwards), also show affinities with the Pilumnidae (see below). These similarities (and exceptions) between the Pilumnidae and the remaining eumedonine genera (Group A of Gordon, 1934) are given as follows:

1. Cephalothorax a little broader than long. Anterolateral margins of the carapace are usually shorter than the posterolateral margins. The regions of the carapace are usually only partially defined, but may be distinct in some species.
2. The frontal margin of the carapace is broad and (except in Group A) exceeds by half or greater the maximal carapace length. The margin is lamellate and deflexed in some species.
3. A median notch is present, and the two lateral notches in which antennal flagella are usually placed (except in Group A) result in a four-lobed structure.
4. The inner suborbital angle is often prominent (except in Group A).
5. The chelipeds are not pressed tightly against the anterolateral margin of the carapace, but may be folded against or beneath the buccal cavity when in resting position.

6. The ischio-meral articulation of the chelipeds is fused, but the suture is well-marked.
7. The fingers of the chelipeds of all pilumnids and of some species of *Harrovia* are dark.
8. The buccal cavity is quadrangular; the epistome is short, wide, and produced forward medially; the endostome bears a longitudinal ridge.
9. A sterno-abdominal cavity is present, as is a functional locking system of the abdomen.
10. The abdominal segments are not fused, abdominal plates cover the entire space between the coxae of the fifth pereopod.
11. The male first pleopods are very slender, long, and sinous; the second is very small and sigmoid.
12. The sternum is at level III B (following the terminology of Guinot, 1979).
13. The ventral portion of the cephalothorax is rounded posteriorly, so that the coxae of the last pair of pereopods are elevated and visible from above, as are the two proximal abdominal segments.

The differences between pilumnids and eumedonines are as follows:

1. In eumedonines the carapace is subhexagonal or subpentagonal, but in pilumnids is transversely oval or subquadrilateral. The cephalothorax is more flattened in eumedonines.
2. The anterolateral carapace margins of pilumnids are arcuate and dentate (usually with at least three prominent teeth behind the postocular angle). In eumedonines the margin is usually straight or even concave (as in *Echinoecus* Rathbun) and with (e.g. *Harrovia*) or without spines, but with one to three lobes and a very distinct spine at the junction of the anterolateral and posterolateral margins (except *Rhabdonotus* A. Milne Edwards).
3. In pilumnids the surface of the carapace is usually granular, spinose, or hairy, whereas in eumedonines it is smooth and rarely with spines on the dorsal surface.
4. The antennules fold obliquely in eumedonines, transversely in pilumnids.
5. The basal antennal article (2+3) may fill the suborbital hiatus in some eumedonines, but in pilumnids it is almost always much larger and not only fills the suborbital hiatus but may just reach the frontal margin as well.
6. The orbits of pilumnids are elliptical and of moderate size; those of eumedonines are small and subcircular. The eyestalks are of moderate size in pilumnids, but short and thick in eumedonines.
7. In eumedonines the chelipeds are equal or subequal in size, not robust and smooth, whereas in pilumnids they are more or less dissimilar, strongly granulated or even spinose, at least partly covered with setae, and robust. In pilumnids the fingers of the chelipeds are directed less obliquely downward than those of eumedonines.
8. The pereopods of eumedonines are often provided with triangular tubercles or even spines, whereas those of pilumnids, if armed, show only reduced spinulation. In addition, eumedonine walking legs are prehensile.
9. The inner ends of the 4/5 and 5/6 sternal sutures are closer in pilumnids than in eumedonines.
10. The male first pleopod of eumedonines is relatively stouter than that of pilumnids.

11. Eumedonines are small symbiotic crabs (i.e. establishing close, obligate, and often specific association with an invertebrate host as defined by Castro, 1986), often variegated in colour, and much less active than the larger, more uniformly coloured and active pilumnids, almost all of which are free-living.

*Larval characters and development in eumedonine, parthenopid, and xanthoid crabs*

The only species of eumedonine crab of which the larval development has been published is *Echinoecus pentagonus* (A. Milne Edwards) (see Castro, 1978; Van Dover, *et al.*, 1986). Larvae of *Harrovia elegans* de Man have been reared and described by Y. Fukuda (unpublished). A detailed examination of the larval development and zoeal characters shows that *E. pentagonus*, at least, is not a parthenopid. Having no more than three (or rarely four) zoeal stages (whereas most parthenopid crabs pass through at least five stages) and exhibiting zoeal features that seem to align *E. pentagonus* more closely with the Xanthoidea (*sensu* Guinot, 1978) rather than the Parthenopidae, supports this removal. Specifically, the setation of the maxillary endopod, and the maxillulary endopod do not agree with known parthenopid zoeae. General carapace configuration is not parthenopid, but xanthoid, and is nearly identical to the larvae of some pilumnids (e.g. *Pilumnus dasypodus* Kingsley) in nearly every appendage feature, including positioning and number of setae (see Sandifer, 1974). Additional similarities are seen in pilumnid and *E. pentagonus* larval telsons and most abdominal somite armature. Indeed, these similarities taken as a whole would make it very difficult to separate the larvae of *E. pentagonus* from several species of *Pilumnus* Leach or its relatives.

