ZOOTAXA

643

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Magnolia Press
Auckland, New Zealand

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(*Zootaxa* 643)

70 pp.; 30 cm.

16 September 2004

ISBN 1-877354-54-6 (Paperback)

ISBN 1-877354-55-4(Online edition)

FIRST PUBLISHED IN 2004 BY

Magnolia Press
P.O. Box 41383
Auckland 1030
New Zealand
e-mail: zootaxa@mapress.com
http://www.mapress.com/zootaxa/

ISSN 1175-5326 (Print edition)
ISSN 1175-5334 (Online edition)

Zootaxa 643: 1–70 (2004)
www.mapress.com/zootaxa/

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ZOOTAXA
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Phylogeny and systematics of the Trapeziidae Miers, 1886 (Crustacea: Brachyura), with the description of a new family

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Accepted by K. Larsen: 14 Aug. 2004; published: 16 Sept. 2004

ABSTRACT

A revision of the family Trapeziidae Miers, 1886, has shown that it consists of three clades, one of which is elevated to family status, Tetraliidae *fam. nov.*, for the genera *Tetralia* Dana, 1851, and *Tetraloides* Galil, 1986. The genera *Trapezia* Latreille, 1828, *Calocarcinus* Calman, 1909, *Hexagonalia* Galil, 1986, *Philippicarcinus* Garth & Kim, 1983, *Quadrella* Dana, 1851, and *Sphenomerides* Rathbun, 1897, remain in the Trapeziidae; *Domecia* Eydoux & Souleyet, 1842, *Jonesius* Sankarankutty, 1962, *Maldivia* Borradaile, 1902, *Palmyria* Galil & Takeda, 1986, and the fossil genus *Eomaldivia* Müller & Collins, 1991, in Domeciidae Ortmann, 1893. Cladistic analysis shows that Trapeziidae *sensu* Miers, 1886, consists of three clades that show convergence as a result of similar habits as symbionts of reef corals and other cnidarians. A list of all recognised genera and species in the three families and their primary synonyms is provided. Keys are also included for four families of Brachyura symbiotic with reef corals, and for the genera and species of Domeciidae, Tetraliidae, and Trapeziidae. Some rare colour figures are reproduced. Three name changes have resulted within the Tetraliidae: *Cancer glaberrimus* Herbst, 1790, for *Tetralia fulva* Serène, 1984, and *Cancer mutus* Linnaeus, 1758, for *Tetralia armata* Dana, 1852, and *Tetralia vanninii* Galil & Clark, 1988. Nomenclatural problems associated with the repeated use of "forma *typica*" for various species of *Trapezia* and *Tetralia* are resolved. To stabilise the nomenclature of a number of well-known species, neotypes are designated for 13 species of Trapeziidae for which type material is not extant: *Trapezia cymodoce* (Herbst, 1801), and its three synonyms (*Trapezia dentifrons* Latreille, 1828, *Trapezia dentata* var. *subintegra* Dana, 1852, *Trapezia cymodoce* var. *ornatus* Chen, 1933); *Trapezia bidentata* (Forskål, 1775), and one of its synonyms (*Trapezia ferruginea* Latreille, 1828); *Trapezia digitalis* Latreille, 1828, and one of its synonyms (*Trapezia nigrofusca* Stimpson, 1858); *Trapezia septata* Dana, 1852, and one of its synonyms (*Trapezia reticulata* Stimpson, 1858); *Trapezia areolata* Dana, 1852; *Trapezia bella* Dana, 1852; and *Trapezia speciosa* Dana, 1852. Neotypes are also designated for seven species of Tetraliidae: *Tetralia glaberrima* (Herbst, 1790), and three synonyms (*Trapezia integra* Latreille, 1828, *Trapezia serratifrons* Jacquinot, 1846, *Tetralia laevissima* Stimpson, 1858); *Tetralia muta* (Linnaeus, 1758), and one of its synonyms (*Tetralia armata* Dana, 1852); and *Tetraloides nigrifrons* (Dana, 1852).

Key words: Crustacea, Brachyura, revision, new family, Trapeziidae, Domeciidae, Tetraliidae fam. nov., cladistics, coral symbionts, keys

INTRODUCTION

The coral symbionts of the family Trapeziidae Miers, 1886, are among the best-known brachyuran crabs in tropical coral reef ecosystems. Not surprisingly, they have been well studied, both from the taxonomic as well as the ecological perspectives (review by Castro 1976). Borradaile's (1900: 39) assessment of the family as a "very difficult little group" paraphrased the challenge for the generations of subsequent investigators. To this effect, numerous taxonomic papers have been published over the last 20 years, and many new species have been described. Yet, there has been no single family-wide revision or treatment since Ortmann (1897), while the monograph (of mostly Indian Ocean species) by Serène (1984) is still a standard reference for most marine biologists, even though it is now quite dated with the numerous discoveries and developments since. There have also been many shorter papers reporting new species, discussing small groups of taxa, and overviews of selected regions (see partial listing by Castro 2003). The history and taxonomic issues with the classification of the Trapeziidae and other families grouped under the superfamily Xanthoidea has been discussed in depth by Guinot (1978, 1979), and many workers since have regarded the Trapeziidae as a distinct family (not a subfamily as has been traditionally regarded, see Balss 1957) (also see Ng 1998, Davie 2002). This was reviewed by Martin & Davis (2001). Despite this extensive interest, there has not been a comprehensive analysis testing the hypothesis that morphological similarities are the result of convergent evolution. Such similarities may have evolved among species that share the use of live reef corals and other colonial cnidarians as habitats and food sources. In an unpublished thesis, Ng (1983) suggested that the Trapeziidae was not a monophyletic taxon and argued that one of the constituent genera, *Tetralia*, belonged to a separate group. However, there was no follow-up until the present authors decided to re-examine this matter.

The family Trapeziidae was originally established by Miers (1886) to include the known species of *Trapezia* Latreille, 1828. Ortmann (1897) revised the family and added *Tetralia* Dana, 1851, and *Quadrella* Dana, 1851, to the family, while *Domecia* Eydoux & Souleyet, 1842, was placed in a separate subfamily, Domeciinae Ortmann, 1893. Borradaile (1902) regarded the Trapeziidae only as a subfamily within the Xanthidae MacLeay, 1838, a position followed by most subsequent authors (*viz* Klunzinger 1913; Balss 1922, 1957; Sakai 1976; Dai & Yang, 1991). Balss (1957), however, placed *Domecia* in the Menippinae Ortmann, 1893. Guinot (1978) resurrected the family Trapeziidae and suggested removing *Domecia* from the Menippinae, adding that *Domecia* together with *Maldivia* Borradaile, 1902 (which had been placed in the Xanthinae by Balss 1957) constituted a group of their own (Guinot 1978: 269). Serène (1984) subsequently recognized two subfamilies in the Trapeziidae: Trapeziinae (for *Trapezia, Quadrella, Tetralia*, *Calocarcinus* Calman, 1909, and *Sphenomerides* Rathbun, 1897) and Domeciinae. He followed Guinot (1978) by including *Maldivia* and *Jonesius* Sankarankutty, 1962 (as *Maldivia triunguiculata* Borradaile, 1902), in the Domeciinae.

Subsequent authors have tended to follow Serène (1984). Two more genera were added. Galil (1986c) established *Hexagonalia* with *Quadrella brucei* Serène, 1973, as the type species, and Galil and Takeda (1986) established *Palmyria* with *Maldivia palmyrensis* Rathbun, 1923, as the type species. Castro (1997a, 1999a, 1999b, 2000, 2003) questioned the inclusion of *Domecia*, *Jonesius*, *Maldivia,* and *Palmyria* in the Trapeziidae and stated that the Trapeziidae consisted of three separate groups, one comprising *Trapezia*, *Quadrella*, *Hexagonalia*, *Calocarcinus*, *Philippicarcinus*, and *Sphenomerides*, a second with *Tetralia* and *Tetraloides*, and a third with *Domecia*, *Jonesius*, *Maldivia*, and *Palmyria* (see comments in Appendix I, Martin & Davis, 2001: 113). More recently, Davie (2002) argued that the subfamily Domeciinae was quite distinct and raised it to family status, Domeciidae Ortmann, 1893, to include *Domecia*, *Jonesius*, *Maldivia*, and *Palmyria.*

The eight genera that remained in the Trapeziidae after the separation of the Domeciidae, however, still represent a heterogeneous group of mostly coral associated crabs. They share some characters that are closely correlated to their live-coral habitat. As we have determined here, *Tetralia* and *Tetraloides* nevertheless share some unique characters that set them apart from *Trapezia* and the other five genera.

There are also many nomenclatural and taxonomic problems within the Trapeziidae *sensu* Miers, 1886, which, surprisingly, still remain unresolved after so many papers have been published on them. Many names which had been used by Linnaeus, Forskål, Dana, and Stimpson for species ultimately placed in the Trapeziidae have been forgotten or ignored for many decades, even though for nomenclatural purposes they are still valid. This is due to a variety of reasons, including the great difficulty in ascertaining the exact identities of some of these taxa because of the extreme brevity of the original descriptions, incorrect or imprecise locality data provided, and loss of the original material. Some of these names clearly have precedence over presently used ones.

The present paper reviews these ecologically significant crabs and provides an updated list of the genera and species in the Domeciidae, Tetraliidae *fam. nov.*, and Trapeziidae. Also provided is a key to the four families of brachyuran crabs which are among the most common obligate and facultative symbionts of reef corals and other colonial cnidarians, namely the three families originally grouped in Trapeziidae *sensu* Miers, 1886, and the coral-gall crabs, Cryptochiridae Paulson, 1875. We also redefine the various suprageneric taxa based on results of cladistic analysis. Opportunity is also taken here to resolve the outstanding nomenclatural problems among the families and, in the process, stabilise their taxonomy. As the taxonomy of most of the genera and species have been treated in detail in many previous papers, it is not necessary to provide complete synonymies for all of them. Instead, we have included primary synonyms in most cases.

Specimens examined are deposited in the Australian Museum, Sydney (AM); Museo di Zoologia "La Specola," Università di Firenze, Florence, Italy (ZMF); Muséum national d'Histoire naturelle, Paris, France (MNHN); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); The Natural History Museum, London, U.K. (BMNH); Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt-am-Main, Germany (SMF); University Museum of Zoology, University of Cambridge, Cambridge, U.K. (UMZC); Zoological Reference Collection, Raffles Museum, National University of Singapore (ZRC); and Zoologisch Museum, Humboldt-Universität, Berlin, Germany (ZMB).

The measurements provided are of the carapace length (cl) and width (cw) in millimetres respectively. Carapace length was measured across the middle of the carapace from the middle portion of the frontal margin to the middle portion of the posterior margin. The width of the carapace was measured across the widest breadth of the carapace. Abdominal somites are referred to by the abbreviation AS, the first and second pairs of male pleopods by G1 and G2 respectively, maxillipeds by MXP, and pereopods by P1 (chelipeds) and P2 to P5 (ambulatory legs).

PHYLOGENETIC ANALYSIS

Terminal taxa and outgroup selection

All recognised genera that are or have been included in the Trapeziidae, Tetraliidae *fam.nov.*, and Domeciidae were included in the ingroup, exemplified by their respective type species. The respective sister groups to the Trapeziidae, Tetraliidae *fam. nov.*, and Domeciidae, however, have not yet been robustly identified through comprehensive phylogenetic analysis. Serène's (1984) classification implies a close relationship between the trapeziids, tetraliids, and domeciids, which together would have a xanthoid sister group. Conversely, Balss (1957), Sakai (1976), and Dai & Yang (1991) imply that the domeciid sister group is within the Eriphiidae MacLeay, 1838. On the basis of sperm morphology, Jamieson (1991) suggested that the Trapeziidae was sister to a clade containing Xanthidae, Panopeidae Ortmann, 1893, and Thoracotremata Guinot, 1977 (Fig. 1A). In a cladistic study of somatic morphology, Sternberg *et al.* (1999) found Trapeziidae to be more closely related to Thoracotremata and various Heterotremata Guinot, 1977, exclusive of eriphiids or any xanthoid families (Fig. 1B). Schubart *et al.* (2000), using partial 16S rRNA sequences, found Trapeziidae to be phenetically more similar to Xanthidae and Panopeidae than to a selection of other brachyuran families including Eriphiidae (as Menippidae, see Ng 1998). Wetzer *et al.* (2003) studied relationships of carpiliids and selected xanthoids using 12S and 16S rDNA sequences analysed via parsimony and maximum likelihood analysis. Of the various analyses performed by Wetzer et al. (2003), the best resolved tree (their fig. 2, based on maximum likelihood analysis of 16S sequences), found Trapeziidae to be sister to a clade containing eriphiids, panopeids, xanthids, and thoracotremes (Fig. 1C) and thus Jamieson's (1991) results are similar for the taxa he studied. Hence, sister group relationships of Trapeziidae *s.lato* remain ambiguous, confounding explicit identification of a suitable outgroup. Common to all studies, however, is the placement of portunids outside of the suite of possible sister groups to the xanthoid families, recognition of heterotreme paraphyly, and more significantly, the implication of xanthoid paraphyly. Therefore, analyses were rooted to the basal portunid, *Carcinus maenas* (Linnaeus, 1758) (Portunidae Rafinesque, 1815). Multiple xanthoid exemplars were also included in the ingroup to permit testing of trapeziid, tetraliid, and domeciid monophyly, and potential identification of respective sister groups. Two non-xanthoids, the heterotreme *Potamon fluviatilis* (Potamidae Ortmann, 1893), and the thoracotreme *Varuna litterata* (Varunidae Alcock, 1900), were included in the ingroup to test xanthoid monophyly. Ingroup and outgroup taxa are given in Table 1.

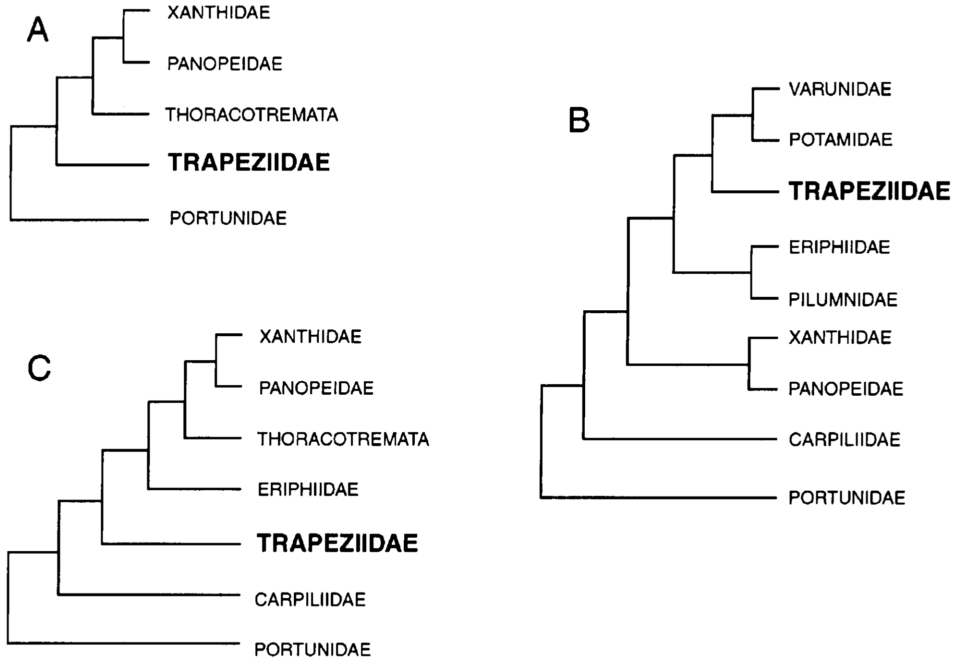

FIGURE 1. Phylogenetic position of Trapeziidae among other taxa represented in the present analysis as depicted by (A) Jamieson (1991); (B) Sternberg *et al.* (1999) using morphology (based on their fig. 2); and (C) Wetzer *et al.* (2003) using 16S rDNA sequences (based on their fig. 2).

TABLE 1. Terminal taxa used in cladistic analysis. *Carcinus maenas* Linnaeus, 1758 (Portunidae) is the outgroup.

Family	**Species** (* denotes type species of genus)	**Sources**
Carpiliidae Ortmann, 1893	*Carpilius maculatus* (Linnaeus, 1767)*	AM P8583, AM P17092
Domeciidae Eydoux & Souleyet, 1842	*Domecia hispida* Eydoux & Souleyet, 1842*	ZRC 1965.11.17.115–124, ZRC 1984.6112–6114
Domeciidae Eydoux & Souleyet, 1842	*Jonesius triunguiculatus* (Borradaile, 1902)*	ZRC 1965.10.8.2, MNHN-B 8355
Domeciidae Eydoux & Souleyet, 1842	*Maldivia symbiotica* Borradaile, 1902*	UMZC holotype
Domeciidae Eydoux & Souleyet, 1842	*Palmyria palmyrensis* (Rathbun, 1923)*	MNHN-B 8376
Eriphiidae Macleay, 1838	*Eriphia sebana* (Shaw & Nodder, 1803)*	ZRC 1999.1023
Panopeidae Ortmann, 1893	*Panopeus herbstii* H. Milne Edwards, 1834	AM P45627
Pilumnidae Samouelle, 1819	*Pilumnus hirtellus* (Linnaeus, 1761)*	ZRC 1968.684–686
Portunidae Rafinesque, 1815	*Carcinus maenas* Linnaeus, 1758*	AM P67929
Potamidae Ortmann, 1896	*Potamon fluviatilis* (Herbst, 1785)	AM P51455
Tetraliidae *fam. nov.*	*Tetralia glaberrima* (Herbst, 1790)*	MNHN-B 25234, AM P44621
Tetraliidae *fam. nov.*	*Tetraloides nigrifrons* (Dana, 1852)*	MNHN-B 25322, MNHN-B 25719
Trapeziidae Miers, 1886	*Trapezia cymodoce* (Herbst, 1801)*	ZRC 1964.81810–11
Trapeziidae Miers, 1886	*Hexagonalia brucei* (Serène, 1973)*	MNHN-B 8191
Trapeziidae Miers, 1886	*Quadrella coronata* Dana, 1852*	ZRC 1968.2.13.1
Trapeziidae Miers, 1886	*Sphenomerides trapezoides* (Wood-Mason & Alcock, 1891)*	MNHN-B 8206
Trapeziidae Miers, 1886	*Philippicarcinus oviformis* Garth & Kim, 1983*	USNM 195357, USNM 195360
Trapeziidae Miers, 1886	*Calocarcinus africanus* Calman, 1909*	ZRC (ex MNHN-B 25214)
Varunidae Alcock, 1900	*Varuna litterata* (Fabricius, 1798)*	AM P7958, AM P56328
Xanthidae Macleay, 1838	*Cymo andreossyi* (Andouin, 1826)*	ZRC 1999.1186, ZRC 1999.0377
Xanthidae Macleay, 1838	*Etisus dentatus* (Herbst, 1785)*	ZRC 2000.0693
Xanthidae Macleay, 1838	*Tweedia laysani* (Rathbun, 1906)	ZRC 2000.0509
Xanthidae Macleay, 1838	*Xantho poressa* (Olivi,1792)	AM P21823

Analytical methods

The data matrix was constructed in MacClade 4 (Maddison & Maddison 2000) and includes 23 taxa and 45 characters (Appendix 1). All characters were unordered (non-additive) and equally weighted, missing data were scored unknown and polymorphisms were scored as such rather than assuming a plesiomorphic state. We employed exemplar scoring for terminal taxa in order to avoid *a priori* assumptions of monophyly of supraspecific taxa. Characters were unordered, so the score given for each state (i.e., 0, 1, 2) implies nothing about plesiomorphy or apomorphy. Trees were generated in PAUP 4 (Swofford 2002) under the heuristic search (MULPARS, TBR, delayed transformation, 100 replications with random input order).

Relative stability of clades was assessed using Bremer support analyses (Bremer 1994), implemented through MacClade 4.

