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A new classification of the Galatheoidea (Crustacea: Decapoda: Anomura)

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Abstract

The high level classification of the Galatheoidea, popularly known as squat lobsters, has been relatively stable for almost a century. Multiple recent studies of their interrelationships, however, have revealed significant incongruities between the traditional classification and phylogeny. The Aeglidae, Chirostylidae and Kiwaidae were recently removed to other superfamilies. On the basis of previous phylogenetic analyses, we herein revise the higher classification of the remaining Galatheoidea to comprise four families: Galatheidae, Munididae **fam. nov.**, Munidopsidae, and Porcellanidae. The galatheoid families are both morphologically and ecologically distinct. Members of the Munidopsidae are distinguished by the absence or reduction of the maxilliped 1 flagellum and usually occur in outer slope or abyssal habitats. Members of the Munididae **fam. nov.** are united by the trifid or trispinous anterior margin of the carapace and usually occur at outer shelf or slope depths. The Galatheidae includes primarily shallow water species, united by a broad, triangular rostrum, and is most closely related to the porcelain crabs, Porcellanidae. The families of the Galatheoidea are diagnosed and a diagnostic key provided. Extant and fossil genera are listed for each galatheoid squat lobster family.

Key words: Galatheoidea, Galatheidae, Munididae **fam. nov.**, Munidopsidae, Porcellanidae, squat lobsters, phylogeny, classification

Introduction

Phylogenetic concepts underpinning the higher classification of the squat lobsters have been remarkably stable for the best part of a century (Baba 2005; Baba *et al.* 2008; Ahyong *et al.* 2009). Rank assignments have varied but higher taxonomies of the Anomura consistently reflected the widespread view that porcelain crabs and all squat lobsters were closely related. As recently as 2001, the monophyly of the Galatheoidea Samouelle, 1819, including families Aeglidae Dana, 1852, Chirostylidae Ortmann, 1892, Galatheidae Samouelle, 1819, and Porcellanidae Haworth, 1825, was almost universally accepted (Martin & Davis 2001). Correspondingly, the family Kiwaidae Macpherson, Jones & Segonzac, 2005, was also placed in the Galatheoidea. Recent decades, however, have not only witnessed increased interest in the evolution of Decapoda, with a focus on hermit crabs in the case of Anomura (e.g., Cunningham *et al.* 1992; McLaughlin & Lemaitre 1997; Morrison *et al.* 2002), but also the widespread development of powerful methods for studying phylogenetic relationships. As a result, phylogenetic analyses of Anomura have often significantly challenged prevailing concepts of squat lobster interrelationships, although these results have been slower to affect formal classifications (De Grave *et al.* 2009). Pérez-Losada *et al.* (2002) and Ahyong & O'Meally (2004) showed that the freshwater squat lobsters, Aeglidae, are not closely related to the marine squat lobsters and should be excluded from the Galatheoidea; this, McLaughlin *et al.* (2007) formally recognised by establishing the Aegloidea, as well as an independent superfamily for the Kiwaidae in Kiwaoidea. More recent phylogenetic analyses, corroborated by spermatozoal (Tudge 1997) and larval data (Guerao *et al.* 2006; Clark & Ng 2008), went further, revealing significant polyphyly among remaining squat lobsters, widely separating

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the Chirostylidae and Kiwaidae from Galatheidae and Porcellanidae (Ahyong *et al.* 2009; Bracken *et al.* 2009; Schnabel *et al.* in press). Clearly, the traditional classification was significantly incongruent with phylogeny. In this light, the chirostylids and kiwaids were recently removed from the Galatheoidea to a separate superfamily, Chirostyloidea (Schnabel *et al.* in press; Schnabel & Ahyong, in press).

Within the remaining galatheoids, Ahyong *et al.* (2009), Bracken *et al.* (2009) and Schnabel *et al.* (in press) found the porcelain crabs, Porcellanidae, to be nested within the galatheids, rendering the Galatheidae paraphyletic. The galatheid genera fell into three main clades (Fig. 1A). The first clade corresponded to Munidopsinae/Shinkaiinae and *Leiogalathea*, and includes species typically found at outer slope to abyssal depths. The second clade included *Munida* and allies, genera united by the slender rostrum and supraocular spines producing a trifid or trispinous front; they typically occur at outer shelf to slope depths. The third clade comprises genera with a broad-rostrum, including the nominotypical genus, *Galathea*. These forms typically occur at shallow depths, and comprise the sister group to the Porcellanidae. The internal nesting of the porcellanids among galatheid genera results in significant paraphyly of the Galatheidae *sensu lato*, requiring changes to the classification.

Although more detailed phylogenetic analyses of the galatheoids are currently underway, studies now in progress across several disciplines require access to an updated taxonomic system. Since the three major clades of galatheoid squat lobsters are both morphologically and ecologically distinct, we herein recognise each as a separate family. Family group names are already available for the first and third clades, Munidopsidae and Galatheidae. The second clade, however, is herein named *de-novo*, as Munididae **fam. nov.** The families of the Galatheoidea, as now restricted, are diagnosed below. Extant and fossil genera are listed for each galatheoid squat lobster family. All species of extant squat lobsters known at the time were listed by Baba *et al.* (2008) but several others have been described since. Known species of fossil galatheoids are given by Schweitzer *et al.* (2010).

Systematics

Galatheoidea Samouelle, 1819

Diagnosis. Rostrum well-developed or obsolete. Cephalothorax and abdomen symmetrical. All abdominal somites distinct, freely articulating, sclerotized. Thoracic somite 8 with well-developed sternite. Ocular acicles absent. Antennal peduncle 4-articulate (articles 1 and 2 of 5 articles fused); acicle absent. Mandible incisor margin entire. Maxilliped 3 with or without epipod. Pereopod 1 chelate. Telson and uropods laminar, forming tailfan. Telson subdivided into plates. Gills phyllobranchiate.