The observed similarities between *E. pentagonus* and, for example, *P. dasypodus*, pose some interesting and vexing questions. If larval characters are conservative, as is traditionally held, then the xanthid features of *Echinoecus* Rathbun suggest that this genus is non-parthenopid (see Van Dover *et al.*, 1986 for discussion). Until larvae from the type genus of the family (*Eumedonus* H. Milne Edwards) and other eumedonine genera become known, it is not certain at present whether eumedonine larvae (*sensu lato*) are a consequence of convergent evolutionary trends, and/or whether the eumedonine and the pilumnid crabs shared a common ancestor. There is no agreement at present as to which larval features are plesiomorphic and which are apomorphic and little further can be said. Examination of more eumedonine larvae would therefore provide much needed additional data.

*Ecology*

Eumedonine crabs differ sharply from parthenopids in terms of their respective habitats. Whereas parthenopids are found free-living on various types of substrates (particularly sand, shell hash, and mud), eumedonines appear to live in obligate symbiotic associations with echinoderms and cnidarians. Although in almost all eumedonines the nature of these associations remains unknown, the term symbiosis is used here to encompass all types of close heterospecific associations irrespective of harm or benefit to the partners (see Castro, 1986). Nevertheless, eumedonines are often referred to in the literature as commensals or parasites even when information on their feeding habits and other aspects of the symbiont-host relationship is not known.

Most of the early records in the literature provide little information on the habitats of eumedonines. Many specimens were obtained from dredged material and no records of hosts are given. With the advent of scuba diving, the symbiont-host relationship can be preserved during collection, thus affording more reliable information on microhab-

itats and host specificity. These crabs, however, easily remain unnoticed as a result of their characteristic small size and cryptic colouration. Table 1 summarizes all recorded hosts from the literature and from specimens examined by P. Castro from several collections.

Echinoderms are by far the most common hosts. Echinoids are the almost exclusive hosts of *Echinoecus* Rathbun, *Eumedonus* H. Milne Edwards, *Gonatonotus* White, *Proechnoecus* Ward, and *Zebrida* White, whereas *Ceratocarcinus* White, *Harrovia* Adams and White, and *Rhabdonotus* A. Milne Edwards have almost always been recorded from crinoids. Soft corals have been recorded as additional hosts in two species, and a scleractinian coral in another.

Information on habitat and/or hosts is scant for eight of the species. Two records of one of these species, *Glyptocarcinus truncatus* (Rathbun), were found free-living under rocks by scuba divers at depths of 21 and 23 m from the island of Oahu, Hawaii (see Takeda, 1979). A closely related species has been recorded in Japan from a 'coral fishing net' (Takeda, 1973) and from a lobster net (as *Harrovia truncata*, Sakai, 1976). A young female of *Harrovia elegans* de Man was collected 'on the surface of rock in intertidal zone' in central Japan (Imanaka *et al.*, 1984).

Eumedonines have been recorded only from the Indo-west Pacific region (see Table 1). *Ceratocarcinus dilatatus* A. Milne Edwards, however, has been reported from South Australia (Hale, 1927; Griffin and Yaldwin, 1968). Eumedonines range from the intertidal zone (as in *Proechnoecus sculptus* Ward) to a depth of 426 m, the maximum depth recorded for *Glyptocarcinus truncatus* (Rathbun) (see Rathbun, 1906). *Echinoecus pentagonus* (A. Milne Edwards) appears to be the most widely distributed species.

Eumedonines are characterized by walking legs provided with a highly flexible dactylo-propodal articulation, an adaptation which provides them with a prehensile mechanism for clinging to the host. A subchelate positioning of the dactylus against a distally enlarged merus (as in *Zebrida*) and the presence of hairs or spinules along the merus and dactylus are of similar adaptive significance. Similar morphological adaptations are observed among symbiotic xanthid crabs (Serène, 1961).

Locomotion of eumedonines on sandy or muddy substrates is difficult or impossible, as has been observed for *Z. adamsi* White (Suzuki and Takeda, 1974), *E. pentagonus* (P. Castro, personal observation), and *C. longimanus* White and *H. albolineata* Adams and White (P. Ng and G. Lim, personal communication). The cryptic colouration and spinulation of the carapace in many eumedonines and their small size (carapace length not often exceeding 1.0 cm) are additional (although not necessarily exclusive) adaptations for living in close association with a host (see Wicksten, 1983).

Very little is known about the biology of eumedonines. *E. pentagonus* is the species most widely studied. Males and immature females inhabit the peristome and the test of their sea urchin host, feeding on epithelial tissue and most probably on the tube feet (Castro, 1971). Tissue destroyed by the small crabs is rapidly regenerated by the host. The much larger adult females are confined to the host's rectum, typically inducing the conspicuous, gall-like calcification of the host's periproct. They feed on the host's fecal pellets and on host coelomocytes that accumulate as a pigmented layer on the lumen of the rectum. *Z. adamsi* was recorded by Mortensen (1943) as feeding on 'spines, tubefeet, and pedicellariae, cleaning the test completely along its way' in *Salmacis bicolor* L. Agassiz, a sea urchin from the Gulf of Thailand (also see Rathbun, 1910). The crab is similarly described by Suzuki and Takeda (1974) as responsible for creating

Table 1. Geographical distribution and hosts of eumedeonids as recorded in the literature and from specimens in collections in the Australian Museum, Sydney (AM), British Museum (Natural History) (BMNH), Bernice P. Bishop Museum, Honolulu, Hawaii (BPBM), and Muséum national d'Histoire naturelle, Paris (MNHN).