Morphological characters

Character 1. Carapace frontal margin: well-developed lobes (0), well-developed teeth (1), at most with minute teeth (2).
Character 2. Carapace tuberculation: weak (0), distinct (1), absent (2).
Character 3. Carapace regions: well-defined (0), indistinct (1), absent (2).
Character 4. Carapace posterior carina: high and sharp (0), narrow and distinct (1), low and indistinct (2).
Character 5. Carapace dorsum: convex (0), flat, depressed (1).
Character 6. Carapace surface: glabrous (0), pubescent (1).
Character 7. Carapace supraorbital notch: present (0), absent (1).
Character 8. Carapace inner suborbital tooth: low (0), distinct (1), undiscernable (2).
Character 9. Carapace antero- and posterolateral margins: demarcated (0), not demarcated (1).
Character 10. Carapace anterolateral teeth form: lamelliform (0), otherwise, smooth (1).
Character 11. Carapace anterolateral teeth number: 3 or 4 (0), fewer than two (1).
Character 12. Anterior thoracic sternites: broad (0), narrow (1).
Character 13. Anterior sternal grooves: shallow (0), deep (1).
Character 14. Sternites 1 and 2: short, semicircular (0), high, pointed, triangular (1).
Character 15. Male abdominal somites 3, 4: free (0), fused (1).
Character 16. Male abdominal somites 4, 5: free (0), fused (1).
Character 17. Lateral margins of male abdominal somites 3–6: faintly concave (0), deeply concave (1).
Character 18. Male telson: semicircular (0), triangular (1).
Character 19. Female abdominal somite 2 width: slightly narrower, higher than AS1 (0), much narrower and higher than AS1 (1), slightly wider but higher than AS1 (2).

Character 20. Male abdominal somite 3 edge: simple, like AS2, 3 (0), thick, enlarged, saddle-like (1).

Character 21. Cheliped dactylus and pollex apices: pointed (0), hollowed (1).

Character 22. Cheliped propodal spines: absent (0), present (1).

Character 23. Cheliped propodus outer surface: smooth (0), granulate or tubercular (1).

Character 24. Cheliped carpus inner angle: with spine (0), blunt tooth or tubercle (1), unarmed (0).

Character 25. Cheliped carpus outer tooth: absent (0), present (1).

Character 26. Cheliped carpus dorsal tooth: absent (0), present (1).

Character 27. Cheliped merus spines: absent (0), present (1), minute (0).

Character 28. Cheliped merus length: about half of carapace width (0), as long as or longer than carapace width (1).

Character 29. P2–P5 dactylus transverse setal rows: absent (0), present (1).

Character 30. P2–P5 dactylus apex: pointed (0), hoof-like, hollowed (1).

Character 31. P2–P5 dactylus ventral row of teeth: absent (0), present (1).

Character 32. P2–P5 dactylus ventral setae: soft (0), robust (1).

Character 33. P2–P5 dactylus-propodus lock: absent (0), present (1).

Character 34. Basal antennal article: narrow (0), very broad (1).

Character 35. MXP2 dactylus: vertically broad (0), elongated, pointed (1).

Character 36. MXP2 endopod dactylus-propodus: articulating (0), fused (1).

Character 37. MXP3 exopod width: broad, 0.5 ischium width (0), narrow (1).

Character 38. MXP3 exopod length: reaching tip of merus (0), not reaching tip of merus (1).

Character 39. MXP3 ischium sulcus: shallow (0), deep (1), absent (2).

Character 40. MXP3 merus shape: squarish (0), reduced, rectangular (1).

Character 41. MXP3 ischium inner proximal margin: square or nearly square (0), strongly oblique (1).

Character 42. G1 apex: tapering (0), fluted, expanded (1).

Character 43. G1 distal portion: simple (0), with elaborate, folds, setae and spines (1).

Character 44. G2 length: less than half G1 (0), about half G1 (1), subequal to G1 (2).

Character 45. G2 apex: slender, pointed (0), blunt (1).

RESULTS AND DISCUSSION

Parsimony analysis of the data resulted in a single minimal length tree (length 152, CI 0.362, RI 0.630) (Fig. 2). Domeciidae was found to be the sister to Trapeziidae + Tetraliidae. Trapeziidae, Tetraliidae and Domeciidae are each monophyletic (Bremer support of 4, 8, 3 respectively) and their interrelationships are supported by Bremer support of 2. Bremer support recorded for monophyly and interrelationships of Trapeziidae, Tetraliidae, and Domeciidae thus indicate stability even in suboptimal trees up to 2 steps longer. *Varuna* (Varunidae) + *Potamon* (Potamidae) are allied to Trapeziidae + Tetraliidae +

Domeciidae rendering Xanthoidea paraphyletic. Additionally, present results suggest that Trapeziidae + Tetraliidae + Domeciidae are more closely related to "higher" heterotremes and thoracotremes than to other xanthoids. *Carpilius* (Carpiliidae), *Eriphia* (Eriphiidae), and *Pilumnus* (Pilumnidae) were found to be closer to trapeziids and domeciids than to a xanthid + panopeid clade. The positions of xanthids, eriphiids, and pilumnids received low Bremer support, but nevertheless provide some interesting hypotheses, notably, that trapeziids, tetraliids, and domeciids appear to be closer to "higher" heterotremes and thoracotremes than to the Xanthidae, and that Xanthoidea is paraphyletic. Additionally, *Panopeus* (Panopeidae) is nested among the other xanthid genera, suggesting that the status of Panopeidae requires reevaluation.

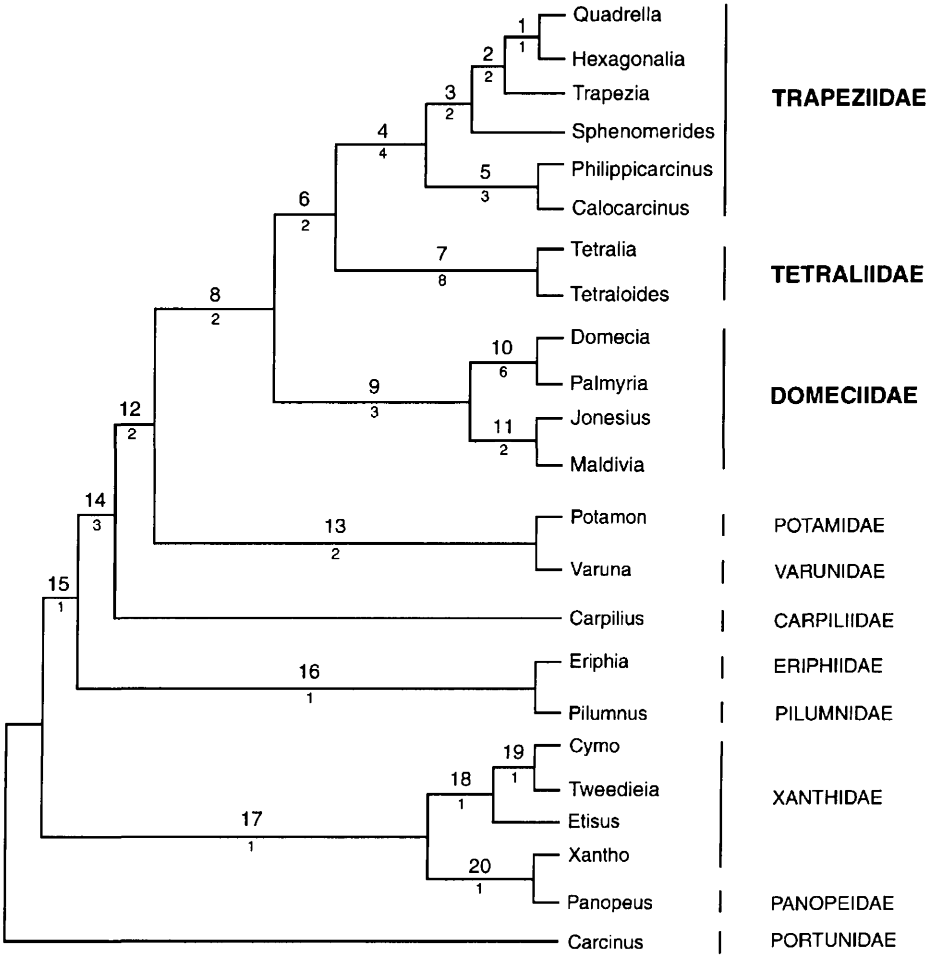

FIGURE 2. Phylogenetic relationships of Trapeziidae, Tetraliidae, and Domeciidae. Single most parsimonious tree (length 152, CI 0.362, RI 0.630). Numbers above and below branches indicate branch number and Bremer support respectively.

The present results are largely consistent with the topology of Sternberg *et al.* (1999) except in the position of Carpiliidae. Our results agree with the 16SrDNA topology of Wetzer *et al.* (2003) in the positions of Carpiliidae and Thoracotremata relative to Trapeziidae, but not with that of Eriphiidae, Panopeidae, and Xanthidae. Both Sternberg *et al.* (1999) and Wetzer *et al.* (2003) agree with our present findings in placing Thoracotremata closer to Trapeziidae than other xanthoids, and in finding Xanthoidea to be paraphyletic. Although monophyly of the Trapeziidae, Tetraliidae, and Domeciidae are clearly supported in the present analysis, the positions of Xanthidae, Panopeidae, Eriphiidae, and Pilumnidae remain open.

In the present study, we have elected to remove *Tetralia* and *Tetraloides* from Trapeziidae to the new family, Tetraliidae. Tetraliidae is sister to Trapeziidae and a case could be made for retaining *Tetralia* and *Tetraloides* in Trapeziidae. Such a position, however, would leave the current system in the unsatisfactory state that previous studies have failed to address, namely, that Trapeziidae *s.lato* cannot be easily diagnosed for all constituent taxa. In particular, the heterogeneity in abdominal segmentation within Trapeziidae *s.lato* is problematic. Removal of *Tetralia* and *Tetraloides* to Tetraliidae enables a more uniform diagnosis of Trapeziidae, and permits recognition of the fused abdominal somites 3–5 as a trapeziid synapomorphy that has been acquired independently of the xanthids. Several traits shared by members of Tetraliidae and some members of Trapeziidae appear to be convergences, possibly related to their coral habitats (we note that the specific habitats of two deep-water trapeziid genera, *Philippicarcinus* and *Sphenomerides*, remain unknown). In particular, tetraliids, and the three shallow-water trapeziid genera, *Trapezia*, *Quadrella,* and *Hexagonalia,* share transverse rows of robust feeding setae on the dactyli of the ambulatory legs (as well as on the chelipeds in *Tetralia*). These setae are used by the crabs to gather coral-mucus and host-tissue as food (see Borradaile 1902, Knudsen 1967, Galil 1987). The most parsimonious interpretation of the cladogram indicates that the feeding setae are independent derivations. On the other hand, if these setae were interpreted as being present in the common ancestor of Trapeziidae and Tetraliidae, this would require two independent losses of the feeding setae, first in *Calocarcinus+Philippicarcinus* and second in *Sphenomerides*. Similarly, the characteristic carapace outline in tetraliids and the three shallow water trapeziid genera, *Trapezia*, *Quadrella*, and *Hexagonalia*, also appears to be convergent since the carapace outline of the intervening taxa (*Sphenomerides*, *Philippicarcinus,* and *Calocarcinus*) is quite different. The smooth and relatively flat carapace of members of the two families appears to be an adaptation to life among the branches of colonial cnidarians, particularly scleractinian corals. Conspicuous, species-specific colour patterns appear to be involved in interspecific and intraspecific recognition in the sibling, typically sympatric species of both families (Preston 1973; Castro 1976, 2000). It appears that the strong similarities between tetraliids and the three shallow-water trapeziid genera are convergences related to their branching-coral hosts. The dactylo-propodal lock present in Tetraliidae, Trapeziidae, and Domeciidae is an adaptation present in other symbiotic or hard-substrate brachyurans (see Ng & Clark 2000a, b, for discussion).

Schweitzer *et al.* (2002) recently described a new fossil genus and species, *Amydrocarcinus dantei,* from the Eocene Tepetate Formation, Mexico, which Schweitzer & Karasawa (2004) subsequently assigned to Goneplacidae. Similarities to the Trapeziidae were noted by Schweitzer *et al.* (2002) in the ill-defined carapace regions, but the new genus was excluded on the basis that trapeziids have abdominal somites 3–5 fused in males, the frontal and anterolateral margins of the carapace are dentate or spined, and the eyes are located on the margins. The abdominal segmentation certainly excludes *Amydrocarcinus* from Trapeziidae, but it should be noted that the other distinguishing features are variable in the trapeziids and are not applicable to the basal taxa. The apparently unfused abdominal somites in *Amydrocarcinus* are also consistent with Tetraliidae, and although the orbits are not on the anterolateral margins as in *Tetralia* and *Tetraloides*, the general carapace outline is not dissimilar to extant tetraliids. While we do not challenge Schweitzer & Karasawa's (2004) placement of *Amydrocarcinus* in the Goneplacidae we draw attention to the fact that it could ultimately prove allied to tetraliids. This is especially with regards to whether the third to fifth abdominal male somites are free or fused. Ng & Chia (1994) highlighted the difficulty of using this character in xanthoids accurately when they showed that while the sutures between the somites may be clear and visible externally, they may in fact be immovable (and effectively fused) as the ventral parts (normally covered with tissue in life) are actually partially fused. To ascertain if these somites are actually fused, one needs to handle them and check for fusion points under the tissue (also see Ng & Guinot 1999, Ng & Chan 2000, Ng & Ho 2003, Crosnier & Ng 2004). With fossils, this uncertainty cannot be resolved.

TAXONOMY

Key to families of Brachyura symbiotic with reef corals and other colonial cnidarians

1 Chelipeds very small, equal or almost equal in size. Carapace narrow, longitudinally rectangular in shape; front very short, shorter than posterior margin of carapace. Females with greatly expanded abdomen visible dorsally. Obligate symbionts of many families of scleractinian corals, where they form galls or pits of different shapes and sizes. Circumtropical in distribution .... Cryptochiridae

\- Chelipeds large or very large in relation to carapace size, almost equal or conspicuously unequal in size. Carapace broad, trapezoidal, transversely oval, hexagonal, or octagonal in shape; front wide, typically longer than posterior margin. Females with moderately expanded abdomen where only first few somites are visible dorsally below posterior margin of carapace. Obligate or facultative symbionts of corals and other colonial cnidarians, living on external surface, very rarely modifying coral skeleton to produce galls or pits. Mostly Indo–West Pacific and Eastern Pacific regions 2

2 Chelipeds conspicuously dissimilar in size. Male abdomen with 6 freely articulating

somites (excluding telson) (Fig. 3A). Exclusively Indo–West Pacific in distribution, always on zooxanthellate (hermatypic) scleractinian corals of the family Acroporidae .... Tetraliidae

- Chelipeds equal or slightly unequal in size. Male abdomen with somites 3–5 fused (although sutures may be visible). Mostly Indo–West Pacific and Eastern Pacific regions, on scleractinian corals and other colonial, mostly anthozoan cnidarians........ 3

3 Propodus of chelipeds with conspicuous pointed or round tubercles or granules; merus short, barely showing dorsally, without row of teeth along anterior margins. Circumtropical in distribution. Facultative or obligate symbionts of shallow-water scleractinian corals .... Domeciidae

- Propodus of chelipeds smooth, without tubercles along outer surface; merus long or very long, always showing a third or more dorsally and showing row of conspicuous teeth or tubercles along each anterior margin (except *Calocarcinus*). Exclusively Indo–West Pacific and Eastern Pacific regions, obligate symbionts of scleractinian corals and other colonial, mostly anthozoan, cnidarians............................. Trapeziidae

Family Domeciidae Ortmann, 1893

Domoeciinae Ortmann 1893: 429, 478; Serène 1984: 291.
Domeciidae — Davie 2002: 152.

Type genus — *Domecia* Eydoux & Souleyet, 1842

Diagnosis

Carapace transversely ovate, posterior portion rounded as posterolateral margins diverge posteriorly only gradually, making posterior margin not conspicuously narrower than frontal margin; dorsal surface granular or smooth; regions not marked; moderately convex, frontal margin straight or nearly straight, finely denticulate or smooth; anterolateral teeth present, 2 or more teeth or small tubercles on each anterolateral margin (Plate 1A–C). Thoracic sternites 1 and 2 fused, triangular, as wide as high, suture between second, third thoracic sternites absent (see Guinot 1964: figs. 13–16). Basal antennal article slender, not expanded, leaving orbital hiatus open (see Forest & Guinot 1961: fig. 123). Antennules transversely folded. Eyes relatively large, rounded, exposed, only partially protected by orbits (Plate 1A). Third maxillipeds with merus narrow, much shorter than ischium; ischium elongated, smooth inner margin, lower inner margin oblique (see Guinot 1964: figs. 7, 9, 10). Second maxillipeds with endopod fused with dactylus, propodus in *Domecia* (four distinct somites in *Jonesius, Palmyria*). Chelipeds unequal in size; tips of fingers pointed; propodus with conspicuous pointed or round tubercles or granules; merus short, barely showing dorsally when folded (Plate 1A–C), smooth anterior margins. P2–P5 relatively short, stout; dactylo-propodal lock; dactyli curved, claw-like, without rows of setae (see Guinot 1964: fig. 8). Male abdomen with somites 3–5 fused but sutures visible. Abdominal holding system of males consisting of small fosette in somite 6 fitting into small, round press-button on abdominal sternite 5 plus raised saddle on slightly widened somite 3 fitting onto abdominal sternite 8 (saddle absent in *Jonesius, Palmyria*). G1 stout, slightly sinuous, tip blunt, truncated (see Serène 1984: figs. 201–203). G2 proximally thick, total length about half G1. Females with moderately expanded abdomen where only first few somites are visible dorsally below posterior margin of carapace. Male genital openings coxal, female openings sternal.

Genera included: *Domecia* Eydoux & Souleyet, 1842, *Jonesius* Sankarankutty, 1962, *Maldivia* Borradaile, 1902, *Palmyria* Galil & Takeda, 1986, and *Eomaldivia* Müller & Collins, 1991 (fossil).

Remarks

As discussed earlier, the genera now included in the Domeciidae have been grouped together since Ortmann (1893) recognised it as a subfamily of the Trapeziidae. Their carapace features are all very different from typical trapeziids, but they have probably been classified together for so long mainly because of their shared habitats and habits (see Serène 1984, Castro 1976). Davie (2002) concluded that the similarities were superficial and raised the Domeciinae to full family status as he felt it was a distinct group in itself (P. Davie, pers. comm.). The present cladistic analysis supports this action.

Key to extant genera of Domeciidae

1 Frontal and anterolateral margins of carapace with numerous acute teeth (Plate 1A). Merus of third maxillipeds about twice as broad. Facultative symbionts of shallow-water scleractinian corals .... *Domecia*

\- Anterolateral margins of carapace between outer orbital angle and anterolateral teeth each with 2 teeth or small tubercles; frontal margin smooth or with microscopic denticles or tubercles, margin complete and nearly straight or with shallow median indentation. Merus of third maxillipeds as long as broad. Obligate symbionts of scleractinian and hydrozoan corals and gorgonians 2

2 Chelipeds conspicuously unequal 3

\- Chelipeds equal (see Borradaile 1902: fig. 60)... *Maldivia* (monotypic, *M. symbiotica*)

3 Rounded tubercles on propodus of chelipeds (Plate 1B) .... *Jonesius* (monotypic, *J. triunguiculatus*)

\- Pointed tubercles on propodus of chelipeds (Plate 1C)... .... *Palmyria* (monotypic, *M. palmyrensis*)

Genus *Domecia* Eydoux & Souleyet, 1842

Domecia Eydoux & Souleyet 1842: 234 (type species *Domecia hispida* Eydoux & Souleyet, 1842, by monotypy; gender feminine)
Domaecius — Dana 1851: 128 (incorrect spelling)
Domaecia — Dana 1851: 128 (incorrect spelling)
Domoecia — A. Milne Edwards 1873: 263 (incorrect spelling)
Neleus Desbonne & Schramm 1867: 35 (type species *Neleus acanthophorus* Desbonne & Schramm, 1867, by monotypy; gender masculine)
Eupilumnus Kingsley 1880: 397 (type species *Eupilumnus websteri* Kingsley, 1880, by monotypy; gender masculine; junior homonym of *Eupilumnus* Kossmann, 1877, Crustacea: Brachyura: Pilumnidae)

Diagnosis

Frontal and anterolateral margins of carapace with many acute teeth (Plate 1A). Chelipeds unequal. Outer margins of propodus and carpus of chelipeds spinose; merus short, barely showing dorsally (Plate 1A). Merus of third maxillipeds very short, about twice as broad as long (see Guinot 1964: figs. 7, 9, 10). Symbionts of shallow-water scleractinian corals (particularly *Pocillopora*; *Acropora* in Western Atlantic) but also found free-living on dead corals and rocks.

Species of *Domecia* (species discussed separately are marked with an asterisk)

1. *Domecia acanthophora* (Desbonne & Schramm, 1867) (as *Neleus acanthophorus*) [type locality Guadaloupe, West Indies; geographical distribution: tropical Western Atlantic region]
   Pilumnus melanacanthus Kingsley, 1879
   = *Eupilumnus websteri* Kingsley, 1880
2. *Domecia africana* Guinot in Manning & Holthuis, 1981*
   = *Domecia acanthophora* forma *africana* Guinot, 1964 (invalid name) [no holotype; geographical distribution: tropical Eastern Atlantic region]
3. *Domecia glabra* Alcock, 1899 [type locality Andaman Islands; geographical distribution: across Indo–West Pacific region]
4. *Domecia hispida* Eydoux & Souleyet, 1842* [type locality Hawaiian Islands; geographical distribution: across Indo–West Pacific region] (Plate 1A)

Key to species of *Domecia*

1 Anterior portion of thoracic sternite plate broadly triangular, with almost straight sides, forming an almost equilateral triangle (see Guinot 1964: fig. 14) .... *D. glabra*
\- Anterior portion of thoracic sternite plate narrowly triangular, with convex sides...... 2
2 Region of carapace posterior to median anterior lobes without conspicuous spines (Plate 1A). Anterior portion of thoracic sternite plate acute, with long, narrow and pointed tip (see Guinot 1964: fig. 13) .... *D. hispida*
\- Region of carapace posterior to median anterior lobes with many small spines. Anterior portion of thoracic sternite plate with short, rounded tip 3
3 Third maxilliped merus with median spines and short tubercles along each inner margin. Anterior portion of thoracic sternite plate slightly long (see Guinot 1964: fig. 15) .... *D. acanthophora*
\- Third maxilliped merus with median spines but no tubercles. Anterior portion of thoracic sternite plate slightly short (see Guinot 1964: fig. 16) .... *D. africana*

Domecia africana Guinot in Manning & Holthuis, 1981

Domecia acanthophora forma *africana* Guinot, 1964: 272, figs. 6, 10–12, 16, 17.
Domecia acanthophora africana Manning & Holthuis, 1981: 122.

Remarks. This taxon was originally described only as a form of *Domecia acanthophora* (Desbonne & Schramm, 1867) by Guinot (1964), and as such, the name is not nomenclaturally available under current zoological rules (Article 15.2). It was only first used as a valid name by Manning and Holthuis (1981) (who recognised the taxon as a subspecies), but credit the authorship and original description to Guinot.

Domecia hispida Eydoux & Souleyet, 1842 (Plate 1A)

Domecia hispida Eydoux & Souleyet, 1842: 235, pl. 2, figs. 5–10.

Remarks. There is a problem with the nomenclature of this well-known and widely distributed species as there appears to be an older name, *Cancer tridentatus* Forskål, 1775. The original description of *Cancer tridentatus* Forskål, 1775 (from Suez, Red Sea), is too brief to be certain of its identity, but as it is, it fits the genus *Domecia* as presently understood. The description best fits *Domecia hispida* Eydoux and Souleyet, 1842, which is present in the Red Sea. As Forskål's material is no longer extant, we can never be certain. However, to have the senior name replacing the widely used name of *Domecia hispida* serves no real purpose in our opinion, and we invoke Article 23.9.2 of the current zoological code in suppressing the senior name. Certainly, the name *Cancer tridentatus* Forskål, 1775, has never been used since its description while the name *Domecia hispida* has been regularly used over the last few decades.

Genus *Jonesius* Sankarankutty, 1962

Jonesius Sankarankutty, 1962: 141 (type species *Jonesius minuta* Sankarankutty, 1962, by monotypy; gender masculine)

Diagnosis

Frontal margin of carapace smooth; anterolateral margins with short, blunt teeth (Plate 1B). Chelipeds unequal. Outer margins of propodus and carpus of chelipeds with conspicuous tubercles, not spinous (Plate 1B). Merus of chelipeds short, barely showing dorsally. Merus of third maxillipeds nearly as broad as long (see Galil & Takeda 1986: fig. 2). Symbiont of many genera of shallow-water scleractinian corals (see Galil & Takeda 1986: 165).

Species of *Jonesius*

Jonesius triunguiculatus (Borradaile, 1902) (as *Pseudozius triunguiculatus*) [type locality Laccadive Islands, India; geographical distribution: across Indo–West Pacific and Eastern Pacific regions] (Plate 1B)
= *Jonesius minuta* Sankarankutty, 1962
= *Maldivia gardineri* Rathbun, 1911
= *Maldivia galapagensis* Garth, 1939

Genus *Maldivia* Borradaile, 1902

Maldivia Borradaile, 1902: 269 (type species *Maldivia symbiotica* Borradaile, 1902, by monotypy; gender feminine)

Diagnosis

Frontal margin of carapace with microscopic teeth; anterolateral margins with short teeth (see Borradaile 1902: fig. 60). Chelipeds equal. Outer margins of propodus and carpus of chelipeds with short teeth. Merus of chelipeds short, barely showing dorsally. Obligate symbiont of gorgonians.

Species of *Maldivia*

Maldivia symbiotica Borradaile, 1902 [geographical distribution: known only from type locality, Maldive Islands]

Fossil species of *Maldivia*

Maldivia plana Müller, 1996 [Miocene]

Genus *Palmyria* Galil & Takeda, 1986

Palmyria Galil & Takeda 1986: 168 (type species *Maldivia palmyrensis* Rathbun, 1923, by original designation; gender feminine)

Diagnosis

Frontal margin of carapace smooth; anterolateral margins with acute teeth (Plate 1C). Chelipeds unequal. Outer margins of propodus of chelipeds with pointed tubercles (Plate 1C). Merus of chelipeds short, barely showing dorsally. Merus of third maxillipeds nearly as broad as long (see Galil & Takeda 1986: fig. 6). Obligate symbiont of shallow-water scleractinian and hydrozoan corals (see Serène 1984, as *Maldivia palmyrensis*).

Species of *Palmyria*

Palmyria palmyrensis (Rathbun, 1923) (as *Maldivia palmyrensis*) [type locality Palmyra Atoll, Line Islands, central Pacific Ocean; geographical distribution: across Indo–West Pacific region] (Plate 1C)

Fossil Genus *Eomaldivia* Müller & Collins, 1991

Eomaldivia Müller & Collins, 1991: 81 (type species *Eomaldivia pannonica* Müller & Collins, 1991, original designation; gender feminine)

Diagnosis

Carapace subhexagonal; 2 or 3 pairs of anterolateral teeth; frontal margin with median notch.

Fossil species of *Eomaldivia*

1. *Eomaldivia pannonica* Müller & Collins, 1991. [Eocene]
2. *Eomaldivia trispinosa* Müller & Collins, 1991 [Eocene]

Family Tetraliidae *fam. nov.*

Trapeziinae Miers, 1886: 163 (part); Borradaile 1902: 238 (part); Klunzinger 1913: 304 (part); Balss 1922: 133 (part);1957: 1653 (part); Sakai 1976: 506 (part); Dai & Yang 1991: 262, 379 (part).
Trapeziidae — Ortmann 1893: 430 (part); 1897: 201 (part); Guinot 1978: 275 (part); Serène 1984: 265 (part); Ng 1998: 1074 (key), 1081 (part); Martin & Davis 2001: 75 (part); Davie 2002: 493 (part).
Trapezoida — Alcock 1898: 177, 217 (part).

Type genus — *Tetralia* Dana, 1851

Diagnosis

Carapace longitudinally ovate, posterior portion conspicuously narrower than anterior portion as posterolateral margins sharply diverge posteriorly; frontal margin straight or nearly straight, finely denticulate; dorsal surface smooth, polished, regions not marked; relatively flattened; anterolateral teeth present only in juveniles, no teeth or tubercles on anterolateral margins (Plate 1D, 2B). Thoracic sternites 1 and 2 fused, triangular, as wide as high, suture between second and third thoracic sternites absent (see Galil 1986a: fig. 2C; 1986b: fig. 2A). Basal antennal articles laterally expanded, reaching orbital margin, closing orbital hiatus (see Galil 1986a: fig. 2B;1986b: fig. 2B). Antennules transversely folded. Eyes relatively large, elongated, exposed, only partially protected by orbits (Plate 1D, 2B). Third maxillipeds with merus much shorter than ischium; merus nearly round; ischium elongated, smooth inner margin, lower inner margins oblique (see Galil 1986a: fig. 2A; 1986b: fig. 2C). Second maxillipeds with endopod consisting of distinct dactylus, propodus, carpus, merus. Chelipeds conspicuously unequal in size, different in shape, largest large or very large in relation to carapace size; tips of fingers pointed, propodus smooth; merus short, a third or less showing dorsally when folded, row of very small teeth along each anterior margin; larger cheliped with curved fingers, swollen, enlarged propodus (Plate 1E); smaller cheliped much shorter, with nearly straight fingers, narrow propodus (Plate 1D, 2B). P2–P5 relatively short, stout; dactylo-propodal lock; dactyli with hoof-like tip, horizontal rows of setae (see Galil 1986a: fig. 3; 1986b: fig. 3; 1987: figs. 3, 4). Male abdomen with 6 freely articulating somites excluding telson (Fig. 3A; also see Serène & Dat 1957: fig. 1). Abdominal holding system of males consisting of small fosette in somite

6 fitting into small, round press-button on abdominal sternite 5 plus thick saddle with anterior spur on widened, slightly elongated somite 3 (Figs. 3B, C) fitting onto abdominal sternite 8. G1 short, stout, slightly sinuous or straight, tip rounded in *Tetralia* (see Serène 1984: fig. 188; Galil 1986b: fig. 3A); slender, slightly sinuous, tip pointed in *Tetraloides* (see Serène 1984: fig. 189, as *Tetralia heterodactyla lissodactyla*; Galil 1986b: fig. 3A). G2 stout, slightly curved, spoon-like tip (Fig. 3D), total length less than half G1. Females with moderately expanded abdomen (see Serène & Dat 1957: figs. 1B, C) where only first few somites are visible dorsally below posterior margin of carapace. Male genital openings coxal, female openings sternal.

Genera included: *Tetralia* Dana, 1851, and *Tetraloides* Galil, 1986.

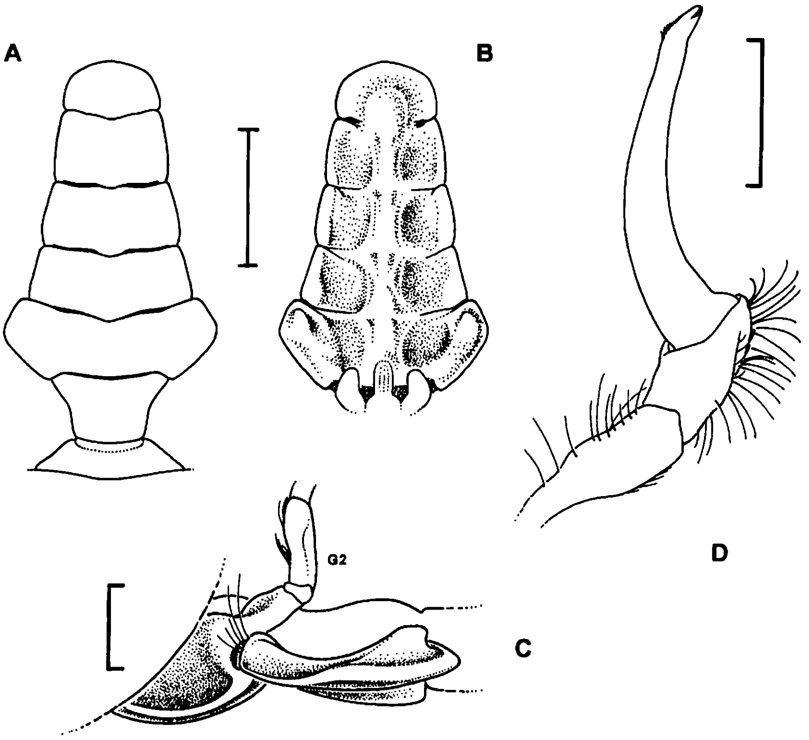

FIGURE 3. *Tetralia glaberrima* (Herbst, 1790), ♂ (cl 9.4 mm, cw10.1 mm), on *Acropora* sp., New Caledonia (22°19.90'S, 166°22.30'E), P. Castro coll., 26.04.1995 (MNHNB 24125): A, external (ventral) view of abdomen; B, internal (dorsal) view of abdomen, showing the characteristic saddle with anterior spur on abdominal somite 3; C, lateral view of abdominal somite 3. *Tetralia glaberrima* (Herbst, 1790), ♂ (cl 9.2 mm, cw10.1 mm), same data as specimen above: D, left male second pleopod (G2), ventral view. Scale bars: A, B = 2 mm; C, D = 0.5 mm.

Key to genera of Tetraliidae

1 Larger cheliped with setae-filled depression on dorsal, proximal surface of propodus (Plate 1E). Distinct median longitudinal groove on thoracic sternites 4 and 5 ... *Tetralia*

- Larger cheliped without setae-filled depression (Plate 2B). Thoracic sternites 4 and 5 entire, without visible median longitudinal groove .... *Tetraloides*

Genus *Tetralia* Dana, 1851

Tetralia Dana, 1851: 224 (type species *Cancer glaberrimus* Herbst, 1790, by monotypy; gender feminine)

Diagnosis

Carapace smooth, longitudinally ovate; frontal margin nearly straight, with minute teeth; anterolateral margins smooth in adults (Plate 1D). Chelipeds conspicuously dissimilar in size. Larger cheliped with setae-filled depression on dorsal, proximal surface of propodus (Plate 1E). Distinct median longitudinal groove on thoracic sternites 4 and 5 (see Galil 1986b: fig. 2A). Male abdomen with 6 freely articulating somites excluding telson (Fig. 3A). Obligate symbiont of shallow-water scleractinian corals (numerous species of *Acropora*).

Remarks

Several morphological differences have been described between the first-stage zoea of Tetraliidae and those of Trapeziidae (e.g. Clark & Galil 1988, Shikatani & Shokita 1990). For example, there is only one spine on each side of the carapace in trapeziids, but two in tetraliids. The first stage zoea of *Quadrella*, however, has been found to have two spines on each side of the carapace instead of one spine as in *Trapezia* (Clark & Ng, in press). In the present analysis, however, *Quadrella* is clearly allied with *Trapezia* and not *Tetralia.* But as Clark & Ng (in press) note, the zoeae of too few genera have been described and more will need to be obtained before a more complete picture develops. Interestingly, a separate preliminary study of the molecular phylogeny of the Trapeziidae *s. lato* (excluding the Domeciidae) has shown that there are two distinct groups, corresponding to what are here defined as two families, Trapeziidae *s. str.* and Tetraliidae (M.-S. Jeng, pers. comm.).

Species of *Tetralia* (species discussed separately are marked with an asterisk)

1. *Tetralia cavimana* Heller, 1861 [type locality Red Sea; geographical distribution: Red Sea, northwestern Indian Ocean]
2. *Tetralia cinctipes* Paulson, 1875 (as *Tetralia cavimana* var. *cinctipes*) [type locality Red Sea; geographical distribution: across Indo–West Pacific region except Hawaiian Islands]
   = *Tetralia glaberrima* forma *pullidactyla* Patton, 1966 (invalid name)
   = *Tetralia glaberrima pullidactyla* Garth, 1971
3. *Tetralia glaberrima* (Herbst, 1790) (as *Cancer glaberrimus*) * [original type locality unknown, type(s) lost; neotype locality (following present designation) Queensland, Australia; geographical distribution: across Indo–West Pacific region except Hawaiian Islands] (Fig. 3A–D, Plate 1D, E, 2A; Fig. 3A–D)
   = *Trapezia integra* Latreille, 1828
   = *Trapezia serratifrons* Jacquinot, 1846
   = *Tetralia laevissima* Stimpson, 1858
   = *Tetralia glaberrima* forma *fulva* Patton, 1966 (invalid name)
   = *Tetralia glaberrima fulva* Serène, 1984
   = *Tetralia sanguineomaculata* Galil & Clark, 1990
4. *Tetralia muta* (Linnaeus, 1758) (as *Cancer mutus*) * [original type locality "*mari mediterraneo*", type(s) lost; neotype locality (following present designation) Guam, Mariana Islands; geographical distribution: across Indo–West Pacific region except Hawaiian Islands]
   = *Tetralia armata* Dana, 1852
   = *Tetralia vanninii* Galil & Clark, 1988
5. *Tetralia nigrolineata* Serène & Dat, 1957 (as *Tetralia glaberrima* forma *nigrolineata*) [type locality Queensland, Australia based on neotype selection by Castro (1997a); geographical distribution: across Indo–West Pacific region except Hawaiian Islands]
   = *Tetralia glaberrima* forma *obscura* Patton, 1966 (invalid name)
   = *Tetralia glaberrima obscura* Serène, 1984
6. *Tetralia rubridactyla* Garth, 1971 (as *Tetralia glaberrima* forma *rubridactyla*) [type locality Queensland, Australia based on neotype selection by Castro (1997a); geographical distribution: across Indo–West Pacific region except Hawaiian Islands]
   = *Tetralia rubridactyla* Garth, 1971
   = *Tetralia innamorata* Galil & Clark, 1988

Fossil species of *Tetralia*

Tetralia loerentheyi (Müller, 1975) (as *Trapezia loerentheyi*) [Eocene]

Key to extant species of *Tetralia*

1 Ambulatory legs banded brown. Carapace light brown with broad, blue band across frontal margin when alive (see Castro 1997b: pl. A, fig. a [colour]; Jones & Morgan 2002: 179 [colour]) .... *T. cinctipes*

- Ambulatory legs not distinctly banded. Black band or red line across frontal margin of carapace or no distinctive line at all 2

2 Outer edges of frontal margin of carapace with teeth much larger than minute teeth along central portion (see Galil 1988a: fig. 1a). Endopod of first maxilliped with oblique distal margin (see Galil 1988a: fig. 2a) .... *T. cavimana*

- Outer edges of frontal margin of carapace with minute teeth similar or nearly similar in form along entire margin. Endopod of first maxillipeds with round, straight or concave distal edge 3

3 Conspicuous black band across frontal margin of carapace 4

- No thick black band across frontal margin of carapace (a thin red or dark brown line may be present) 5

4 Black band followed by thin blue-green line along both frontal and anterolateral margins of carapace (see Castro 1997a: pl. 1, fig. D [colour]). Cheliped propodus evenly coloured, with microscopic granules. Endopod of first maxillipeds each with rounded distal margin (see Galil 1988a: fig. 2e) .... *T. nigrolineata*

- Black band followed by thin-blue line only along frontal margin of carapace (except small specimens, where it may extend along anterolateral margins). Cheliped propodus with red tubercle on dorsal surface, conspicuous granules, particularly visible along inner margin. Endopod of first maxillipeds with concave distal margin (see Castro 1997b: fig. 1, as *T. vanninii*) .... *T. muta*

5 Distal portion of cheliped dactyli light brown (Plate 1E) .... *T. glaberrima*

- Distal portion of cheliped dactyli orange-red ((see Castro 1997a: pl. 1, fig. E [colour]) .... *T. rubridactyla*

Tetralia glaberrima (Herbst, 1790) (Plate 1D, E, 2A)

Cancer glaberrimus Herbst, 1790: 262, pl. 20, fig. 115 (colour) (see Plate 2C).
Trapezia integra Latreille, 1828: 696.
Trapezia serratifrons Jacquinot, in Hombron & Jacquinot 1846: pl. 4, fig. 20 (colour)—23; Jacquinot, in Lucas 1853: 47.
Tetralia laevissima Stimpson,1858: 38 [35]; Stimpson 1907: 73, pl. 9, figs. 4, 4a.
Tetralia glaberrima forma *fulva* Patton, 1966: 286 (invalid name)
Tetralia glaberrima fulva Serène, 1984: 282.
Tetralia sanguineomaculata Galil & Clark, 1990: 375, figs. 4, 5, 6b.