Species	Geographical distribution	Recorded hosts
<i>Ceratocarcinus</i> White, 1847		
<i>C. dilatatus</i> A. Milne Edwards, 1872	Singapore (Walker, 1887); Borneo and Flores Sea (Flipse, 1930); Philippine Is. (Roxas, 1930 as <i>C. longimanus</i> , <i>vide</i> P. Ng, personal communication); Moluccas (de Man, 1888); Roebuck Bay, Western Australia (AM); Torres Strait, northern Australia (McCulloch, 1913); Queensland, Australia (Rathbun, 1918; McNeill, 1968); South Australia (Hale, 1927); New Caledonia: type locality (Milne Edwards, 1872)	CRINOIDEA: <i>Zygometra</i> sp., Western Australia (AM)
<i>C. intermedius</i> Zehntner, 1894	Moluccas: type locality (Zehntner, 1894)	unknown
= <i>C. dilatatus</i> A. Milne Edwards, 1872 ( <i>vide</i> P. Ng, personal communication)		
<i>C. longimanus</i> White, 1847	Strait of Malacca (Alcock, 1895); Viet Nam (Serène <i>et al.</i> , 1958); north Borneo (White, 1847a, 1847c; Adams and White, 1848); Moluccas (Gordon, 1934; Serène and Romimoharto, 1963); Aru Is., eastern Indonesia (Miers, 1886); Townsville, Queensland, Australia (AM)	CRINOIDEA: unidentified species, Viet Nam (Serène <i>et al.</i> , 1958); unidentified species, Queensland, Australia (AM)
<i>C. speciosus</i> Dana, 1853	Fiji: type locality (Dana, 1853; Balss, 1938)	CRINOIDEA: unidentified species, Fiji (Dana, 1853)



Table (continued)\*

Species	Geographical distribution	Recorded hosts
<p><i>C. spinosus</i> Miers, 1879</p>	<p>Red Sea (Bass, 1924); Christmas I., eastern Indian Ocean (AM); 'Eastern Seas': type locality (Miers, 1879a); Sparty I., South China Sea (Serène <i>et al.</i>, 1958); Flores Sea, Indonesia (Flipse, 1930); Japan (review by Sakai, 1976)</p>	<p>CRINOIDEA: <i>Decametra chadwicki</i> (A. H. Clark) (adults and megalopae), <i>Heterometra savignii</i> (J. Müller), and <i>Lamprometra klunzingeri</i> (Hartlaub), Red Sea (Fishelson, 1974); unidentified species, Japan (Sakai, 1938b); ANTHOZOA: <i>Dendronephthia</i> sp., Japan (Sakai, 1976)</p>
<p><i>C. trilobatus</i> (Sakai, 1938) = <i>Harrovia trilobata</i> Sakai, 1938</p>	<p>Fuzhou, China, East China Sea (BMNH); Japan: type locality (Sakai, 1938a; review by Sakai, 1976)</p>	<p>CRINOIDEA: <i>Comanthus japonicus</i> (J. Müller), Japan (Sakai, 1938a, 1976)</p>
<p><i>Echinoecus</i> Rathbun, 1894 <i>E. pentagonus</i> (A. Milne Edwards, 1879) (for complete synonymy see Serène <i>et al.</i>, 1958 and Sakai, 1976)</p>	<p>Red Sea (Klunzinger, 1906); Madagascar (Gravier, 1922); Mauritius: type locality (Milne Edwards, 1879); Nicobar Is. (Sastry, 1977, 1981); Phuket I., Andaman Sea (P. Castro, unpublished); Gulf of Thailand (Naiyanetr, 1980); Cocos Is., eastern Indian Ocean (Tweedie, 1950); Viet Nam (Serène <i>et al.</i>, 1958); South China Sea (Anonymous, 1974); Moluccas (Serène <i>et al.</i>, 1974); New Guinea (Bouvier and Seurat, 1905); Solomon Is., Line Is. (R. U. Gooding, unpublished); South Korea (Kim and Chang, 1985); Japan (review by Sakai, 1976); Ogasawara (Bonin) Is. (Rathbun, 1894; Miyake, 1939); Hawaiian Is. (Rathbun, 1906; Caëstro, 1971); Tuamotu Archipelago (Bouvier and Seurat, 1905; Nobili, 1907; Holthuis, 1953; Morrison, 1954)</p>	<p>ECHINOIDEA: adult females in rectum of <i>Echinothrix</i> spp. and <i>Diadema</i> spp. throughout its distribution (partial review by Serène <i>et al.</i>, 1958); 'anal region' of <i>Phyllacanthus dubius</i> Brandt, Ogasawara Is. (Miyake, 1939); on the surface of <i>Anthocidaris crassispina</i> (A. Agassiz) (Imanaka <i>et al.</i>, 1984) and <i>Pseudocentrotus depressus</i> (A. Agassiz), Japan (review by Sakai, 1976); on <i>Heterocentrotus mammillatus</i> (Linnaeus), Red Sea (Zool. Museum, Tel Aviv University)</p>