Remarks. The taxonomic history of *Cancer glaberrimus* Herbst, 1790, has been very confusing. In recent times, the name has been used loosely for a number of species of *Tetralia*, and despite the several revisions and taxonomic studies (including the establishment of a separate genus *Tetraloides*) by several authors, the exact identity of *T. glaberrima* has never been discussed. This is all the more unfortunate and surprising since *Cancer glaberrimus* is the type species of *Tetralia*. In fact, as late as 1918, Rathbun (1918: 254) regarded *Cancer glaberrimus* as a junior synonym of the grapsid *Planes minutus* (Linnaeus, 1758)!

Unfortunately, only its colour provides a clue to the identity of *C. glaberrimus*. The smooth carapace was described as brown with a bluish colour that gave it a porcelain-like shine (*"porzellanähnliches Ansehen"*; Herbst 1790: 262). A colour figure (Herbst 1790: pl. 20, fig. 115) shows a large, blue spot centered on the anterior half of the carapace (Plate 2A). The spot surrounds a smaller, round spot of the same colour, perhaps a hole on the carapace. No such colour pattern has ever been observed or described in any trapeziid so it is most probably an artefact. A blue band across the frontal margin of the carapace has been described in *T. cinctipes* Paulson, 1875, but this is evident only on live specimens (Castro 1997b: pl. 1, fig. A [colour]), something Herbst most probably could not observe. A uniform brown colour without black or dark brown bands agrees best with the colour pattern of *T. fulva* Serène, 1984 (see Castro 1997a: 67, pl. 1, fig. C [colour]). As such, on the basis of the available information, *Cancer glaberrimus* can be referred to either *T. cinctipes* Paulson, 1875, or *T. fulva* Serène, 1984. However, we believe that in the interests of nomenclatural stability, *C. glaberrimus* and *T. fulva* should be regarded as synonymous (see below). The type locality of *C. glaberrimus* was stated as unknown, although it was probably obtained from the Indian Ocean as much of his material was from there (see Ng 1996, Sakai 1999). There are no extant type(s). The first two authors have searched in vain for the types on separate occasions over the last decade, and Sakai (1999: 41) also recorded that it was lost. This has also been confirmed by the former and present crustacean curators of the Zoologisch Museum, Humboldt-Universität, Berlin, Hans Gruner and Oliver Coleman respectively (pers. comm.).

The identity of *Trapezia integra* Latreille, 1828, is also a mystery. There is no type material in the Muséum national d'Histoire naturelle, Paris. The species was described from an unknown location and it was seemingly a new or replacement name for *Cancer glaberrimus* (Latreille 1828: 696). As such, *Trapezia integra* Latreille, 1828, shares the same type series as *Cancer glaberrimus* Herbst, 1790.

Castro (1997b) suggested that *T. serratifrons* Jacquinot, 1846 (type locality Marquesas Islands, French Polynesia) is likely to be conspecific with *T. fulva* Serène, 1984. It is here regarded as a junior synonym of *T. glaberrima*. The colour figure of *T. serratifrons* (which shows a brown carapace without dark bands) is diagnostic for *T. glaberrima* (as *T. fulva*). No type material of this species (supposedly in the MNHN) exists.

Tetralia laevissima Stimpson, 1858, described from southern Japan, is very likely to be a junior synonym of *T. glaberrima* as well. Although Stimpson's type material is no longer extant, the drawings, presumably made by Stimpson himself or under his supervision (Stimpson, 1907: pl. 9, figs. 4, 4a), do not show any distinctive, obvious colour pattern on the carapace, chelipeds, or ambulatory legs. This is diagnostic for *T. fulva* (*sensu* Galil 1988a: fig. 1b; Castro 1997a: pl. 1, fig. C [colour]) (= present *T. glaberrima*), which is uniformly brown to tan except a thin orange to red-orange line along the anterior border of the carapace and along the distal margins of carpi and anterior margins of meri of chelipeds. The ambulatory legs are uniformly brown to tan except a black spot on the articulations of the carpi visible in most specimens. We doubt that Stimpson would have missed a characteristic colour pattern such as a wide band along the anterior portion of the carapace (if present) in his figure of the species, especially since he clearly indicated the honeycomb-like network of lines in his drawing of the carapace of *Trapezia septata* (Stimpson 1907: pl. 9, fig. 5, as *Trapezia reticulata* Stimpson, 1858). The chelipeds of *T. laevissima* were described as "glossy", which also agree with those of *T. fulva*. In *T. cinctipes* Paulson, 1875, a species where the carapace (but not the chelipeds and ambulatory legs) is also uniformly brown to tan in preserved specimens, the chelipeds cannot be described as glossy since they are covered by small but distinct tubercles. Serène (1984) synonymised *T. rubridactyla* Garth, 1971 with *T. laevissima* without comment, an action we do not agree with. *Tetralia rubridactyla* typically has a prominent crest along the anterior margins of the cheliped merus, and the distal edge of the cheliped merus as well as the dorsal surface of the cheliped merus and propodus are dark brown in colour when alive, characters that are clearly absent in Stimpson's figure or description. The posterior portion of the carapace of *T. laevissima* appears very narrow, as in members of *Tetraloides*, but we believe this is due merely to the figure being schematic. A setae-filled depression on the dorsal proximal surface of the cheliped propodus, diagnostic for *Tetralia* is absent in *Tetraloides*, but is clearly indicated in Stimpson's drawings (Stimpson 1907: pl. 9, figs. 4, 4a).

As already discussed by Castro (1997a: 67), the name *Tetralia glaberrima* forma *fulva* Patton, 1966, is invalid under the current zoological code. Its first valid use was apparently by Serène (1984), who also used Patton's name as a subspecies, *T. glaberrima fulva*. As Patton's material was no longer extant, Castro (1997a: 65) designated a neotype of *T. fulva* Serène, 1984, from Queensland, Australia. It is also worthwhile to note that the first nomenclaturally valid use of "*fulva*" may in fact be by Ribes (1978: 14) who used the name "*Tetralia glaberrima fulva*" in her doctoral thesis. This thesis, however, had a very limited circulation and is not well known outside France, and is not here regarded as a valid publication. Even if Ribes' thesis is considered a valid publication (as might be shown later), it will not affect the taxonomy of the species because on the basis of the present study *Tetralia glaberrima fulva* is an objective junior synonym of *Cancer glaberrimus* Herbst, 1790 (see below).

Castro (1997a: 68) had shown that *T. sanguineomaculata* Galil & Clark, 1990 (type locality New Caledonia), is a junior subjective synonym of *T. fulva*.

The recognition of the poorly understood *C. glaberrimus* Herbst, 1790, as a senior synonym of *Tetralia fulva* Serène, 1984, *Trapezia integra* Latreille, 1828, *Trapezia serratifrons* Jacquinot, 1846, and *Tetralia laevissima* Stimpson, 1858, does not cause any problems. The name and taxonomic concept of *Tetralia fulva* was only established with certainty relatively recently (Galil 1988a) and the name has been seldom used. In any case, as discussed earlier, *Tetralia fulva* Serène, 1984, has to be replaced by *Trapezia integra* Latreille, 1828, anyway. We believe that our present action best serves the interest of long-term nomenclatural stability.

To this effect and to maintain stability, we hereby designate the neotype of *Tetralia fulva* Serène, 1984, designated by Castro (1997a: 65), a male (MNHN-B 25234; cl 7.3 mm, cw 8.4 mm) from Heron Island (23°26'N, 151°55'E), Queensland, Australia, as the simultaneous neotype of *Cancer glaberrimus* Herbst, 1790. We also designate this specimen as the neotype for *Trapezia integra* Latreille, 1828, *Trapezia serratifrons* Jacquinot, 1846, and *Tetralia laevissima* Stimpson, 1858. This action effectively makes all five names objective synonyms of *C. glaberrimus* Herbst, 1790.

Tetralia muta (Linnaeus, 1758)

Cancer mutus Linnaeus, 1758: 625.
Tetralia armata Dana, 1852: 264, pl. 16, fig. 4.
Tetralia vanninii Galil & Clark, 1988: 146, figs. 1C, 2B, 3C, 4C, 4H, 6C.

Remarks. *Cancer mutus* Linnaeus, 1758, is a name which has hardly been used since 1758. When naming this species, Linnaeus described it as having a brown frontal margin and a smooth carapace with a flattened, truncated posterior margin ("... *thorace laevi integerrimo, margine antico transverso brunneo ... postice complanato-truncata* ..." (Linnaeus, 1758: 625). The name was subsequently used by Herbst (1783: 116), who merely listed this species, but without any figures. This species was then forgotten until the name was used again by Sakai (1999: 14), this time for a dromiid. Sakai (1999: pl. 4A, fig. F) figured a specimen in the Zoologisch Museum, Humboldt-Universität, Berlin which apparently had been identified and labelled as "*Conchoecetes mutus* Linnaeus, 1758". The specimen figured is clearly conspecific with *Conchoecetes intermedius* Lewinsohn, 1984, as currently understood and bears absolutely no resemblance to the description of Linnaeus (1758). Clearly, Herbst (or someone else) had misidentified the Berlin specimen and Sakai (1999) had followed suit without question. The type specimen(s) of *Cancer mutus* Linnaeus, 1758, is no longer extant (S. H. Tan, pers. comm.).

The characters noted by Linnaeus (1758) for *Cancer mutus* are clearly that of a *Tetralia* (or *Tetraloides*). He recorded it from the Mediterranean with doubt. This is important as the Mediterranean does not have any known records of trapeziids or tetraliids, and this probably confused workers or caused them to ignore the name. In the present instance, we believe that the locality data Linnaeus obtained was incorrect. Certainly there is no crab we know of from the Mediterranean which has the characters Linnaeus described for *C. mutus*.

The characters enumerated by Linnaeus, although brief, clearly indicate that *C. mutus* could be one of the following recognised trapeziid species: *Tetralia armata* Dana, 1852, *Tetralia vanninii* Galil & Clark, 1988, or *Tetraloides nigrifrons* (Dana, 1852).

Tetralia armata Dana, 1852, itself is a problem, especially since the type is lost. Although described from Tonga in the central Pacific Ocean, the name has somehow been ignored by almost all workers, even though Dana provided a reasonably detailed description (for the time) and an uncoloured figure. It was described as "pale, with anterior margin brownish black" (Dana 1852: 264). The specimen illustrated by Dana (1852: pl. 16, figs. 4 a–c) was a juvenile or small adult with one anterolateral spine on each side of the carapace and two pointed spines on the inner side of each cheliped carpus. Dana's drawing also showed the outer margin of the cheliped merus having thin, spine-like teeth. The colour pattern and morphological characters of *T. armata* are shared with *T. vanninii*, which has been collected through most the Indo–West Pacific region (see Castro 1997b: 113, fig. 1; 1999b: 103). *Tetralia vanninii* Galil & Clark, 1988, is thus likely to be a junior subjective synonym of *T. armata* Dana, 1852.

All of the characters used to describe *C. mutus*, most particularly the brown frontal margin, could also apply to *Tetraloides nigrifrons* (Dana, 1852), although the brown frontal margin of this species often extends along the anterolateral sides of the carapace.

Therefore, as things are, the name *Cancer mutus* Linnaeus, 1758, can be used for either *Tetralia armata* Dana, 1852 (= *Tetralia vanninii* Galil & Clark, 1988) or *Tetraloides nigrifrons* (Dana, 1852). *Tetraloides nigrifrons* (Dana, 1852), however, is a relatively common species and the name has been used more frequently used by taxonomists and ecologists than either *T. armata* or *T. vanninii*. In addition, *Tetraloides nigrifrons* is also the designated type species of *Tetraloides* Galil, 1986. Since the name *T. vanninii* Galil & Clark, 1988, has to be replaced by the senior but hardly used name *T. armata* Dana, 1852, anyway, and since this species is generally less common, replacing both names with *Cancer mutus* Linnaeus, 1758, seems to be the most parsimonious action to take and will cause the least problems for taxonomy.

To this effect, we hereby select an ovigerous female specimen (ZRC 2000.2330; cl 8.0 mm, cw 8.8 mm) from Pago Bay, Guam (13°30'N, 144°40'E), Mariana Islands, as the neotype for both *T. armata* and *C. mutus*. It was collected by G. Paulay from *Acropora* at a depth of 20–25 m on 1 May 1997. *Cancer mutus* Linnaeus, 1758, and *Tetralia armata* Dana, 1852, thus become objective synonyms. The holotype of *T. vanninii* Galil & Clark, 1988, a male specimen from Somalia, western Indian Ocean, is supposedly extant (ZMF 1263) but is now apparently lost or misplaced. It has been unsuccessfully searched in Florence by the first author and more recently by S. Trautwein (pers. comm.). In the event future studies show that the Indian and Pacific Ocean populations of *Tetralia muta* (Linnaeus, 1758) are separate taxa, the name *T. vanninii* Galil & Clark, 1988, is still available.

Genus *Tetraloides* Galil, 1986

Tetraloides Galil, 1986: 68 (type species *Tetralia nigrifrons* Dana, 1852, by original designation; gender masculine)

Diagnosis

Carapace smooth, longitudinally ovate; frontal margin nearly straight, with minute teeth; anterolateral margins smooth in adults (Plate 2B). Posterior margin conspicuously short. Chelipeds conspicuously dissimilar in size. Larger cheliped entire, without setae-filled depression on dorsal surface of propodus. Thoracic sternites 4 and 5 entire, without median groove (see Galil 1986a: fig. 2C). Male abdomen with 6 freely articulating somites excluding telson (see Serène & Dat 1957: fig. 1A, as *Tetralia nigrifrons* forme *fusca)*. Obligate symbiont of shallow-water scleractinian corals (numerous species of *Acropora*).

Species of *Tetraloides* (species discussed separately are marked with an asterisk)

1. *Tetraloides heterodactyla* (Heller, 1861) (as *Tetralia heterodactyla*) * [type locality Red Sea; geographical distribution: across Indo–West Pacific region except the Hawaiian Islands]
   = *Tetralia pubescens* Klunzinger, 1913
   = *Tetralia nigrifrons* forme *fusca* Serène & Dat, 1957
   = *Tetralia nigrifrons* forme *cyanea* Serène & Dat, 1957
2. *Tetraloides nigrifrons* (Dana, 1852) (as *Tetralia nigrifrons*) * [original type locality Tuamotu Archipelago, French Polynesia, type(s) lost; neotype locality (following present designation) Tuamotu Archipelago, French Polynesia; geographical distribution: across Indo–West Pacific region except the Hawaiian Islands] (Plate 2B)
   = *Tetralia nigrifrons* forma *lissodactyla* Serène & Dat, 1957

Key to species of *Tetraloides*

1 Dorsal surface of carapace with dark brown anterior portion (Plate 2B; also see Castro 1997a: pl. 1, fig. F [colour]; Jones & Morgan 2002: 178 [colour]). Ambulatory legs of live specimens with white or tan spots. Lower margin of smaller chela entire .... *T. nigrifrons*

\- Dorsal surface of carapace with light brown (see Castro 1997b: pl. 1, fig. B [colour]). Ambulatory legs of live specimens with blue spots (black in preserved specimens). Lower margin of smaller chela serrated .... *T. heterodactyla*

Tetraloides heterodactyla (Heller, 1861)

Tetralia heterodactyla Heller, 1861: 14.
Tetralia pubescens Klunzinger, 1913: 316, pl. 7, fig. 15.
Tetralia nigrifrons forma *fusca* Serène & Dat, 1957: 290.
Tetralia nigrifrons forma *cyanea* Serène & Dat, 1957: 116.

Remarks. *Tetralia nigrifrons* forma *cyanea* Serène & Dat, 1957 (type locality Vietnam), is almost certainly identical with *Tetraloides heterodactyla* Heller, 1861. Serène & Dat (1957) described the taxon as having bright blue spots on the ambulatory legs ("... *le vif de ses taches bleues sur les péreiopodes*)", a diagnostic characterisation of live or freshly preserved specimens (Castro 1997b: 46). The type material (a female lectotype and a female paralectotype, NMV 11a) is in the Naturhistorisches Museum, Vienna.

Tetraloides nigrifrons (Dana, 1852) (Plate 2B)

Tetralia nigrifrons Dana, 1852: 83, pl. 16, figs. 2a (colour)—d.
Tetralia nigrifrons forma *lissodactyla* Serène & Dat, 1957: 283, pl. 1.

Remarks. Dana's type material is lost. Since this is the type species of *Tetraloides* Galil, 1986, and there is the possibility that it may be confused with species like *T. muta* (Linnaeus, 1758) (see discussion for that species), it is best that a neotype be selected. The type locality is Pukapuka Island (= Honden Island) in the Tuamotu Archipelago, French Polynesia (Dana, 1852: 263). A male (MNHN-B 25322; cl 8.2 mm, cw 8.9 mm; Plate 2B) from Fangataufa Atoll (22°11.3S, 138°45.1W), Tuamotu Archipelago, is herein designated as the neotype of *Tetralia nigrifrons* Dana, 1852. It was collected by J. Poupin from *Acropora* on 4 May 1997.

Family Trapeziidae Miers, 1886

Trapezides Milne Edwards, 1862: 40 (French vernacular, name invalid).
Trapeziden Nauck, 1880: 64 (German vernacular, name invalid).
Trapeziinae Miers, 1886: 163 (part); Borradaile 1902: 238 (part); Klunzinger 1913: 304 (part); Balss 1922: 133 (part); 1957: 1653 (part); Sakai 1976: 506 (part); Dai & Yang, 1991: 262, 379 (part).
Trapeziidae — Ortmann 1893: 430 (part); 1897: 201 (part); Guinot 1978: 275 (part); Serène 1984: 265 (part); Ng 1998: 1074 (key), 1081 (part); Martin & Davis 2001: 75 (part); Davie 2002: 493 (part).
Trapezioida — Alcock 1898: 177, 217 (part).

Type genus — *Trapezia* Latreille, 1828 (by monotypy)

Diagnosis

Carapace trapezoidal (Plate 2C), hexagonal (Plate 4A, B), octagonal (Plate 4C), or transversely ovate (Plate 4D, E); posterior portion rounded or rectangular as posterolateral margins diverge posteriorly only gradually, making posterior margin not conspicuously narrower than frontal margin; frontal margin straight or nearly straight, typically with 4 lobes or broad teeth; dorsal surface smooth, polished, or finely granular; regions not marked; relatively flattened (convex in *Sphenomerides*); anterolateral margins smooth or 1 tooth or tubercle on each margin. Thoracic sternites 1 and 2 fused, much wider than high (see Guinot 1979: pl. 12, fig. 7; Castro 1997a: figs. 2B, D, F), suture between second and third thoracic sternites present (see Castro 1997a: fig. 2B) or absent. Basal antennal articles slender, not expanded (see Garth & Kim 1983: fig. 13c). Antennules transversely folded. Eyes relatively large, rounded, exposed, only partially protected by orbits (Plate 2C, 4 A–E). Third maxillipeds with merus shorter than ischium; merus nearly square; ischium strongly rectangular, denticulate inner margin, lower inner margins bent at nearly 90° angle (see Castro 1997a: fig. 3B). Second maxillipeds with endopod consisting of distinct dactylus, propodus, carpus, merus. Chelipeds large or very large in relation to carapace size, equal or slightly unequal in size, similar shape; tips of fingers pointed; propodus smooth; merus long or very long, third or more showing dorsally when folded, row of conspicuous teeth or tubercles along each anterior margin (Plates 2C; smooth in *Calocarcinus*, Plate 4C). P2–P5 long or moderately long, slender; dactylo-propodal lock; dactyli with pointed tip (hoof-like in *Trapezia*; see Galil 1987: figs. 1, 2), horizontal rows of setae (see Galil 1987: figs. 1, 2) (absent in *Calocarcinus, Philippicarcinus,* and *Sphenomerides*). Male abdomen with somites 3–5 fused but faint sutures visible (see Serène 1984: fig. 190). Abdominal holding system of males consisting of anteriorly-thickened fosette in somite 6 fitting into conspicuous, round press-button on abdominal sternite 5. G1 slender, slightly sinuous or straight, tip pointed (see Serène 1984: figs. 178–187, 191–196) (stout in *Calocarcinus*; see Serène 1984: figs. 197, 198). G2 stout, slightly curved or nearly straight, slender, spoon-like tip (see Serène 1975: fig. 9) (slender, curved tip in *Calocarcinus*; see Serène 1984: figs. 199–200), total length less than half G1 (about half length in *Calocarcinus*, about same length in *Philippicarcinus*). Females with moderately expanded abdomen (see Serène 1959: pl. 2, fig. B) where only first few somites are visible dorsally below posterior margin of carapace. Male genital openings coxal, female openings sternal.

Genera included: *Calocarcinus* Calman, 1909, *Hexagonalia* Galil, 1986, *Quadrella* Dana, 1851, *Philippicarcinus* Garth & Kim, 1983, *Sphenomerides* Rathbun, 1897, and *Trapezia* Latreille, 1828.

Key to genera of Trapeziidae

1 Anterior margins of cheliped merus with well-developed teeth or tubercles.............. 2

\- Anterior margins of cheliped merus without teeth 3

2 Frontal margin of carapace with conspicuous, V- or U-shaped median emargination, and 2 or more lobes, which are dentiform if more than 2 lobes present 4

\- Frontal margin of carapace with relatively short, rounded lobes or no lobes at all (if lobes are triangular, carapace and chelipeds covered with conspicuous spots) 5

3 Carapace octagonal, anterolateral margins with 2 teeth, the posterior tooth placed immediately below anterior tooth, thus forming 2 parallel, straight sides along middle portion of carapace (Plate 4C). On deep-water corals and other colonial cnidarians .... *Calocarcinus*

\- Carapace ovoid, with acuminate anterolateral sides each, with blunt tooth at tip; posterior portion of each anterolateral margin behind first tooth distinctly convex (Plate 4D). Not known to be associated with other invertebrates; deep water .... *Philippicarcinus*

4 Anterolateral margins of carapace each with 1 tooth (small specimens may also have 1 small intermediate spine on one or both sides), directed obliquely outwards (Plate 4A). Male first pleopod with distal spines or setae. On antipatharians (black corals), gorgonians, alcyonaceans (soft corals) or azooxanthellate (ahermatypic) scleractinian corals .... *Quadrella*

\- Anterolateral margins of carapace each with 2 prominent, acute teeth directed anteriorly (Plate 4B). On stylasterid (hydrozoan) corals and possibly gorgonians .... *Hexagonalia*

5 Anterolateral margins of carapace each with 1 tooth (Plate 2C) or no tooth at all. On shallow-water, zooxanthellate (hermatypic) scleractinian corals of family Pocilloporidae .... *Trapezia*

\- Anterolateral margins of carapace each with 2 small teeth (Plate 4E). Not known to be associated with other invertebrates; relatively deep water .... *Sphenomerides* (monotypic, *S. trapezoides*)

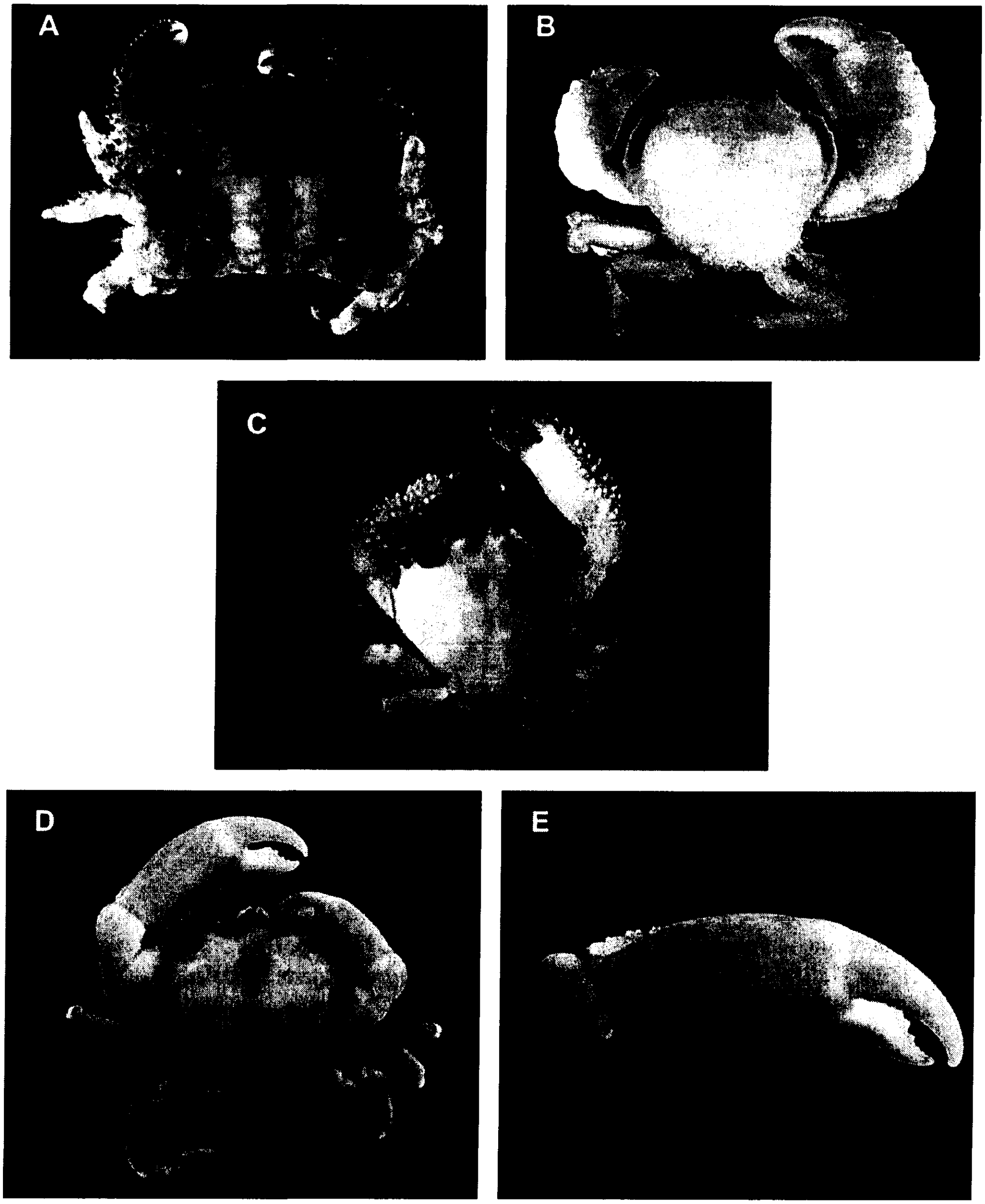

PLATE 1. Domeciidae: A, *Domecia hispida* Eydoux & Souleyet, 1842, ♂ (cl 6.5 mm, cw 9.1 mm), on *Pocillopora* sp., Hiva Oa I. (09°45'S, 139°00'W), Marquesas Is., French Polynesia, J. Poupin coll., 15.02.1996 (MNHNB 25813); B, *Jonesius triunguiculatus* (Borradaile, 1902), ♀ (cl 4.9 mm, cw 5.8 mm), New Caledonia, C. Vadon coll., 09.1978 (MNHNB 29171); C, *Palmyria palmyrensis* (Rathbun, 1923), ♂ (cl 2.9 mm, cw 3.9 mm), on *Galaxea fascicularis*, La Réunion (Indian Ocean), S. Ribes coll., 20.1.1977 (MNHNB 8376). Tetraliidae: D, *Tetralia glaberrima* (Herbst, 1790), ♂ (cl 9.4 mm, cw10.1 mm), on *Acropora* sp., New Caledonia (22°19.90'S, 166°22.30'E), P. Castro coll., 26.04.1995 (MNHN-B 24125); E, *Tetralia glaberrima*, left cheliped, same specimen as in D.

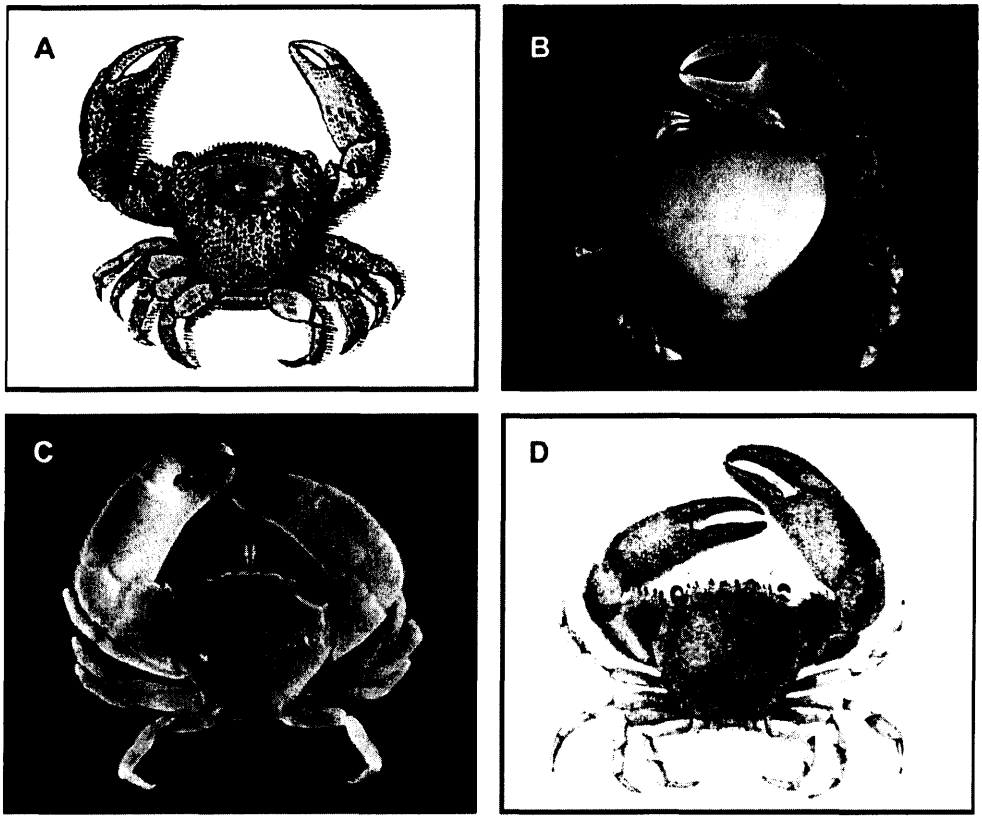

PLATE 2. Tetraliidae: A, *Cancer glaberrimus* Herbst, 1790 [= *Tetralia glaberrima* (Herbst, 1790)], plate 20, fig. 115 of Herbst (1790); B. *Tetraloides nigrifrons* Dana, 1851, ♂ neotype (cl 8.2 mm, cw 8.9 mm), on *Acropora* sp., Fangataufa Atoll (22°11.3'S, 138°45.1'W), Tuamotu Archipelago, French Polynesia, J. Poupin coll., 04.05.1997 (MNHNB 25322). Trapeziidae: C, *Trapezia cymodoce* (Herbst, 1801), ♂ (cl 9.7 mm, cw 11.9 mm), on *Pocillopora* sp., New Caledonia (22°19.80'S, 166°25.10'E), P. Castro coll., 24.04.1995 (MNHN-B 24961); D, *Cancer cymodoce* Herbst, 1801 [= *Trapezia cymodoce* (Herbst, 1801)], plate 51, fig. 2 of Herbst, 1801.

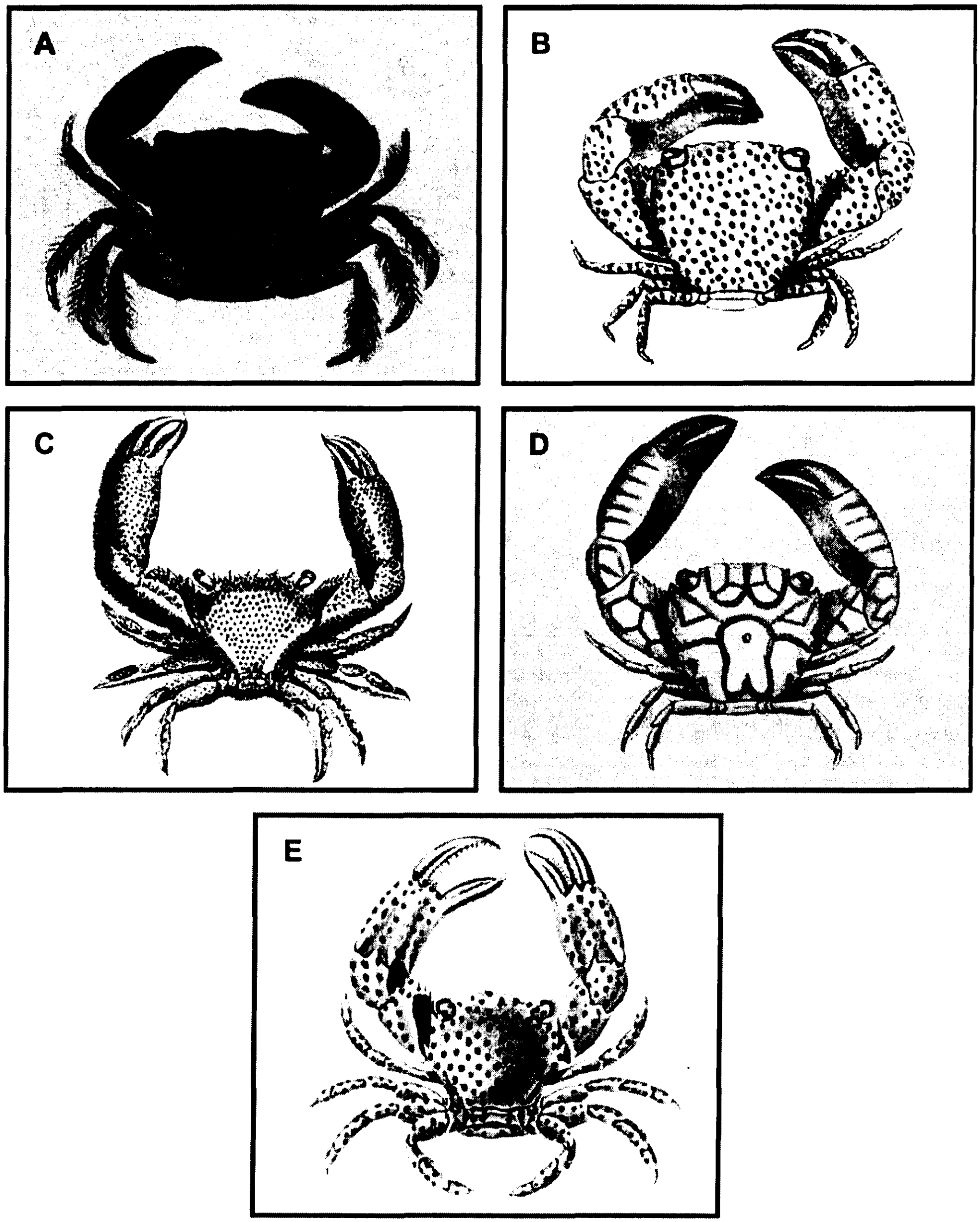

PLATE 3. Trapeziidae: A, *Trapezia dentata* var. *subintegra* Dana, 1852 [= *Trapezia cymodoce* (Herbst, 1801)], plate 17, fig. 7a of Dana (1852) [*Atlas* published in 1855]; B, *Trapezia bella* Dana, 1852, plate 15, fig. 2 of Dana (1852) [*Atlas* published in 1855]; C, *Trapezia flavopunctata* Eydoux & Souleyet, 1842, plate 2, fig. 3 of Eydoux & Souleyet (1842); D, *Trapezia speciosa* Dana, 1852, plate 15, fig. 1 of Dana (1852) [Atlas published in 1855]; E, *Trapezia tigrina* Eydoux & Souleyet, 1842, plate 2, fig. 4 of Eydoux & Souleyet (1842).

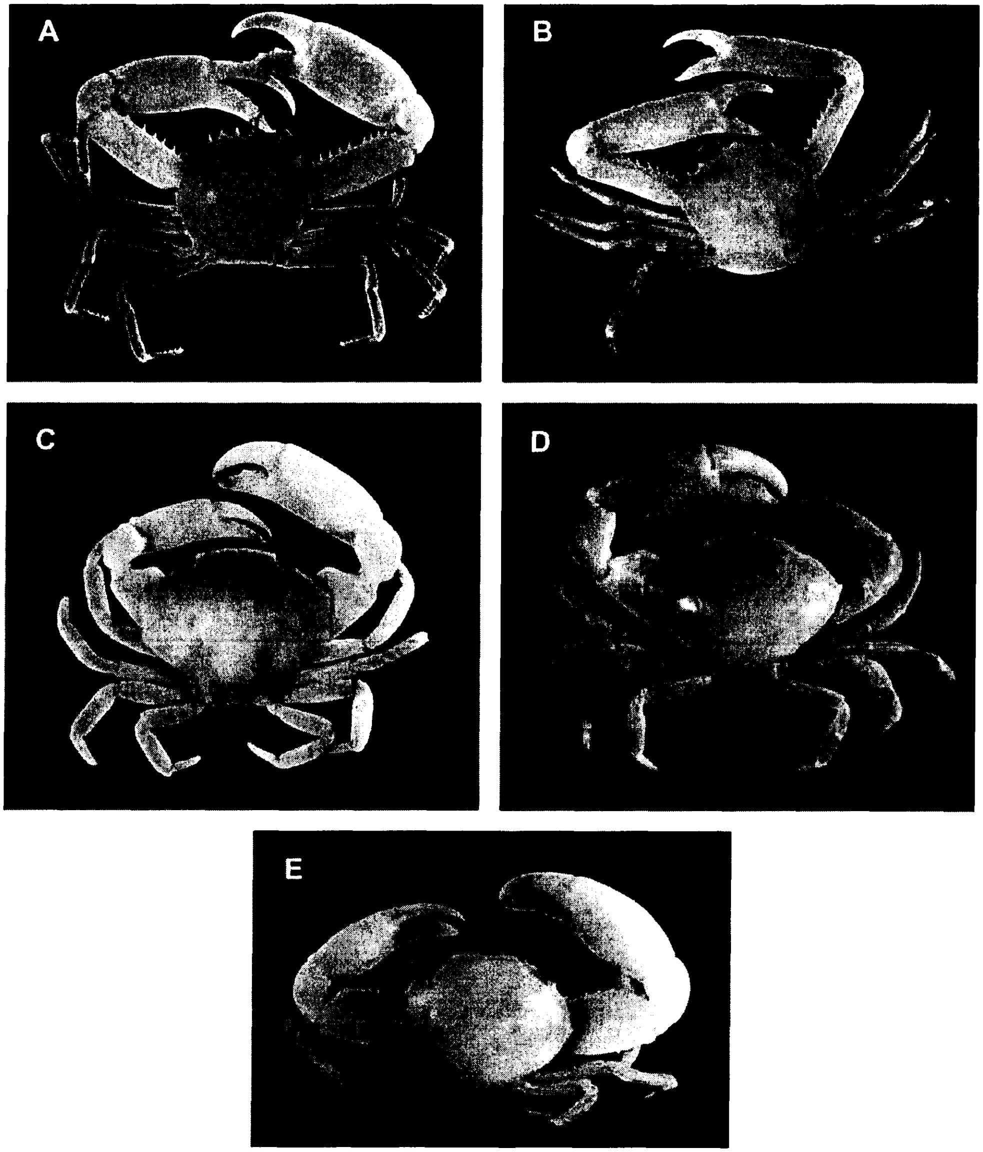

PLATE 4. Trapeziidae: A, *Quadrella coronata* Dana, 1852, ♂ (cl 9.5 mm, cw 10.7 mm), off northwest coast, Madagascar, A. Crosnier coll., 06.1959 (MNHN-B 25732); B, *Hexagonalia brucei* (Serène, 1973), ♀ (cl 4.6 mm, cw 6.5 mm), Kenya (02°33.0'S, 40°54.0'E), A.J. Bruce coll., 09.01.1972 (MNHN-B 8190); C, *Calocarcinus africanus* Calman, 1909, ♂ (cl 11.8 mm, cw 15.0 mm), off Tanimbar I. (08°42'S, 131°53'E), Arafura Sea, Indonesia, KARUBAR, 02.11.1991 (MNHN-B 29172); D, *Philippicarcinus oviformis* Garth & Kim, 1983, ♂ holotype (cl 9.4 mm, cw 13.5 mm), off Mindanao (08°47'S, 123°31'E), Philippine Islands, Albatross, 09.08.1909 (USNM 195357); E, *Sphenomerides trapezoides* (Wood-Mason & Alcock, 1891), ♀ (cl 5.9 mm, cw 7.7 mm), off northwest coast (12°41.7'S, 48°14.5'E), Madagascar, A. Crosnier coll., 11.10.1974 (MNHN-B 8206).