Table (continued)

Species	Geographical distribution	Recorded hosts
<p><i>Eumedonus</i> H. Milne Edwards, 1834  <i>E. crassimanus</i> (Haswell, 1880)  = <i>E. villosus</i> Rathbun, 1918 (<i>vide</i> Griffin, 1972)</p>	<p>East China Sea (Takeda and Miyake, 1972); Queensland, Australia (Rathbun, 1918); New South Wales, Australia: type locality (Haswell, 1880; Griffin, 1972)</p>	<p>ECHINOIDEA: <i>Prionocidaris australis</i> Ramsay, eastern Australia (Rathbun, 1918; Griffin, 1972)</p>
<p><i>E. granulosus</i> MacGilchrist, 1905  = <i>E. zebra</i> Lenz, 1905 (<i>vide</i> Barnard, 1954)</p>	<p>Red Sea (Guinot, 1964), Persian Gulf: type locality (MacGilchrist, 1905); Zanzibar (Lenz, 1905); Mozambique (Barnard, 1954); Amirante Is., western Indian Ocean (Rathbun, 1911); Seychelles (Serène, 1977); Mauritius (Ward, 1942); Japan (review by Sakai, 1976); Ogasawara (Bonin) Is. (Ooishi, 1970)</p>	<p>ECHINOIDEA: unidentified species, Zanzibar (Lenz, 1905); ANTHOZOA: <i>Stylophora pistillata</i> (Esper), Japan (Sakai, 1976)</p>
<p><i>E. niger</i> H. Milne Edwards, 1834  ? = <i>E. crassimanus</i> (Haswell, 1880)</p>	<p>*China: type locality (Milne Edwards, 1834)</p>	<p>unknown</p>
<p><i>E. vicinus</i> Rathbun, 1918  = <i>E. zebra</i> Sakai, 1938 (<i>vide</i> Sakai, 1976)</p>	<p>Red Sea (Monod, 1938); East China Sea (Sakai, 1932; Takeda and Miyake, 1972); Queensland, Australia: type locality (Rathbun, 1918)</p>	<p>unknown</p>
<p><i>E. zebra</i> Alcock, 1895  <i>nec E. zebra</i> Lenz, 1905 (<i>vide</i> Barnard, 1954)  <i>nec E. zebra</i> Sakai, 1938 (<i>vide</i> Sakai, 1976)</p>	<p>Sri Lanka: type locality (Alcock, 1895); Philippine Is. (Serène and Vadon, 1981); Japan (review by Sakai, 1976)</p>	<p>ECHINOIDEA: <i>Gonocidaris biserialis</i> (Döderlein), Japan (review by Sakai, 1976)</p>
<p><i>Gonatonotus</i> White, 1847  <i>G. pentagonus</i> White, 1847  = <i>Eumedonus pentagonus</i> Buitendijk, 1950 (<i>vide</i> Serène <i>et al.</i>, 1958)</p>	<p>Gulf of Thailand (Rathbun, 1910); Singapore (Walker, 1887; Buitendijk, 1950); Belitung I., Java Sea (Miers, 1879c); north Borneo: type locality (White, 1847a, 1847c; Adams and White, 1848); Torres Strait, northern Australia (Ortman, 1894); Queensland, Australia (Haswell, 1880)</p>	<p>ECHINOIDEA: <i>Prionocidaris bispinosus</i> (Lamarck), Gulf of Thailand (Rathbun, 1910); unidentified cidaroid, Singapore (P. Ng, personal communication)</p>

Table (continued)

Species	Geographical distribution	Recorded hosts
<i>Glyptocarcinus</i> Takeda, 1973 <i>G. lophopus</i> Takeda, 1973	Ogasawara (Bonin) Is.: type locality (Takeda, 1973; 1979); Japan (Sakai, 1974; 1976)	unknown (free-living?)
<i>G. truncatus</i> (Rathbun, 1906) = <i>Harrovia truncata</i> Rathbun, 1906 ( <i>vide</i> Takeda, 1979)	Hawaiian Is.: type locality (Rathbun, 1906; Edmondson, 1951)	unknown (free-living?)
<i>Harrovia</i> Adams and White, 1848 <i>H. albolineata</i> Adams and White, 1848 = <i>Ceratocarcinus albolineata</i> Stimpson, 1857 = <i>Harrovia albolineata longipes</i> Lanchester, 1900	south India (Jones and Sankarankutty, 1961; Sankarankutty, 1966, probably <i>Harrovia elegans</i> , <i>vide</i> P. Ng, personal communication); Sri Lanka (Laurie, 1906); Singapore Lanchester, 1900; Buitendijk, 1950; Viet Nam (Serène <i>et al.</i> , 1958) Hong Kong (Stimpson, 1857); Borneo (and Philippine Is.): type locality (Adams and White, 1848); Philippine Is. (White, 1847c—list only)	CRINOIDEA: <i>Lamprometra</i> sp., south India (Jones and Sankarankutty, 1961); <i>Comaster gracilis</i> (Hartlaub), Singapore (G. Lim, personal communication) unidentified species, Viet Nam (Serène <i>et al.</i> , 1958)
<i>H. bituberculata</i> Dai and Chen, 1982	Hainan I., south China: type locality (Shen <i>et al.</i> , 1982)	unknown but possibly from crinoids (A. Dai, personal communication)
<i>H. egeriae</i> Gordon, 1947	Macclesfield Bank, South China Sea: type locality (Gordon, 1947)	unknown
<i>H. elegans</i> de Man, 1887 = <i>H. japonica</i> Balss, 1921	Somalia (Castro, in press); north Arabian Sea (Tirmizi and Kazmi, 1982); Mergui Archipelago, Andaman Sea: type locality (de Man, 1887); Singapore (Buitendijk, 1950 as <i>Harrovia</i> sp., <i>vide</i> P. Ng, personal communication); Philippine Is. (Serène and Vadon, 1981); Moluccas (de Man, 1902); Taiwan (Lin, 1949); South Korea (Kim, 1970); Japan (review by Sakai, 1976); Marshall Is. (Garth, 1964; Castro, in press)	CRINOIDEA: <i>Comanthus japonicus</i> (J. Müller), Japan (review by Sakai, 1976); <i>Comaster multifidus</i> (J. Müller), Marshall Is. (Castro, in press); unidentified species, Andaman Sea (Castro, in press)