Genus *Trapezia* Latreille, 1828

Trapezia Latreille, 1828: 695 (type species *Trapezia dentifrons* Latreille, 1828, designation by Rathbun, 1930; gender feminine)
Grapsillus Macleay, 1838: 67 (type species *Grapsillus maculatus* Macleay, 1838, designation by Rathbun, 1930; gender masculine)

Diagnosis

Carapace trapezoidal, smooth; frontal margin with short, rounded (rarely triangular) lobes or no lobes at all; anterolateral margins each with1 tooth (Plate 2C) or no tooth at all. Chelipeds only slightly dissimilar in size, merus relatively long, at least a third visible dorsally; anterior margin of merus with well-developed teeth (Plate 2C). Dactyli of P2–P5 pointed, hoof-like tip, horizontal rows of setae (see Galil 1987: figs. 1, 2). Male abdomen with somites 3–5 fused (see Serène 1984: fig. 190). Obligate symbiont of shallow-water scleractinian corals (species of *Pocillopora*, *Seriatopora*, and *Stylophora*).

Remarks

The genus *Trapezia* was established by Latreille (1828) for five species, viz. *Cancer rufopunctatus* Herbst, 1799, *T. ferruginea* Latreille, 1828, *T. dentifrons* Latreille, 1828, *T. integra* Latreille, 1828, and *T. digitalis* Latreille, 1828. No type species was named. The first valid type species was designated by Rathbun (1930: 556), who selected *Trapezia dentifrons* Latreille, 1828. This species, however, has generally being regarded as a junior synonym of *Cancer cymodoce* Herbst, 1801 (see later for nomenclatural action to make both names objective synonyms, resulting in *Cancer cymodoce* Herbst, 1801, becoming type species of genus). Serène (1984: 267), however, stated that the type species of *Trapezia* was *T. ferruginea* Latreille, 1828. Rathbun's action clearly has priority, although the concept of the genus is not affected.

Macleay (1838: 67) established *Grapsillus* for three new species from South Africa, *G. dentatus*, *G. maculates*, and *G. subinteger*, but did not designate a type species. Rathbun (1930: 556) selected the type species *Grapsillus maculatus* Macleay, 1838, as the type species of *Grapsillus* Macleay, 1838. Rathbun (1897: 165) commented that *Trapezia* Latreille, 1825, was a preoccupied name, with the name of a mollusc genus, *Trapezium* Humphrey, 1797, having priority; and as such, *Grapsillus* Macleay, 1838, should be used instead. However, under the modern zoological code, *Trapezia* Latreille, 1825, and *Trapezium* Humphrey, 1797, are not homonyms (different spelling). As such, *Trapezia* Latreille, 1825, still has priority over *Grapsillus* Macleay, 1838.

Notes on the use of the epithet "*typica*"

In the late 1800s and the 1900s, there was a tendency among several authors to recognise varieties and colour forms for the various species of *Trapezia* (as well as *Tetralia*). Many of the currently recognised species were then defined as such. The state of the taxonomy of the three clades also resulted in many incorrect identifications and identified material often consisted of several species. One habit was to name the typical or nominate form or variety (nomenclaturally equivalent to the modern subspecies) as "forma *typica*". The modern method is simply to repeat the specific epithet when referring to the nominate subspecies, e.g. *Trapezia cymodoce cymodoce*; rather than *Trapezia cymodoce* forma *typica*. Unfortunately, under the modern zoological code, such names, at least those established before 1960, are nomenclaturally valid (ICZN 1999). That is, the epithet *typica* is an available name, and can be used as a specific name distinct from its original combination or intention.

The following are the earliest authors to have used the epithet "*typica*" for trapeziids and tetraliids and to have validated the names in various combinations:

Ortmann (1893: 482): *Trapezia cymodoce* var. *typica*
Ortmann (1894: 54): *Trapezia cymodoce typica*
Wedenissow (1894: 411): *Trapezia cymodoce typica*
Ortmann (1897: 203, 205, 208, 213): *Trapezia digitalis typica*, *Trapezia ferruginea typica*
Borradaile (1900: 589): *Trapezia ferruginea typica*
Borradaile (1902: 264, 265): *Trapezia ferruginea* var. *typica*, *Trapezia digitalis* var. *typica*
Bouvier (1915: 272, 273): *Trapezia digitalis* forme *typica*, *Trapezia ferruginea* forme *typica*, *Trapezia rufopunctata* forme *typica*

As such, the epithet "*typica*" has been used for four different species of *Trapezia*, viz. *T. cymodoce* (Herbst, 1801), *T. bidentata* Forskål, 1775 (= *T. ferruginea* Latreille, 1828), *T. digitalis* Latreille, 1828, and *T. rufopunctata* (Herbst, 1799). All the above uses of "*typica*" must thus be considered homonyms. The earliest use of the name "*typica*" was by Ortmann (1893) for *T. cymodoce*, and as he was clearly referring to the nominate subspecies, its type should also be the type of *T. cymodoce* (Herbst, 1801). The holotype of *T. cymodoce* is no longer extant and a neotype has been selected here (see below). This neotype of *T. cymodoce* (Herbst, 1801) thus becomes the simultaneous neotype of *T. cymodoce* forma *typica* Ortmann, 1893.

The first author has examined Borradaile's (1900, 1902) material deposited in the Museum of Zoology, Cambridge University, England and it is clear that Borradaile's *Trapezia ferruginea typica* and *T. digitalis typica* are clearly identical with the nominate form. Bouvier's (1915) forms are less homogeneous. His *Trapezia digitalis* forme *typica* actually contains specimens of three species from two families and two genera: *Trapezia digitalis* Latreille, 1828, *Tetralia cinctipes* Paulson, 1875, and *Tetralia glaberrima* (Herbst, 1790) (= *Tetralia glaberrima fulva* Serène, 1984) (see Castro 1999b: 101, 107). *Trapezia rufopunctata* forme *typica* Bouvier, 1915, contains material of *T. rufopunctata* (Herbst, 1799), and *Trapezia richtersi* Galil & Lewinsohn, 1983 (Castro 1999b: 112, 113). Only

Bouvier's *Trapezia ferruginea* forme *typica* is *T. ferruginea s. str.* (Castro 1999b: 108). None of these elucidations, however, affect the modern nomenclature as *Trapezia cymodoce* var. *typica* Ortmann, 1893, *Trapezia ferruginea typica* Borradaile, 1900, *Trapezia digitalis* var. *typica* Borradaile, 1902, and *Trapezia rufopunctata* forme *typica* Bouvier, 1915, are all homonyms, with Ortmann's name having clear priority.

Species of *Trapezia* (species discussed separately are marked with an asterisk)

1. *Trapezia areolata* Dana, 1852 * [type locality Tuamotu Archipelago, French Polynesia; geographical distribution: southeastern Pacific Ocean]
2. *Trapezia bella* Dana, 1852 * [type locality Tuamotu Archipelago, French Polynesia; geographical distribution: southeastern Pacific Ocean] (Plate 3B)
3. *Trapezia bidentata* (Forskål, 1775) (as *Cancer bidentatus*) * [type locality Red Sea; geographical distribution: across Indo–West Pacific and Eastern Pacific regions]
   = *Trapezia ferruginea* Latreille, 1828
   = *Trapezia miniata* Jacquinot, 1846
   = *Grapsillus subinteger* Macleay, 1838
   = *Trapezia subdentata* Gerstaecker, 1857
4. *Trapezia cheni* Galil, 1983 [geographical distribution: known only from type locality, Taiwan]
5. *Trapezia corallina* Gerstaecker, 1857 [type locality Pacific Ocean coast of Panamá; geographical distribution: Eastern Pacific region]
6. *Trapezia cymodoce* (Herbst, 1801) (as *Cancer cymodoce*) * [type locality Singapore; geographical distribution: across Indo–West Pacific region except central Pacific Ocean east of Caroline Islands] (Plate 2C, D, 3A)
   = *Trapezia dentifrons* Latreille, 1828
   = *Grapsillus dentatus* Macleay, 1838
   = *Trapezia dentata* var. *subintegra* Dana, 1852
   = *Trapezia coerulea* Rüppell, 1830
   = *Trapezia hirtipes* Jacquinot, 1846
   = *Trapezia cymodoce* var. *ornatus* Chen, 1933
7. *Trapezia digitalis* Latreille, 1828 * [type locality Red Sea; geographical distribution: across Indo–West Pacific and Eastern Pacific regions]
   = *Trapezia leucodactyla* Rüppell, 1830
   = *Trapezia fusca* Jacquinot, 1846
   = *Trapezia nigrofusca* Stimpson, 1858
8. *Trapezia flavopunctata* Eydoux & Souleyet, 1842 [type locality Hawaiian Islands; geographical distribution: across Indo–West Pacific region except Indian Ocean] (Plate 4A)
9. *Trapezia formosa* Smith, 1869 * [type locality Pacific Ocean coast of Panamá; geo-

graphical distribution: across Indo–West Pacific and Eastern Pacific regions]

= *Trapezia cymodoce* var. *edentula* Laurie, 1906

10. *Trapezia garthi* Galil, 1983 [type locality Taiwan; geographical distribution: western Pacific Ocean]
11. *Trapezia globosa* Castro, 1997 [type locality Marquesas Islands, French Polynesia; geographical distribution: southeastern Pacific Ocean]
12. *Trapezia guttata* Rüppell, 1830 * [type locality Red Sea; geographical distribution: across Indo–West Pacific region except Hawaiian Islands]

= *Trapezia davaoensis* Ward, 1941

= *Trapezia ferruginea* var. *ceylonica* Chen, 1933

= *Trapezia miersi* Ward, 1941

13. *Trapezia intermedia* Miers, 1886 [known only from the type locality, Hawaiian Islands]
14. *Trapezia lutea* Castro, 1997 [type locality New Caledonia; geographical distribution: across Indo–West Pacific region except Hawaiian Islands]
15. *Trapezia plana* Ward, 1941 [type locality Mindanao, Philippine Islands; geographical distribution: eastern Indian and western Pacific oceans]

= *Trapezia punctipes* Castro, 1997

16. *Trapezia neglecta* Castro, 2003 [type locality Guam, Mariana Islands, geographical distribution: northwestern and central Pacific Ocean]
17. *Trapezia punctimanus* Odinetz, 1983 * [type locality Tuamotu Archipelago, French Polynesia; geographical distribution: southeastern Pacific Ocean]
18. *Trapezia richtersi* Galil & Lewinsohn, 1983 [type locality Somalia; geographical distribution: Indian Ocean to Andaman Sea]

= *Trapezia richtersi* Serène, 1984

19. *Trapezia rufopunctata* (Herbst, 1799) (as *Cancer rufopunctatus*) * [type locality Singapore; geographical distribution: across Indo–West Pacific region]

= *Grapsillus maculatus* Macleay, 1838

= *Trapezia acutifrons* A. Milne Edwards, 1867

= *Quadrella rufopunctata* Chen, 1933

20. *Trapezia septata* Dana, 1852 * [type locality Luzon, Philippine Islands; geographical distribution: Indian Ocean east of Sri Lanka and western and central Pacific Ocean to Marshall Islands and Samoa]

= *Trapezia reticulata* Stimpson, 1858

= *Trapezia areolata* var. *inermis* A. Milne Edwards, 1873

21. *Trapezia serenei* Odinetz, 1984 * [type locality Guam, Mariana Islands; geographical distribution: Pacific Ocean except Hawaiian Islands]
22. *Trapezia speciosa* Dana, 1852 * [type locality Tuamotu Archipelago, French Polynesia; geographical distribution: Indian Ocean, western and southeastern Pacific Ocean] (Plate 3D)

23. *Trapezia tigrina* Eydoux & Souleyet, 1842 * [type locality Hawaiian Islands; geographical distribution: across Indo–West Pacific region] (Plate 3E)
   = *Trapezia punctata* Coulon, 1864
   = *Trapezia wardi* Serène, 1971
   = *Trapezia danae* Ward, 1939

Fossil species of *Trapezia*

1. *Trapezia brevispina* Karasawa, 1993 [Cenozoic]
2. *Trapezia glaessneri* Müller, 1975 [Miocene]

Key to extant species of *Trapezia*

1 Dorsal margin of cheliped propodus with conspicuous tomentum that consists of numerous long setae (Plate 2C); propodus with keel-like (subacute) upper margin 2

- Dorsal margin of cheliped propodus without conspicuous tomentum along entire length, although microscopic or visible but short setae may be present; propodus with rounded upper margin 3

2 Conspicuous suture between second and third thoracic sternites always present. Carapace with almost straight anterolateral margins (Plate 2C) except in largest specimens; anterolateral teeth acute except in largest specimens. Dorsal surface of carapace purplish to brownish blue, with row of orange-red spots across (Plate 2C; also see Castro 1997a: pl. 2, fig. A; pl. 3, fig. A [colour]); dactylus of chelipeds distally black only to about two-thirds its length (Plate 2C) .... *T. cymodoce*

- Suture between second and third thoracic sternites present only in smaller specimens, partially or completely fused in larger ones. Carapace with rounded anterolateral margins; anterolateral teeth acute in smaller specimens, blunt (obtuse) in larger ones. Carapace orange; dactylus of chelipeds almost entirely black (see Castro 1997a: pl. 2, fig. C; pl. 5, fig. A [both in colour]; Jones & Morgan 2002: 178–179 [colour]) ...... *T. lutea*

3 Dorsal surface of carapace of live individuals or recently preserved specimens without coloured spots, dots, bands or lines, other than very thin line along frontal margin of carapace or distinctive band in post-larvae and juveniles 4

- Dorsal surface of carapace ornamented with distinctive coloured spots, dots, bands or lines that very often remain in preserved specimens (if frontal margin of carapace is coloured differently from rest of carapace, it is as broad band, not very thin line, and ambulatory legs are ornamented with coloured dots) 12

4 Carapace and chelipeds dark brown (see Castro 1997a: pl. 3, fig. B; 1998: fig. 1F [both in colour]) (broad cream band may be present across carapace in post-larvae and juveniles). Frontal margin of carapace with very slight emarginations and minute teeth .... *T. digitalis*

\- Carapace orange, orange-pink or red-brown. Frontal margin of carapace with well demarcated emarginations and no visible teeth (microscopic in some specimens) 5

5 Carapace with anterolateral margins almost parallel to each other or only slightly curved, not having globose appearance. Anterolateral teeth distinct but may be obtuse and slight in largest individuals 6

\- Carapace with anterolateral margins strongly curved, giving carapace distinctively rounded or globose appearance, often without anterolateral teeth 10

6 Chelipeds or ambulatory legs with many dots 7

\- Chelipeds and ambulatory legs without many dots (single orange-red spot may be present on distal end of propodi of ambulatory legs) 8

7 Ambulatory legs without dots. Chelipeds orange with red dots throughout inner, dorsal surface (see Castro 1997b: pl. 1, fig. E [colour]) .... *T. punctimanus*

\- Ambulatory legs orange with many orange-red dots. Chelipeds orange without dots (see Castro 1997a: pl. 2, fig. D [colour]; as *T. punctipes*) .... *T. plana*

8 Carapace and chelipeds dark orange-brown (see Castro 1998: fig. 1C [colour]). Cheliped propodus with irregular, dark reticulations on inner, dorsal surface. Ischium of endognath of third maxillipeds with small granules on distal inner margin .... *T. corallina*

\- Carapace and chelipeds orange, light brown-orange or orange-pink. Chelipeds without reticulations. Ischium of endognath of third maxillipeds smooth 9

9 Carapace orange to brown-orange (see Castro 1998: fig. 1D; as *T. ferruginea*). Orange-red spot on distal end of propodi of ambulatory legs. Suture between second and third thoracic somites present only in very small specimens .... *T. bidentata*

\- Carapace orange-pink with conspicuous pink or purplish edges that remains in preserved specimens (see Jones & Morgan 2002: 178 [colour]). No spot on propodi of ambulatory legs. Suture between second and third thoracic somites present except in largest specimens .... *T. serenei*

10 Carapace and chelipeds bright orange, faint red reticulations on ambulatory legs of freshly-preserved specimens (see Castro 1998: figs. 1A, B, E; 2 [all in colour]) .... *T. formosa*

\- Carapace orange-yellow and chelipeds deep red or both carapace and chelipeds uniformly red brown 10

11 Carapace orange-yellow and chelipeds deep red .... *T. cheni*

\- Carapace and chelipeds red-brown (see Castro 1997b: pl. 1, fig. D [colour]) *T. globosa*

12 Lower margin of cheliped propodus armed with thick, teeth-like tubercles 13

\- Lower margin of cheliped propodus smooth or with microscopic tubercles 14

13 Frontal teeth of carapace rounded. Dorsal surface of carapace red to red-orange with large yellow spots (see Castro & Huber 2005: 113 [colour]) .... *T. flavopunctata*

\- Frontal teeth of carapace triangular. Dorsal surface of carapace light orange to orange-white with red spots (see Castro 1997a: pl. 5, fig. B; Jones & Morgan 2002: 179

[colour]) .... *T. rufopunctata*

14 Dorsal surface of carapace white to orange-white without any spots or dots, but with brown band across frontal margin between eyes (see Castro 1997a: pl. 2, fig. B; pl. 4 [all in colour]). Ambulatory legs ornamented with red dots .... *T. guttata*

\- Dorsal surface of carapace with dots, spots or network of lines 15

15 Carapace, chelipeds and ambulatory legs with red dots or spots 16

\- Carapace and chelipeds not ornamented exclusively with small red dots or spots ... 18

16 Carapace and chelipeds with small, not very numerous spots. Anterolateral teeth acute .... *T. tigrina*

\- Carapace and chelipeds with very small and numerous dots and no well-defined spots. Dorsal surface of cheliped propodus may have irregular, red reticulations. Anterolateral teeth obtuse or absent 17

17 Carapace with distinctively rounded anterolateral margins, without anterolateral teeth (except juveniles), giving carapace globose appearance. Chelipeds short and thick .... *T. bella*

\- Carapace with parallel or slightly rounded anterolateral margins. Anterolateral teeth obtuse but always present. Chelipeds slender .... *T. richtersi*

18 Anterolateral margins of carapace always parallel to each other, not rounded .... *T. areolata*

\- Anterolateral margins of carapace rounded (except in juveniles) 19

19 Carapace ornamented with lines on light background 20

\- Carapace ornamented with spots or dots 21

20 Carapace and chelipeds with honeycomb-like network of red-brown lines interconnected as pentagons or hexagons on pink to orange-white background (see Castro 1997a: pl. 2 fig. A; pl. 6 [all in colour]) .... *T. septata*

\- Carapace and chelipeds with maze-like arrangement of sinuous, red or red-purple (magenta) lines on light-orange or pinkish background (see Castro 1997b: pl. 1, fig. F [colour]) .... *T. speciosa*

21 Carapace with square to irregular orange spots surrounded by dark red-purple (magenta) lines .... *T. garthi*

\- Carapace and chelipeds with irregular, faint, light-brown spots 22

22 Irregular, faint, light-brown spots on dorsal surfaces of carapace and chelipeds .... *T. intermedia*

\- Red, well-defined spots on dorsal surfaces of carapace and chelipeds (see Castro 2003: figs. 2, 3 [colour]) .... *T. neglecta*

Trapezia cymodoce **(Herbst, 1801) (Plate 2C, D, 3A)**

Cancer cymodoce Herbst, 1801: 22, pl. 51, fig. 2 (colour) (see Plate 2D).
Trapezia dentifrons Latreille, 1828: 695.

Trapezia coerulea Rüppell, 1830: 27, pl. 5, fig. 7; pl. 6, fig. 22.
Grapsillus dentatus Macleay, 1838: 67, pl. 3.
Trapezia hirtipes Jacquinot, in Hombron & Jacquinot 1846: pl. 4, figs. 14 (colour)–16; Jacquinot, in Lucas 1853: 44.
Trapezia dentata var. *subintegra* Dana, 1852: 259, pl. 15, figs. 7a (colour), b (see Plate 3A).
Trapezia cymodoce var. *ornatus* Chen, 1933: 108, fig. 53.

Remarks. This well-known species has a long synonymy. The above synonymy has been accepted by most workers for many decades, although in many cases, the types of the various taxa have never been checked. *Cancer cymodoce* Herbst, 1801, was described on the basis of an unspecified number of specimens from "Ostindien" (Herbst 1801: 23; see Plate 2D). As such, any specimens that may have been reported should be regarded as syntypes. Rathbun (1906: pl. 11, fig. 6) published a photograph of a syntype specimen (also see Castro 1997a: 77) which was deposited in the Zoologisch Museum, Humboldt-Universität, Berlin but this specimen could no longer be located by us during separate visits by the first two authors, and is now regarded as lost (H.E. Gruner *in litt.*, 6 June 1994). Sakai (1999: 41) in compiling the extant Herbst material, also could not locate any specimen of *C. cymodoce* there.

Trapezia dentifrons Latreille, 1828, was most probably described from a juvenile specimen ("*très petite*," anterolateral teeth "*très aiguë*"; Latreille 1828: 695), but because of this, it is impossible to be sure of its identity. The type specimen(s), supposedly in the Muséum national d'Histoire naturelle, Paris, cannot be located by the first author and is here considered to be lost. Latreille himself (1828: 696) nevertheless noted that it was just a variety of *T. cymodoce*: "*n'est peut-être qu'une variété du Cancer cymodoce d'Herbst*".

Galil (1988b: 161) and Castro (1999b: 104) separately examined the type material of *T. coerulea* Rüppell, 1830 (type locality Red Sea) from the Senckenberg Museum, Frankfurt and showed that Rüppell's specimens of "*T. coerulea*" also included *T. ferruginea* [= present *T. bidentata* (Forskål, 1775), see below]. The lectotype designation by Galil (1988b: 162) ensured that *T. coerulea* Rüppell, 1830, remains a junior subjective synonym of *T. cymodoce*.

The identity of *Grapsillus dentatus* Macleay, 1838, and its synonymy with *T. cymodoce*, is less of a problem as Macleay provided a relatively good colour figure of the species. The dried type specimen (a female) is still extant in the Macleay Museum, University of Sydney, and has been examined by us. Ng & Ahyong (2000) provided a photograph of the lectotype designated by them.

The apparent type of *T. hirtipes* Jacquinot, 1846 (a dried male, MNHN-B 2953, type locality Nuku Hiva Island, Marquesas Islands, French Polynesia), is still in good condition. Re-examination of this specimen and consideration of the relatively good colour figure, we have no doubt that it is a junior synonym of *T. cymodoce* (see Castro 1997b: 119).

The identity of *T. dentata* var. *subintegra* Dana, 1852, described from the Tuamotu Archipelago, French Polynesia, is questionable as it was based on a small (cl 3 lines = 7.6 mm) specimen which is no longer extant. Its long accepted synonymy with *T. cymodoce* is not necessarily correct. On the basis of the very brief description and a colour figure (Dana 1852: pl. 15, fig. 7a; see Plate 3A), Dana's variety can just as easily be referred to *T. bidentata* (Forskål, 1775). To resolve this matter, we have selected a neotype for this species that maintains the long established synonymy of *T. dentata* var. *subintegra* with *T. cymodoce* (see below).

On the basis of material collected by L. Plate and ultimately deposited in the Phyletisches Museum, University of Jena (Germany), Chen (1933) described *Trapezia cymodoce* var. *ornatus* (type locality Sri Lanka) which agrees very well with what is presently defined as *T. cymodoce*. Although his figure of *Quadrella rufopunctata* (Chen 1933: fig. 55) seemingly depicts *T. cymodoce*, the description of this taxon demonstrates that it is actually *T. rufopunctata* (Herbst, 1799). Chen had five specimens of *T. cymodoce* var. *ornatus* on hand, but no holotype was designated. Chen's specimens could not be located in the Jena, Senckenberg or Humboldt-Universität museums (Dietrich von Knorre, Michael Türkay, Oliver Coleman, pers. comm.).

It is somewhat unfortunate that Rathbun (1930: 556) selected *Trapezia dentifrons* Latreille, 1828, a somewhat dubious species described on the basis of a juvenile, and which is now lost, as the type species of *Trapezia*. In addition, the type materials of *Cancer cymodoce* Herbst, 1801, *T. dentata* var. *subintegra* Dana, 1852, *T. cymodoce* var. *ornatus* Chen, 1933, and *Quadrella rufopunctata* Chen, 1933, are also lost. As such, the taxonomic situation of the species is far from stable. More recently, Castro (1997a) described *T. lutea* (type locality New Caledonia), a species close to *T. cymodoce* and with which it has been confused with for over a century. While we are convinced that none of the names of Herbst, Latreille, Dana, and Chen (at least on the basis of their descriptions, colour notes and/or figures) are conspecific with *T. lutea*, the lack of type material is very troublesome and can potentially cause nomenclatural problems.

In order to stabilise the taxonomy of *T. cymodoce*, one of the most common and widely distributed species of trapeziids anywhere, neotypes should be designated for all the above names for which type material is not extant. As several of the junior synonyms of what is now regarded as *T. cymodoce s. str.* (see Galil & Clark 1990; Castro 1997a, b) have been recognised as valid taxa for many decades, we believe that the best solution is to designate a neotype simultaneously for *Cancer cymodoce* Herbst, 1801, *Trapezia dentifrons* Latreille, 1828, *Trapezia dentata* var. *subintegra* Dana, 1852, and *Trapezia cymodoce* var. *ornatus* Chen, 1933. All four names thus become objective synonyms; with the oldest name, *Cancer cymodoce* Herbst, 1801, automatically becoming the type species of *Trapezia*. Whilst this action seems drastic, it is the one which we feel will present the least problems and confusion in the long term. We hereby select a male specimen (ZRC 1985.1554; cl 11.7 mm, cw 13.8 mm) collected from Siloso Beach, Sentosa Island, Singapore (01°20'N, 103°50'E), as the neotype of the above five taxa. The specimen was collected by P. K. L. Ng on 25 May 1982 from a colony of *Pocillopora*.

Trapezia areolata Dana, 1852

Remarks. *Trapezia areolata* was described from an unspecified number of specimens from Tahiti, Society Islands, French Polynesia (Dana 1852: 259). Dana's material is no longer extant. The species had been frequently confused with *T. septata* Dana, 1852, until Galil & Lewinsohn (1985) showed the distinctiveness of each taxon. Considering the history of this species, a neotype should be selected to ensure the name remains as is currently used.

A female (MNHN-B 25313; cl 5.3 mm, cw 6.2 mm) from Anuanuraro Atoll (20°25'S, 134°30'W), Tuamotu Archipelago, French Polynesia is herein designated as the neotype of *Trapezia areolata* Dana, 1852. It was collected by J. Poupin from *Pocillopora* at a depth of 1 m on April 1996. The characteristic pattern on the dorsal surface of the carapace (brown lines that form a honeycomb pattern of mostly large rectangles) is visible in the neotype specimen, even if out of focus and barely seen in the colour photograph of the specimen given by Castro (1997b: pl. 1, fig. c).

Trapezia bella Dana, 1852

Trapezia bella Dana, 1852: 254, pl. 15, fig. 2 (colour) (Plate 3B).

Remarks. This species was described from an unspecified number of specimens from Carlshoff Island (= Aratika Island), Tuamotu Archipelago, French Polynesia (Dana 1852: 254). No specimens are extant.

The only colour figure that is known of *T. bella* is that of Dana (1852: pl. 15, fig. 2; see Plate 2B). Forest & Guinot (1961: figs. 129, 130) published an excellent drawing which shows the characteristic colour pattern and morphology of the species. The photograph supposedly of *T. bella* by Serène (1984: pl. 38, fig. F) actually shows *T. formosa* Smith, 1869 (see Castro 1997b, 1998). Although the diagnostic colour pattern (with small red-brown dots) and morphology (adults with rounded anterolateral margins lacking teeth) are unique, juveniles may be confused with juveniles of *T. tigrina*, an often-sympatric species.

A male (MNHN-B 27679; cl 5.3 mm, cw 6.2 mm) from Takapoto Atoll (14°35'S, 145°13'W), Tuamotu Archipelago is herein designated as the neotype. It was collected by O. Odinetz from *Pocillopora* (colony P5–A2) at an unknown depth and date in 1982.

Trapezia bidentata Forskål, 1775

Cancer bidentatus Forskål, 1775: 90.
Trapezia ferruginea Latreille, 1828: 695.
Grapsillus subinteger Macleay, 1838: 67.
Trapezia miniata Jacquinot, in Hombron & Jacquinot 1846: pl. 4, figs. 10 (colour)—13; Jacquinot in Lucas 1853: 43.

Trapezia subdentata Gerstaecker, 1857: 127.
Trapezia bidentata — Davie 2002: 498.

Remarks. Forskål (1775) described *Cancer bidentatus* from an unspecified number of specimens from the Gulf of Suez, in the Red Sea. In his brief description, Forskål (1775: 90) wrote "*Color rubro-flavescens... Thorax...depressus, glaber...Dentes duoab urroque hatere... chelae glabra ... color rubro-flavescens*" [depressed, smooth carapace (orange colour; carapace depressed, smooth; teeth on both sides). Although brief, Forskål's description clearly refers to *T. ferruginea* Latreille, 1828, as currently understood, even if clear, obtuse anterolateral teeth are typically observed among smaller individuals. Specimens were collected between shells ("*inter conchylia*") but it is possible that the reference was to corals. Klunzinger (1913: 307) placed Forskål's species in the genus *Trapezia* and relegated *T. ferruginea* Latreille, 1828, to a junior synonym. Klunzinger obviously worked with live or fresh material, referring to the red spot at the distal end of the propodi of the ambulatory legs, which is diagnostic for *T. ferruginea.* Many authors, however, have incorrectly regarded *T. bidentata* as Klunzinger's species; and have synonymised it with *T. ferruginea* Latreille, 1828. Since *T. ferruginea* Latreille, 1828, was supposedly senior to "*T. bidentata* Klunzinger, 1913", the latter name has been conveniently forgotten. Davie (2002) used the name "*T. bidentata* (Forskål, 1775)" for his Australian material but he based this on an early unpublished manuscript of the present paper by the first two authors. Since *T. bidentata* is a now attributed to Forskål (1775), this name has priority over *T. ferruginea* Latreille, 1828.

Trapezia cymodoce, which is also common in the Red Sea, has often been confused with *T. ferruginea*. Unlike *T. cymodoce* (Plate 2C), however, *C. bidentatus* has smooth chelipeds which lack a conspicuous tomentum. Forskål based his descriptions on fresh specimens he obtained during his stay in Suez, and as such, probably would not have missed this character. As such, we are confident *T. bidentata* (Forskål, 1775) is not *T. cymodoce*.

Trapezia ferruginea Latreille, 1828, was described from the Red Sea on the basis of a female specimen. It has since been reported throughout the Indo–West Pacific and eastern Pacific regions. The type, supposedly in the Muséum national d'Histoire naturelle, Paris, is no longer extant.

Grapsillus subinteger Macleay, 1838, was described from Cape of Good Hope, South Africa on the basis of an unspecified number of specimens. The description was inadequate and no figures were provided. The name has long been regarded as a synonym of *T. digitalis* Latreille, 1828 (see Serène 1984: 278), but Ng & Ahyong (2000), who re-examined and re-figured Macleay's specimen (a dried lectotype male) in the Macleay Museum in the University of Sydney, showed that this was incorrect. This was later verified by the first author. *Grapsillus subinteger* Macleay, 1838, is actually conspecific with *T. ferruginea* (present *T. bidentata*).

Trapezia miniata Jacquinot, 1846, was described from Nuku Hiva, Marquesas Islands, French Polynesia, and from his description (in Lucas 1853: 43) and colour figure (Jacquinot, in Hombron & Jacquinot 1846: pl. 4, fig. 10) and apparent type material (a dried male and female [MNHN-B 2956] and two dried males [MNHN-B 2959]), there is little doubt that it is conspecific with *T. bidentata* (also see Castro 1997b: 120).

Trapezia subdentata Gerstaecker, 1857, was described (but not figured) from two specimens from the Red Sea. Its description leaves little doubt that *T. subdentata* is conspecific with *T. bidentata.* Photographs of Gerstaecker's specimens in the Zoologisch Museum, Humboldt-Universität, Berlin (ZMB 195) confirm this.

Trapezia cymodoce var. *edentula* Laurie, 1915, was described from one specimen from Ceylon (=Sri Lanka). Lauries description of the specimen (location unknown) shows that this variety is identical with *T. bidentata.*

Since the types of the two earliest names, *Cancer bidentatus* Forskål, 1775, and *Trapezia ferruginea* Latreille, 1828, are lost, a neotype is necessary to stabilise the use of these names as presently discussed. Since both species were described from the same area, we hereby designate a male specimen (MNHNB 27680 [ex B 13925]; cl 11.6 mm, cw 13.6 mm) from Abu Latt Island (19°57'N, 40°07'E), Red Sea as the simultaneous neotype of both species. It was collected by the research vessel *Calypso* from *Pocillopora* at an unknown depth and date in 1952. The diagnostic red spot on the distal edge of the propodi of the ambulatory legs is still clearly visible.

Trapezia digitalis Latreille, 1828

Trapezia digitalis Latreille, 1828: 696.
Trapezia leucodactyla Rüppell, 1830: 28.
Trapezia fusca Jacquinot, in Hombron & Jacquinot 1846: pl. 4, figs. 17 (colour)—19; Jacquinot in Lucas 1853: 45.
Trapezia nigrofusca Stimpson, 1858: 219.

Remarks. This well-known species has a wide distribution, and not surprisingly, has been described (as different species) several times. Latreille (1828: 696) described it from a male collected by Fébure de Cérisy from the Red Sea, but the type, supposedly in the Muséum national d'Histoire naturelle, Paris, is lost.

Rüppell (1830) subsequently described *Trapezia leucodactyla* from the Red Sea. Rüppell's syntypes (male lectotype, SMF 4040, cl 8.8 mm, cw 9.4 mm; four females paralectotypes, SMF 25963) were examined by Galil (1988b: 164), who concluded that they were identical with *T. digitalis*. The first author has also examined the lectotype series and concurs with Galils conclusion. *Trapezia fusca* Jacquinot, 1846, is also conspecific with *T. digitalis*, a conclusion reached after examination of its syntypes (four dried specimens, two males and two females, MNHN-B 2951, 2952) by Castro (1997b: 120). Stimpson (1858) then described *T. nigrofusca* from Lower California, Mexico. It seems clear from the description that Stimpson's species is identical to *T. digitalis*. There appears to be no extant type and while we are confident *T. nigrofusca* is identical with *T. digitalis*, absence of figures and the loss of Stimpson's types means that we can never be sure.

A male specimen (MNHN-B 13927; cl 7.5 mm, cw 9.0 mm) from Abu Latt Island (19°57'N, 40°07'E), Red Sea is herein designated as the simultaneous neotype of *Trapezia digitalis* Latreille, 1828, and *Trapezia nigrofusca* Stimpson, 1858. It was collected by the research vessel *Calypso* from *Pocillopora* at an unknown depth and date in 1952. The characteristic colouration of the neotype is still evident. The two names now become objective synonyms.

Trapezia formosa Smith, 1869

Trapezia cymodoce var. *edentula* Laurie, 1915: 461.

Remarks. The taxonomic status of this species was reviewed by Castro (1998). *Trapezia cymodoce* var. *edentula* Laurie, 1915 was described for specimens of *T. cymodoce* in which "... the lateral epibranchial tooth was absent and the hand naked." It was presumed to be identical to *T. bidentata* (as *T. ferruginea*) by Castro (1999b: 108). Both characters are indeed shared by *T. bidentata* and *T. formosa*. In *T. formosa*, however, the anterolateral teeth become barely noticeable or absent in much smaller individuals and the chelipeds are thicker and shorter than in *T. bidentata*. The two syntypes of *T. cymodoce* var. *edentula* (BMNH 1907.5.22.263–264) from Galle, Ceylon (= Sri Lanka) were examined and proved to be identical to *T. formosa*. The male syntype (cl 5.1 mm, cw 4.2 mm) is here designated the lectotype; the female syntype (cl 5.6 mm, cw 7.6 mm) becomes the paralectotype.

Trapezia guttata Rüppell, 1830

Trapezia guttata Rüppell, 1830: 27.
Trapezia ferruginea var. *ceylonica* Chen, 1933: 109.
Trapezia davaoensis Ward, 1941: 14, fig. 27.
Trapezia miersi Ward, 1941: 15.

Remarks. The identity of this species was clarified by Galil (1988b: 166) and Castro (1997a: 82) but some additional notes are necessary. The questionable conspecificity of *T. ferruginea* var. *ceylonica* Chen, 1933 (type locality Sri Lanka) with *T. guttata* Rüppell, 1830 (type locality Red Sea) follows from Chen's brief comments and schematic figure. Since the three specimens Chen examined are now lost (see discussion for *T. cymodoce*), this cannot be verified.

Miers (1886: 167) described specimens of *T. guttata* from Fiji as having "... carapace and chelipeds ... of a uniform reddish or yellowish brown. The ambulatory legs, but not the chelipeds, are covered with small, distinct, red or brownish spots." The species, however, has a characteristic white to orange-white carapace that is rounded anteriorly by a thin, red-brown line (see Castro 1997a: 80, pl. 2, fig. B; pl. 4) in addition to the spotted ambulatory legs. The red-brown line may fade or it can easily be overlooked in preserved specimens. A light orange carapace and ambulatory legs with orange-red spots is characteristic of *T. plana* Ward, 1941 (see Castro 1997a: 88, pl. 2, fig. D, as *T. punctipes*). Miers' species, however, is undoubtedly *T. guttata* as indicated by the straight anterolateral margins of the carapace, postorbital angles that are acute and directed anteriorly, and long cheliped fingers which cross each other when closed (Miers, 1886: pl. 12, fig. 1). Ward (1941), however, was of the opinion that Miers' material belonged to a separate species, to which he applied the name *T. miersi* Ward, 1941, without any explanation or examination of Miers' specimens. The material of *T. guttata* from the Philippines that Ward (1941) had on hand was described as a new species, *T. davaoensis* Ward, 1941. Castro (1997b: 125) examined two paratypes of *T. davaoensis* (MNHN-B 16783) and confirmed that it is conspecific with *T. guttata*. This is also evident from Ward's (1941: fig. 27) photograph of *T. davaoensis*. Both *T. miersi* Ward, 1941, and *T. davaoensis* Ward, 1941, are therefore junior subjective synonyms of *T. guttata* Rüppell, 1830.

Trapezia punctimanus **Odinetz, 1983**

Trapezia punctimanus Odinetz, 1983: 35, 107, 114, 134, 206, 214, photograph 7 (colour).

Remarks. This species was first described in a doctoral thesis (Odinetz 1983) although it was formally described in a publication of much wider circulation a year later (Odinetz 1984). However, Odinetz's (1983) thesis was widely circulated among scientists from different parts of the world. Although she did not intend it to be a proper publication, she did not state emphatically that it was not, and as such it fulfils all the requirements for publication under the current zoological code (ICZN 1999) and as such, the 1983 publication date of her new name is valid.

Trapezia rufopunctata **(Herbst, 1799)**

Cancer rufopunctatus Herbst, 1799: 54, pl. 47, fig. 6 (colour).
Grapsillus maculatus Macleay, 1838: 67.
Trapezia acutifrons A. Milne Edwards, 1867: 281.
Quadrella rufopunctata Chen, 1933: 111, fig. 55 (junior homonym of *Cancer rufopunctatus* Herbst, 1799)

Remarks. The taxonomy of this species is now quite stable. Ng & Ahyong (2000) showed that the lectotype of *Grapsillus maculatus* Macleay, 1838 was still extant (in the Macleay Museum, University of Sydney) and that it fits the concept of *T. rufopunctata* as currently understood (see Galil & Lewinsohn 1985: 209; Castro 1997a: 127).

The dried male and female syntypes of *Trapezia acutifrons* A. Milne Edwards, 1867 (MNHN-B 2913) from the Hawaiian Islands are clearly identical to *T. rufopunctata*.

From its description, but not the figure (Chen 1933: 111, fig. 55), *Quadrella rufopunctata* (type locality Sri Lanka) (not *Cancer rufopunctata* Herbst, 1799) is almost certainly *T. rufopunctata*.

Trapezia septata Dana, 1852

Trapezia septata (var.?) Dana, 1852: 260, pl. 15, fig. 9.
Trapezia reticulata Stimpson, 1858: 37 [35]; Stimpson, 1907: 73, pl. 9, fig. 5.
Trapezia areolata var. *inermis* A. Milne Edwards, 1873: 259, pl. 10, fig. 6.