Table (continued)

Species	Geographical distribution	Recorded hosts
<i>H. frontodentata</i> Chen and Dai, 1982	South China: type locality (Shen <i>et al.</i> , 1982)	unknown but possibly from crinoids (A. Dai, personal communication)
<i>H. plana</i> Ward, 1936 *? = <i>H. albolineata</i> Adams and White, 1848 (fide Serène <i>et al.</i> , 1958)	Queensland, Australia: type locality (Ward, 1936)	CRINOIDEA: unidentified species, Queensland, Australia (Ward, 1936)
<i>H. purpurea</i> Gordon, 1934	Moluccas (Buitendijk, 1939); northwestern New Guinea: type locality (Gordon, 1934); Palau Is. (Castro, in press); Guam (Castro, in press); Marshall Is. (Holthuis, 1953; Castro, in press).	CRINOIDEA: <i>Comanthus parvicirrus</i> (J. Müller), Palau (Castro, in press); <i>Comanthus bennetti</i> (J. Müller), Marshall Is. (Holthuis, 1953); <i>Comanthina schlegeli</i> (Carpenter), Marshall Is. (Castro, in press); unidentified species, Guam (Castro in press)
<i>H. tuberculata</i> Haswell, 1880	Singapore (Lanchester, 1900); Torres Strait, northern Australia: type locality (Haswell, 1880)	CRINOIDEA: <i>Actinometra multiradiata</i> A. H. Clark, Singapore (Lanchester, 1900)
<i>Prochinocetus</i> Ward, 1934 <i>P. sculptus</i> Ward, 1934 = <i>Eumedonus sculptus</i> Buitendijk 1950	Christmas I., eastern Indian Ocean: type locality (Ward, 1934; Buitendijk, 1950; Serène and Romimohtarto, 1963)	ECHINOIDEA: oral region of <i>Colobocentrotus atratus</i> (Linnaeus), Christmas I. (Ward, 1934; Buitendijk, 1950)
<i>Rhabdonotus</i> A. Milne Edwards, 1879 <i>R. pictus</i> A. Milne Edwards, 1879 = <i>Caplyra archeri</i> Walker, 1887 (fide Serène and Romimohtarto, 1963)	south India (Sankarankutty, 1966); Andaman Sea (Lundoer, 1974); Singapore (Walker, 1887; Johnson, 1962; Serène and Romimohtarto, 1963); Viet Nam: type locality (Milne Edwards, 1879); south China (Shen <i>et al.</i> , 1982); Moluccas (de Man, 1888); Western Australia (Z. Števc̃ić, unpublished)	CRINOIDEA: unidentified species, Singapore (Johnson, 1962); unidentified species, Moluccas (de Man, 1888); ANTHOZOA: <i>Virgularia</i> sp., south India (Sankarankutty, 1966)

Table (continued)

Species	Geographical distribution	Recorded hosts
<p><i>Zebrida</i> White, 1847            = <i>Z. adamsi</i> White, 1847            = <i>Z. longispina</i> Haswell, 1880 (<i>vide</i>            Serène <i>et al.</i>, 1958)            = <i>Z. paucidentata</i> Flipse, 1930 (<i>vide</i>            Suzuki and Takeda, 1974)</p>	<p>south India (Henderson, 1893; Alcock, 1895;            Daniel and Krishnan, 1979); Sri Lanka (Laurie,            1906); Andaman Sea (Lundoer, 1974); Gulf of            Thailand (Rathbun, 1910; Serène and            Romimoharto, 1963); Singapore (Johnson,            1962); south China (Shen <i>et al.</i>, 1982); north            Borneo: type locality (White, 1847b, 1847c;            Adams and White, 1848); Celebes (Flipse,            1930); Jolo I., Philippine Is., (BPBM);            Cockburn Sound, Western Australia (AM);            Torres Strait, northern Australia (Haswell,            1880); Queensland, Australia (McNeill, 1968);            New Caledonia (MNHN); Japan (review by            Suzuki and Takeda, 1974)</p>	<p>ECHINOIDEA: <i>Salmacis virgulata</i> L. Agassiz,            south India (Daniel and Krishnan, 1979);  <i>Salmacis bicolor</i> L. Agassiz and <i>Toxopneustes</i>  <i>pileolus</i> (Lamarck), Gulf of Thailand (Rathbun,            1910); <i>Toxopneustes pileolus</i>, south China (Shen  <i>et al.</i>, 1982); <i>Anthocidaris crassispina</i>            (A. Agassiz), <i>Asthenosoma ijimai</i> Yoshiwara,  <i>Diadema setosum</i> (Leske), <i>Salmacis bicolor</i>,  <i>Toxopneustes elegans</i> (Döderlein) and  <i>Toxopneustes pileolus</i>, Japan (review by Suzuki            and Takeda, 1974); <i>Helicidaris erythrogramma</i>            var. <i>armigera</i> (A. Agassiz), Western Australia            (AM); CRINOIDEA?: unidentified species,            Singapore (Johnson, 1962)</p>