Remarks. Dana's type material is lost. The type locality is the Sulu Sea (Dana 1852: 260), collected somewhere between the Philippine Islands and the north coast of Borneo by the U.S. Exploring Expedition. Considering the confusion between this species and *T. areolata* Dana, the designation of a neotype is desirable to stabilise their taxonomy. As such, a male specimen (MNHN-B 27682; cl 8.9 mm, cw 10.8 mm) from the southern coast of Luzon, Philippine Islands, is herein designated as the neotype. It was collected by the MUSORSTOM 2 expedition (unknown station number) during November-December 1980. This specimen is also designated as the neotype of *Trapezia reticulata* Stimpson, 1858.

The examination of the type material of *T. areolata* var. *inermis* A. Milne Edwards 1873 showed it to be a junior synonym of *T. septata* (Castro 1997a).

Trapezia serenei Odinetz, 1983

Trapezia serenei Odinetz, 1983: 34, photograph 6 (colour).

Remarks. The species was first reported in a doctoral thesis (Odinetz 1983) but formally described in a paper a year later (Odinetz 1984) (see discussion for *T. punctimanus* Odinetz, 1983).

Trapezia speciosa Dana, 1852

Trapezia speciosa Dana, 1852: 83, pl. 15, fig. 1 (colour) (Plate 3D).

Remarks. The colour pattern illustrated in the colour figure of Dana (1852: pl. 15, fig. 1) of a French Polynesian specimen depicts a series of red lines in a rather regular geometric pattern (Plate 3D). A similar pattern is shown in the drawings of western Indian Ocean specimens given by Richters (1880: pl. 16, figs. 9, 10). Richter's illustrations, unfortunately, only showed the lines on the anterior part of the carapace. Photographs of preserved Vietnamese specimens in Serène (1959: pl. 2, figs. A, B), however, show a very different pattern of thicker, diffuse and irregular red-brown lines much closer to those of *T. garthi* (see Galil 1983: fig. 9B). Examination of numerous live and preserved specimens from French Polynesia (Castro 1997b) and the western Indian Ocean (Castro 1999b) has demonstrated that the red lines on the carapace are typically sinuous and interconnected (Galil 1983: fig. 9C; Serène 1984: pl. 38, fig. E; Castro 1997b: pl. 1, fig. F [colour]) but they sometimes follow a more regular geometric pattern. Although all the available evidence points to the fact that recent records are conspecific with Dana's species, it would be better if a neotype is designated.

Dana's type material is lost. The type locality is Carlshoff Island (= Aratika Island) in the Tuamotu Archipelago, French Polynesia (Dana 1852: 254). A female (MNHN-B 27681 [ex B 25319]; cl 8.3 mm, cw 10.7 mm) from Moruroa (Mururoa) Atoll (21°50'S, 138°50'W), Tuamotu Archipelago (Castro 1997b: pl. 1, fig. F [colour]) is herein designated as the neotype. It was collected by J. Poupin and SMSRB divers from *Pocillopora* at a depth of 5–10 m on March 1996.

Trapezia tigrina Eydoux & Souleyet, 1842

Trapezia tigrina Eydoux & Souleyet, 1842: 232, pl. 2, fig. 4 (colour) (see Plate 3E).
Trapezia punctata Coulon, 1864: 569.
Trapezia danae Ward, 1939: 13, figs. 17, 18.
Trapezia wardi Serène, 1971: 140.

Remarks. The identity of *T. wardi* Serène, 1971 (type locality Vietnam) and *T. danae* Ward, 1939 (type locality Samoa) with *T. tigrina* Eydoux & Souleyet, 1842, is not in question (see Galil & Lewinsohn 1984: 166; Castro 1997b: 130). *T. punctata* Coulon, 1864 (type locality Red Sea) is almost certainly identical with *T. tigrina*, even if Coulon's description is far too brief. What appears to be Coulon's type, a dried specimen, is in the zoology collections of the University of Neuchâtel, Switzerland. It carries the label "*Trapezia rufopunctata* Herb." made by Coulon himself. This specimen was very likely used by Coulon in his description of *T. punctata*, but Coulon apparently realised later that there was an earlier name (*T. rufopunctata*) and his species was only a junior synonym (J.-P. Haenni, pers. comm. through M. Kottelat).

As *T. tigrina* and *T. rufopunctata* have very similar colour patterns, and as a result were frequently mistaken for each other, Coulon's eventual identification is not at all surprising. Since *T. rufopunctata* is not known from the Red Sea, Coulon's *T. punctata* should be *T. tigrina* instead. The colour description of *T. punctata* also fits better that of *T. tigrina*, orange dots ("*points orange*", Coulon 1864: 569) rather than the distinctly larger spots of *T. rufopunctata*.

Genus *Quadrella* Dana, 1851

Quadrella Dana, 1851: 128 (type species *Quadrella coronata* Dana, 1852, by monotypy; gender feminine)

Diagnosis

Carapace hexagonal, smooth; frontal margin with conspicuous, V- or U-shaped median emargination and 2 conspicuous teeth on each side; anterolateral margins each with 1 tooth (Plate 4A) (small specimens may also have 1 small intermediate spine on one or both sides). Chelipeds dissimilar in size, merus typically very long; anterior margin with conspicuous teeth or tubercles (Plate 4A). Dactyli of P2–P5 ending with acute tooth, horizontal rows of spinules (see Galil 1986c: figs. 3D; 4B, E; 5B, F; 7C, E; 8B). Male abdomen with somites 3–5 fused (see Galil 1986c: fig. 3E). Male first pleopod with distal spines or setae (see Serène 1984: figs. 191, 193–195; Galil 1986c: fig. 6). On antipatharians (black corals), gorgonians, alcyonaceans (soft corals) or azooxanthellate (ahermatypic) scleractinian corals.

Species of *Quadrella*

1. *Quadrella boopsis* Alcock, 1898 [type locality Bay of Bengal, Myanmar; geographical distribution: across most of Indo–West Pacific region except Hawaiian Islands]
   = *Quadrella bispinosa* Borradaile, 1902
2. *Quadrella coronata* Dana, 1852 [type locality Zulu Sea, Philippine Islands; geographical distribution: Indian Ocean, western Pacific Ocean] (Plate 4A)
   = *Quadrella coronata* var. *granulosa* Borradaile, 1902
3. *Quadrella maculosa* Alcock, 1898 [type locality Andaman Islands, Indian Ocean; geographical distribution: western and southeastern Pacific Ocean]
   = *Quadrella cyrenae* Ward, 1942
4. *Quadrella nitida* Smith, 1869 [type locality Pacific coast of Panamá; geographical distribution: Eastern Pacific region]
5. *Quadrella reticulata* Alcock, 1898 [type localities: Andaman Islands, Sri Lanka; geographical distribution: Indian Ocean, western Pacific Ocean]
6. *Quadrella serenei* Galil, 1986 [type locality Madagascar; geographic distribution: western and southeastern Pacific Ocean].
   = *Quadrella lewinsohni* Galil, 1986

Key to species of *Quadrella*

1 Suture between thoracic sternites 2 and distinct, complete 2

- Suture between thoracic sternites 2 and 3 not complete, only evident marginally, except in juveniles and small adults 5

2 Chelipeds relatively short, merus less than two-thirds carapace length, armed with relatively short teeth. Frontal margin of carapace with short teeth provided with rounded tips. Posterior margin of propodi of ambulatory legs smooth, without spines. On dendrophyliid and other azooxanthellate corals.. *Q. boopsis*

- Chelipeds relatively long, merus more than two-thirds carapace length 3

3 Posterior margin of dactyli of ambulatory legs with teeth that conspicuously increase in size toward tip (Plate 4A). Merus of chelipeds always armed with 7–12 long, spine-like teeth (Plate 4A) 4

- Posterior margin of dactyli of ambulatory legs with teeth of similar sizes (see Galil 1986c: fig. 8b). Merus of chelipeds of adults armed for most of length with short and pointed or blunt (obtuse) tubercles, with only 2 or 3 distal tubercles conspicuous and tooth-like (only juveniles and small adults with short teeth along entire length of merus) (see Castro 2002: fig. 2 [colour]). On antipatharians (black corals).. *Q. serenei*

4 Posterior margin of propodi of ambulatory legs armed with spines (see Galil 1986c: fig. 4E). Male first pleopod with curved tip (see Serène 1984: fig. 195). On alcyonaceans, gorgonians, antipatharians (black corals) (Plate 4A) .... *Q. coronata*

- Posterior margin of propodi of ambulatory legs smooth (see Galil 1986c: fig. 7C). Male first pleopod with almost straight tip. On antipatharians (black corals).. *Q. nitida*

5 Chelipeds relatively short; merus armed with 8–12 short triangular teeth that extend along its entire length. Posterior margin of dactylus of fourth ambulatory leg with 12–13 teeth that increase in size toward tip. On antipatharians (black corals) .... *Q. reticulata*

- Chelipeds long; merus armed for most of length with short pointed or blunt (obtuse) tubercles, with only 2 or 3 distal ones conspicuous and tooth-like (only juveniles and small adults with short teeth along entire length of merus). Posterior margin of dactylus of fourth ambulatory leg with 15 or 16 teeth of approximately same size (see Castro 2002: fig. 1 [colour]). On antipatharians (black corals) .... *Q. maculosa*

Genus *Hexagonalia* Galil, 1986

Hexagonalia Galil, 1986: 275 (type species *Quadrella brucei* Serène, 1973, by original designation; gender feminine)

Diagnosis

Carapace hexagonal, smooth; frontal margin with conspicuous, V- or U-shaped median emargination and 1 or 2 broad or teeth-like lobes on each side; anterolateral margins each with 2 conspicuous, anteriorly directed teeth (Plate 4B). Chelipeds dissimilar in size, merus very long; anterior margin with conspicuous teeth (Plate 4B). Dactyli of P2–P5 ending with acute tooth, horizontal rows of spinules (see Galil 1986c: fig.1D). Male abdomen with somites 3–5 fused (see Galil 1986c: fig. 1E). Male first pleopod with distal pinnate appendage (except species being described: see below) (see Serène 1984: fig. 192, as *Quadrella brucei*; Galil 1986c: fig. 2). On stylasterid (hydrozoan) corals and possibly gorgonians.

Species of *Hexagonalia*

1. *Hexagonalia brucei* (Serène, 1973) (as *Quadrella brucei*) [type locality off Kenya; geographical distribution: western Indian Ocean] (Plate 4B)
2. *Hexagonalia laboutei* Galil, 1997 [known only from the type locality, Tuamotu Archipelago, French Polynesia]

A third species is being described from the Solomon Islands (Castro, in press).

Key to species of *Hexagonalia*

1 Frontal margin of carapace with 2 broad, slightly concave teeth (Plate 4B) ... *H. brucei*
- Frontal margin of carapace with 4 triangular teeth .... *H. laboutei*

Genus *Calocarcinus* Calman, 1909

Calocarcinus Calman, 1909: 31 (type species *Calocarcinus africanus* Calman, 1909, by monotypy; gender masculine).

Diagnosis

Carapace octagonal, finely granular; frontal margin entire; anterolateral margins each with 2 teeth placed one above the other, leaving two straight, parallel sides along middle portion of carapace (Plate 4C). Chelipeds dissimilar in size, merus relatively long, at least a third visible dorsally, without teeth along anterior margin (Plate 4C). Dactyli of P2–P5 with pointed tip, no horizontal rows of setae. Male abdomen with somites 3–5 fused. Male first pleopod stout, spinous (see Serène 1984: figs. 199, 200). Obligate symbionts of deep-water precious corals (*Corallium*), deep-water azooxanthellate (ahermatypic) scleractinian corals, and probably deep-water gorgonians, antipatharians (black corals) and alcyonaceans (soft corals) (see Castro 1997a).

Species of *Calocarcinus*

1. *Calocarcinus africanus* Calman, 1909 [type locality western Indian Ocean; geographical distribution: Indian Ocean, western Pacific Ocean to New Caledonia] (Plate 4C)
2. *Calocarcinus crosnieri* Galil & Clark, 1990 [known only from type locality, New Caledonia]
3. *Calocarcinus habei* Takeda, 1980 [type locality off Midway Island, central Pacific; geographical distribution: western Indian Ocean, central and southeastern Pacific Ocean]
4. *Calocarcinus lewinsohni* Takeda & Galil, 1980 [known only from type locality, Izu Is., Japan]

Key to species of *Calocarcinus*

1 Two anterolateral teeth conspicuous and salient; carapace margin between 2 anterolateral teeth convex .... *C. hebei*

\- Two anterolateral teeth not conspicuous and salient; carapace margin between 2 anterolateral teeth straight or slightly convex 2

2 Propodi and dactyli of ambulatory legs with long setae (see Takeda & Galil 1980: fig. 6) .... *C. lewinsohni*

\- Propodi and dactyli of ambulatory legs with short setae 3

3 Cheliped merus long, projecting far beyond lateral margins of carapace (Plate 4C) .... *C. africanus*

\- Cheliped merus short, not projecting far beyond lateral margins of carapace .... *C. crosnieri*

Genus *Philippicarcinus* Garth & Kim, 1983

Philippicarcinus Garth & Kim, 1983: 712 (type species *Philippicarcinus oviformis* Garth & Kim, 1983, by original designation; gender masculine)

Diagnosis

Carapace transversely ovate, finely granular; frontal margin entire; anterolateral margins each with 1 or 2 blunt teeth (Plate 4D). Chelipeds dissimilar in size, merus relatively long, at least a third visible dorsally, without teeth or with a blunt tubercle along anterior margin (see Garth & Kim 1983: figs. 13a, 14a). Dactyli of P2–P5 with pointed tip, no horizontal rows of setae (see Garth & Kim 1983: fig. 13d). Male abdomen with somites 3–5 fused. Male first pleopod stout, spinous tip (see Garth & Kim 1983: fig. 14c). Relatively deep water (333–510 m), no known associations with other invertebrates.

Species of *Philippicarcinus*

1. *Philippicarcinus oviformis* Garth & Kim, 1983 [type locality Mindanao; geographical distribution: Philippine Islands] (Plate 4D)
2. *Philippicarcinus tuberomerus* Garth & Kim, 1983 [known only from the type locality, Mindanao, Philippine Islands]

Key to species of *Philippicarcinus*

1 Anterolateral margins of carapace each with 1 blunt (obtuse) tooth (Plate 4D). Anterior margin of cheliped merus smooth .... *P. oviformis*

\- Anterolateral margins of carapace each with 1 blunt tooth and 2 short, broad, tubercle-like teeth (see Garth & Kim 1983: fig. 14a). Distal, anterior margin of cheliped merus with pointed tubercle (see Garth & Kim 1983: fig. 14a) .... *P. tuberomerus*

Genus *Sphenomerides* Rathbun, 1897

Sphenomerus Wood-Mason & Alcock, 1891: 263 (type species *Sphenomerus trapezoides* Wood-Mason & Alcock, 1891, by monotypy; gender neuter; invalid junior homonym)

Sphenomerides Rathbun, 1897: 164 (replacement name for *Sphenomerus* Wood-Mason & Alcock, 1891)

Diagnosis

Carapace transversely ovate, finely granular, dorsal surface convex; frontal margin entire; anterolateral margins each with 2 small teeth (Plate 4E). Chelipeds dissimilar in size, merus relatively long, at least a third visible dorsally, with teeth along anterior margin (Plate 4E). Dactyli of P2–P5 with pointed tip, no horizontal rows of setae. Male abdomen with somites 3–5 fused. Male first pleopod slender, sinuous (see Serène 1984: fig. 196). Moderately deep water (80–530 m), no known associations with other invertebrates.

Species of *Sphenomerides*

Sphenomerides trapezoides (Wood-Mason & Alcock, 1891) (as *Sphenomerus trapezoides*) [type locality Andaman Sea; geographic distribution: Madagascar and Andaman, Sulu, Moluccas, and Banda seas] (Plate 4E)

ACKNOWLEDGEMENTS

We thank two reviewers and D. Guinot (MNHN) for their valuable comments to the manuscript. The second author is grateful to L. B. Holthuis for his many useful discussions on Linnean names, and for drawing his attention to the name *Cancer mutus*. S. H. Tan (Raffles Museum of Biodiversity Research, National University of Singapore) kindly searched the collections in Uppsala, Sweden to establish which of Linnaeus specimens are still extant. We also thank M. Kottelat for helping us search and check Coulon's material in Switzerland. The following colleagues have been invaluable in their help with material: D. Guinot, R. Cleva, and A. Crosnier (MNHN), A. Allspach (SMF), P. Clark and M. Lowe (BMNH), O. Coleman and H. Gruner (ZMB), P. Dworschak (MNV), R. Lemaitre and K. Reed (USNM), R.C. Preece (UMZC), and M. Vannini (ZMF). We also thank P. Clark (BMNH) for help with the larvae, and M.-S. Jeng (Academia Sinica, Taipei, Taiwan) for sharing with us information on his research on molecular phylogeny. Line drawings and photographs of preserved material were made by J.-F. Dejouannet (MNHN); other photographs by S. H. Tan (Raffles Museum of Biodiversity Research, National University of Singapore).

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APPENDIX 1. Input data matrix. Unknown states are scored "?".

Carcinus	0200000100	0101110120	0000000000	0000100100	10010
Carpilius	0222001200	1101100100	0002000000	0000000120	01020
Eriphia	1101000110	0111000100	0000001000	0000001110	10020
Trapezia	0222101101	1000110000	0000001011	0110001100	00001
Tetralia	2222101011	1101000011	0002002011	0111001100	10001
Tetraloides	2222101011	1101000011	0002002011	0111001100	10001
Quadrella	1222101101	1000110000	0000001110	1110001100	00001
Hexagonalia	1222101100	1000110100	0010001110	1110001100	00001
Domecia	1012111100	0001000011	0110111001	0110011121	00011
Philippicarcinus	2222101201	1100110010	0001000000	0110001000	00021
Calocarcinus	2222101201	1100110000	0001000000	0110001000	00011
Sphenomerides	2222001101	1100110100	0000001100	0010001100	00001
Jonesius	2222101100	1101000020	0012000000	0110000120	10010
Palmyria	2022101100	1101000000	0110111000	0110010121	100?0
Maldivia	2222101100	1101000020	0012000000	0110000120	10010
Cymo	1111110000	1111110001	1011010000	0010100010	11100
Xantho	0001100100	0110111121	0011000000	0000100110	10000
Etisus	0201000100	0110110001	1000000000	0000100110	01100
Tweedia	0101100200	1100110101	1110000000	?010100120	01100
Panopeus	0001000100	0110111120	0001000000	0000101000	11100
Pilumnus	0001010100	0100000101	0000001000	0010000000	10001
Potamon	2012101011	1101000120	0000000000	0000001100	10020
Varuna	2212100000	1001000120	0000000000	0000100000	11101

APPENDIX 2. Unambiguous character state reconstructions for each branch.

Branch 1. 31: 0–1.
Branch 2. 12: 1–0, 29: 1–0.
Branch 3. 27: 0–1, 28: 0–1.
Branch 4. 14: 1–0, 15: 0–1, 16: 0–1, 41: 1–0.
Branch 5. 8: 1–2, 24: 0–1, 38: 1–0.
Branch 6. 18: 1–0, 32: 0–1, 33: 0–1.
Branch 7. 8: 1–0, 9: 0–1, 19: 0–1, 20: 0–1, 24: 0–2, 27: 0–2, 29: 0–1, 30: 0–1, 34: 0–1.
Branch 8. 1: 0–2, 5: 0–1.
Branch 9. 23: 0–1, 39: 0–2, 44: 0–1.
Branch 10. 2: 2–0, 22: 0–1, 25: 0–1, 26: 0–1, 27: 0–1, 36: 0–1, 40: 0–1.
Branch 11. 19: 0–2, 24: 0–2.
Branch 12. 1: 0–2, 5: 0–1.
Branch 13. 3: 2–1, 8: 1–0, 19: 0–2.
Branch 14. 3: 0–2, 4:1–2, 7: 0–1, 11: 0–1.
Branch 15. 16: 0–1, 35: 1–0.
Branch 16. 27: 0–1.
Branch 17. 13: 0–1, 14: 1–0.
Branch 18. 21: 0–1.
Branch 19. 2: 2–1, 5: 0–1, 11: 0–1, 23: 0–1, 33: 0–1.
Branch 20. 2: 2–0, 17: 0–1, 24: 0–1.