small areas devoid of spines on the test of sea urchins in Japan; Daniel and Krishnan (1979) report it as causing damage to the base of the spines of its echinoid host in south India.

Larval settlement and host selection behaviour in laboratory-reared megalopae of *E. pentagonus* were analyzed by Castro (1978). Results suggest that the megalopae are actively involved in host selection and that metamorphosis into juveniles is triggered by contact with material from live hosts. In south-central Japan, immature males and females can be found only on the test of sea urchins. This is apparently the result of larvae that are carried by warm currents and are able to develop into juvenile crabs but which are subsequently unable to survive winter temperatures.

It is apparent that eumedonines are specialists that have evolved morphological and behavioural adaptations to live as obligate symbionts on the surface of echinoderms and cnidarians. In contrast, parthenopids are free-living, relatively unspecialized omnivores and detritivores (Gore and Scotto, 1979). Hosts provide eumedonines with protection and with food sources that may include epithelial and other types of tissue, detritus caught on the surface of the host, fecal material, and mucus. The occupation of the host's rectum by the adult females of *E. pentagonus* represents an additional adaptation paralleling those in some pinnotherid crabs which are symbionts of molluscs, echinoderms, and other invertebrates.

## Discussion

An important consideration is whether the eumedonines should be treated as a separate family (see Dana, 1853; Ortmann, 1893, 1894; Estampador, 1937, 1959), a subfamily of the Parthenopidae (as Neumann, 1878 and most subsequent authors), a subfamily of the Pilumnidae (*sensu* Guinot, 1978) following Ng (1983), or even as an independent superfamily (Guinot, 1985).

There are some general similarities between eumedonines and parthenopids, but the question remains whether these similarities are a result of convergence or of common ancestry. Some of the similarities are shared only by these two taxa; others are common within several families within the Heterotremata (*sensu* Guinot, 1978). The latter include (1) the position of the antennules, (2) the shape of the buccal frame and third maxillipeds, (3) structure of the sternum, (4) position of the gonopores, and (5) position of the basal antennal article. However, there are features common to both groups suggesting that parthenopids and eumedonines are related to some degree. This conclusion is based primarily on particular similarities shared only by these two taxa (i.e., synapomorphies). These include (1) general body shape, (2) shape of frontal margins, (3) size and structure of the orbits, and (4) general shape of the chelipeds, especially the claws. Yet even these characters may have been acquired through convergent evolution.

On the other hand there is evidence indicating relationships of the eumedonines to the Xanthoidea (*sensu* Guinot, 1978) as noted by Tirmizi and Serène (1971) and Ng (1983), who included eumedonine genera in the Pilumnidae (see Ng and Rodriguez, 1986). Both groups share similarities in the morphology of the orbits, the position and shape of the chelipeds, the position of the basal antennal article, and particularly in the shape of the male gonopods. Moreover, xanthid crabs such as *Calmania* Laurie (see below) have been placed in the Eumedoninae, whereas eumedonines such as *Rhabdonotus* A. Milne Edwards have been included in the Xanthidae.

The larval development of eumedonines has been studied only in *Echinoecus pentagonus* (A. Milne Edwards) (Castro, 1978; Van Dover *et al.*, 1986) and the zoeal

stages of this species cannot be considered parthenopid at all but instead are definitely xanthoid-like, and specifically pilumnid suggesting that this genus at least may not even be a eumedonid but a member of the Pilumnidae (*sensu* Guinot, 1978). Studies on the larval development of the genera *Gonatonotus*, *Proechinocus*, *Zebrida*, *Ceratocarcinus*, etc. and a comparison of their larvae with those of *Eumedonus* must be undertaken to provide larval evidence for assessing the relationships of these genera.

Apart from any possible phylogenetical relationships of the eumedonines, parthenopids, and pilumnids, it is obvious that these taxa are very different in their key adaptations to specific modes of life. The symbiotic existence of eumedonines contrasts sharply with the burying (not burrow-forming) mode of life of parthenopids and the omnivorous habits of pilumnids. Their morphological differences are coincident with their ecological differences.

One other problem has been the systematic position of several genera formerly included among the eumedonines. The first is *Calmania*, classified by the author (Laurie, 1906) in the Xanthidae, and accepted therein by Flipse (1930) and Sakai (1939, 1976). Balss (1922) and Gordon (1934), however, included this genus in the Eumedoninae. *Calmania* shares some characters with the eumedonines, such as the bilobed and projecting pseudorostrum, obliquely inserted antennules, position of the basal antennal article in the inner orbital hiatus, and the morphology of the male gonopods. But differences are also salient and include a noticeably hirsute carapace and pereopods covered with long, silky hairs, a lamellate pseudorostrum, the absence of a junctional point between the anterolateral and posterolateral margins of the carapace, and in the form of the chelipeds. This last feature is of most importance, inasmuch as the chelipeds are one of the prime appendages in contact with the environment. In *Calmania* the chelae are most distinctive and quite different from any seen among the eumedonines. Moreover, some species of *Calmania* (e.g. *C. simodaensis* Sakai) are similar to the Pilumnidae.

A similar problem is the systematic position of *Dentoxanthus* (Stephensen, 1945). The most common species, *D. iranicus* Stephensen (a second species, *D. komodoensis* Serène, needs to be revised), shares some common morphological characters with the eumedonines, as noted by Holthuis (see Serène *et al.*, 1958) and Tirmizi and Kazmi (1982). These authors considered this genus to belong to the Eumedoninae. There are similarities in the rhomboid form of its carapace, the junction between the anterolateral and posterolateral margins of the carapace, the anterolateral margin is divided into four lobes, the front bilobed, and the merus of the chelipeds and walking legs dorsally keeled. Ng (1983) included the genus in the Pilumnidae because the male first pleopod is slender and sinuous. *Dentoxanthus* has also the pulley-like dactylopropodal articulation characteristic of many pilumnids. However, the differences between this genus and the eumedonine genera are conspicuous. These include the characteristically sculptured carapace of *Dentoxanthus*, its strongly keeled and lamellate walking legs, and particularly the much expanded chelipeds similar to those seen in *Calappa*, and the tip of the male first pleopod is strongly hooked in contrast to the slightly-hooked pleopod of eumedonines. These differences strongly suggest that *Dentoxanthus* may not be a eumedonine but that it occupies an isolated position within the Pilumnidae (Štević and Ng, in preparation).

Although *Rhabdonotus* was initially included in the Xanthidae (Milne Edwards, 1879), Serène and Romimohtarto (1963) revised its systematic position and it is now firmly established that it should be classified as a eumedonine inasmuch as it shares all principal eumedonine taxonomic features. It is a symbiont of crinoids and soft corals.

It lacks, however, a marked junction between the anterolateral and posterolateral borders, so that the side margins of the carapace are more or less rounded.

It can be concluded, based on all available evidence, that *Eumedonus* and allied genera certainly differ from the parthenopids in adult morphology, as well as in ecological and larval (at least in *Echinoecus*) features. A close affinity to the Pilumnidae (*sensu* Guinot, 1978) is also evident but the peculiar mode of life of eumedonines emphasizes their status as an independent taxon as suggested by the superfamily rank recently given to the group by Guinot (1985). The strong xanthoidean affinities discussed above, however, do not justify this elevation to superfamily level. We thus believe that the group should be elevated instead to family rank by re-establishing the family Eumedonidae Dana, 1853 within the superfamily Xanthoidea (*sensu* Guinot, 1978).

### Description of the Family

#### Family EUMEDONIDAE Dana, 1853

*Eumedonoidea* Guinot, 1853, p. 453.

*Eumedonidae* Dana, 1853, p. 1422; Ortmann, 1893, p. 419; 1894, p. 48; Estampador, 1937, p. 559; 1959, p. 120.

*Eumedoninae* Neuman, 1878, p. 17; Miers, 1879b, p. 670; Haswell, 1882, p. 38; Miers, 1886, p. 104; Alcock, 1895, p. 258, 286; Klunzinger, 1906, p. 56; Borradaile, 1907, p. 481 (key); Rathbun, 1910, p. 321; 1918, p. 27; Balss, 1922, p. 136; Rathbun, 1925, p. 10 (key); Flipse, 1930, p. 18, 20, 70; Sakai, 1932, p. 300; Gordon, 1934, p. 62; Ward, 1934, p. 7; 1936, p. 10; Sakai, 1938a, p. 329, 347; Buitendijk, 1939, p. 266; Ward, 1942, p. 77; Stephensen, 1945, p. 114; Gordon, 1947, p. 111; Lin, 1949, p. 17; Edmondson, 1951, p. 217; Holthuis, 1953, p. 6; Balss, 1957, p. 1631; Serène *et al.*, 1958, p. 136; Serène and Romimohtarto, 1963, p. 1; Sakai, 1965, p. 93 (key), 101; Serène, 1965, p. 21; 1968, p. 63; Glaessner, 1969, p. R508; Lundoer, 1974, p. 5; Suzuki and Takeda, 1974, p. 289; Sakai, 1976, p. 294; Serène, 1977, p. 49; Tirmizi and Kazmi, 1982, p. 308; Ng, 1983, p. 141; Kim and Chang, 1985, p. 50; Ng and Rodríguez, 1986, p. 90.

The family can be described as follows: Cephalothorax subpentagonal or subhexagonal, junction between anterolateral and posterolateral margins of carapace almost always well marked, usually having a spine. Projecting pseudorostrum bilobed or fourlobed, rarely emarginate. Surface of carapace nearly flat, sometimes bearing pointed tubercles, with more or less indistinctly marked regions. Circular orbits well defined but small; floor of orbits not in contact with the front, but leaving a hiatus, usually filled by basal (2+3) antennal article and, in some genera, by the subsequent article. Antennae small, with small, discoidal first (urinal) article; basal antennal article the largest; two following articles smaller, provided with short flagellum. Epistome wide, short; buccal cavity quadrangular, completely covered by third maxillipeds; palp of third maxilliped well-developed, articulated at anterolateral angle of merus; exopod terminating in the flagellum. Chelipeds of moderate size, subequal, and in some genera longer than the carapace; fingers much shorter than palms, bent at an angle toward fixed finger; ischium and merus fused, but suture remaining very distinct and complete. Walking legs of moderate size, with coxae of last pair somewhat elevated over others; chelipeds and walking legs often armed with spines or cusps; dactyls can be flexed against the propodus producing a prehensile effect. Sternoabdominal cavity present; sternites arranged in parallel except last which is arranged radially; sternum with normal breadth; first two sternal sutures (4/5 and 5/6) interrupted; last two (6/7 and 7/8) complete [thus belonging to level III B according to Guinot (1979)]; a median line is present at 8th sternite; a functional abdominal-retaining mechanism present. Male



sexual opening coxal; the female sexual opening sternal, concave; first male gonopod long, slender, curved at middle, hooked apically; second gonopod distinctly shorter and sigmoid. Abdomen with seven non-fused segments in both sexes, the first one or two usually visible from above.

Members of the family are usually small (mostly around 1 cm in carapace length), typically concealed within their hosts (mostly echinoderms) and therefore rarely observed, collected, and studied. Fossils are unknown.

Type genus: *Eumedonus* A. Milne Edwards, 1834

The nine genera and 26 species of eumedonid crabs (see Table 1) can be classified according to the shape of the frontal and anterolateral margins of the carapace, the length of the walking legs and chelipeds, the surface of the carapace, the breadth of the inner orbital hiatus, the relative position of antennae (especially of the basal antennal segment), colouration, and type of hosts. The genera were grouped by some authors (Gordon, 1934; Serène *et al.*, 1958) in two groups, A and B. Flipse (1930) and Sakai (1976) also used 'A' and 'B' in their keys but without any reference to groups.

Subfamily *Eumedoninae* Dana, 1853

Group A Gordon, 1934, p. 62; Serène *et al.*, 1958, p. 138.

Carapace subpentagonal or subhexagonal. Prominent pseudorostrum consists of two median lobes or spines which are more or less divided by median notch or sinus. Distance between orbits at most half total width of carapace. Antennules folded slightly obliquely (almost longitudinally) into their fossae. Antennae rather short; basal article does not reach frontal margin, and together with subsequent articles, it usually fills orbital hiatus. Last two antennal segments (4 and 5) short. In some genera a ridge is present on inner side of shallow antennal groove. Eyes located at indentations formed by junction of anterolateral and frontal margins and are sometimes concealed by margins of carapace. Inner orbital margin not prominent. Anterolateral margin of carapace usually without teeth or lobes. Third pair of maxillipeds completely covers buccal cavity. Longitudinal endostomial ridges feebly marked. Chelipeds of moderate size and equal. Pereopods often have spines. All four walking legs have dactyls that are similar and subequal. The subfamily contains the genera *Echinoecus* Rathbun, 1894; *Eumedonus* H. Milne Edwards, 1834 (type); *Gonatonotus* White, 1847; *Proechnoecus* Ward, 1934; *Rhabdonotus* A. Milne Edwards, 1879; and *Zebrida* White, 1847.

**Ceratocarcininae** new subfamily

Group B Gordon, 1934, p. 62; Serène *et al.*, 1958, p. 138.

Carapace almost subhexagonal. Fronto-orbital margin wide, exceeding by half the total width of carapace. Pseudorostrum consists of four parts: two median lobes (lamellate and curved downwards in some species) and two lateral lobes or spines projecting forward. Pseudorostrum also has frontal median notch plus two lateral grooves enclosing antennae. Eyes are situated laterally behind external lobes or spines. Inner suborbital angle prominent and well developed. Antennules fold obliquely (more transversely) into their fossae. Antennae moderate in size; basal article narrow, short, and does not (or barely) reach border of inner suborbital angle; next antennal articles usually long and narrow, fourth article fills orbital hiatus, and fifth, together with flagellum, lie in frontal grooves. In rare cases antennae are excluded from the very narrow orbital hiatus. Anterolateral margin of carapace has teeth or lobes. Third pair

of maxillipeds does not completely cover buccal cavity. Longitudinal endostomial ridges well defined. Chelipeds very long and subcylindrical, with merus projecting well beyond margin of carapace; tips of fingers, usually light coloured, are dark only in a few rare species. First pair of walking legs has a slender dactylus and is much longer than following pairs. The latter are slender and subcylindrical. Most species have been reported from crinoids but one is known from a soft coral. In addition to the type genus, *Ceratocarcinus* White, 1847, the subfamily consists of the genus *Harrovia* Adams and White, 1848 and possibly *Glyptocarcinus* Takeda, 1973. The latter differs from *Ceratocarcinus* and *Harrovia* in several morphological characters (see Takeda, 1979) and it has been collected as free-living.

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