Composition. Galatheidae Samouelle, 1819; Munididae fam. nov.; Munidopsidae Whiteaves, 1874; Porcellanidae Haworth, 1825.

Remarks. The Galatheoidea as restricted here includes four families, Galatheidae, Munididae **fam. nov.**, Munidopsidae, and Porcellanidae. In most previous uses of the superfamily (e.g., Balss 1957; Martin & Davis 2001; Macpherson *et al.* 2005), the Chirostylidae and Kiwaidae were included, but phylogenetic analyses have shown that these families are not closely related to other marine squat lobsters, and belong in a separate superfamily, Chirostyloidea (Schnabel *et al.* in press). Kiwaids are potentially nested within Chirostylidae *sensu* Baba *et al.* (2008) (Ahyong *et al.* 2009; Schnabel *et al.* in press). A key to the galatheoid families is given below.

Key to families of the Galatheoidea

1. Maxilliped 3 operculiform; epipod absent. Antennal peduncle directed laterally or inclined posteriorly .... Porcellanidae Haworth, 1825
- Maxilliped 3 pediform; epipod present. Antennal peduncle directed anteriorly or anterolaterally 2
2. Maxilliped 1 without flagellum or flagellum strongly reduced ..... .Munidopsidae Whiteaves, 1874

- Maxilliped 1 with well-developed flagellum 3
3. Front trispinous or trilobate, usually composed of slender rostrum flanked by supraorbital spines. ..... Munididae **fam. nov.**
- Rostrum broad, triangular ..... Galatheidae Samouelle, 1819

Galatheidae Samouelle, 1819
(Figs 1B–F, 2A–D)

Galatheadae Samouelle, 1819: 92.
Galatheidae. — Dana, 1853: 1431.
Galatheinae. — A. Milne-Edwards & Bouvier, 1894: 244.

Diagnosis. Rostrum well developed, broad, flattened, usually subtriangular; supraocular spines present or absent. Carapace (excluding rostrum) as long as or longer than wide; dorsally with transverse striae. Tailfan well developed, not folded against preceding somite, telson distinctly or indistinctly subdivided into multiple plates. Eyes with well-developed cornea. Antennal peduncle directed anteriorly or anterolaterally. Maxilliped 1 exopod flagellum well-developed. Maxilliped 3 pediform; ischium and merus elongate, not expanded mesially; epipod present. Chelipeds subcylindical to ovate in cross-section.

Type genus. *Galathea* Fabricius, 1793.

Composition. Extant genera: *Alainius* Baba, 1991; *Allogalathea* Baba, 1969; *Allomunida* Baba, 1988; *Coralliogalathea* Baba & Javed, 1974; *Fennerogalathea* Baba, 1988; *Galathea* Fabricius, 1793; *Janetogalathea* Baba & Wicksten, 1997; *Lauriea* Baba, 1971; *Macrothea* Macpherson & Cleva, 2010; *Nanogalathea* Tirmizi & Javed, 1980; *Phylladiorhynchus* Baba, 1969.

Fossil genera: *Acanthogalathea* Müller & Collins, 1991 [Upper Eocene]; *Lessinigalathea* De Angeli & Garassino, 2002 [Lower Eocene]; *Luisogalathea* Karasawa & Hayakawa, 2000 [Upper Cretaceous]; *Mesogalathea* Houša, 1963 [Upper Jurassic to Cretaceous]; *Palaeomunida* Lőrenthey, 1901 [Upper Jurassic to Oligocene]; *Spathagalathea* De Angeli & Garassino, 2002 [Upper Eocene]; *Lophoraninella* Glaessner, 1945 [Upper Cretaceous].

Remarks. The Galatheidae are distinguished from the Munidopsidae by the presence of a well-developed flagellum on maxilliped 1 (absent or reduced in munidopsids), and from the Munididae **fam. nov.** by the broad and flattened rostrum (versus a usually slender rostrum with supraocular spines). The Galatheidae are herein restricted to the 11 extant and seven fossil genera formerly placed in the Galatheinae, sharing a broad, triangular rostrum. We follow De Angeli & Garssino (2002) in treating *Spathogalathea* as a galatheid, although we suspect it may be better placed in the Porcellanidae on the basis of the raised orbital rims, a feature often present in porcellanids but not galatheids.

Galatheids are more closely related to the porcelain crabs, Porcellanidae, than to other clades of squat lobsters (Ahyong *et al.* 2009). Both families share a broad, flattened rostrum (though considerably shortened in porcellanids). Additionally, both galatheids and porcellanids are typically small (carapace length usually < 15 mm) and usually occupy shallow-water or shelf habitats on rocky substrates or coral reefs, in contrast to outer shelf and slope habitats of typical munidids and munidopsids.

Munididae fam. nov.
(Figs 1G, H, 2H–E)

Diagnosis. Rostrum slender, dorsally ridged, usually spiniform; supraocular spines present. Carapace (excluding rostrum) as long as or longer than wide; dorsally with transverse striae. Tailfan well developed, not folded against preceding somite; telson distinctly or indistinctly subdivided into multiple plates. Eyes with well-developed cornea. Antennal peduncle directed anteriorly or anterolaterally. Maxilliped 1 exopod flagellum well developed. Maxilliped 3 pediform; ischium and merus elongate, not expanded mesially; epipod present. Chelipeds subcylindical to ovate in cross-section.

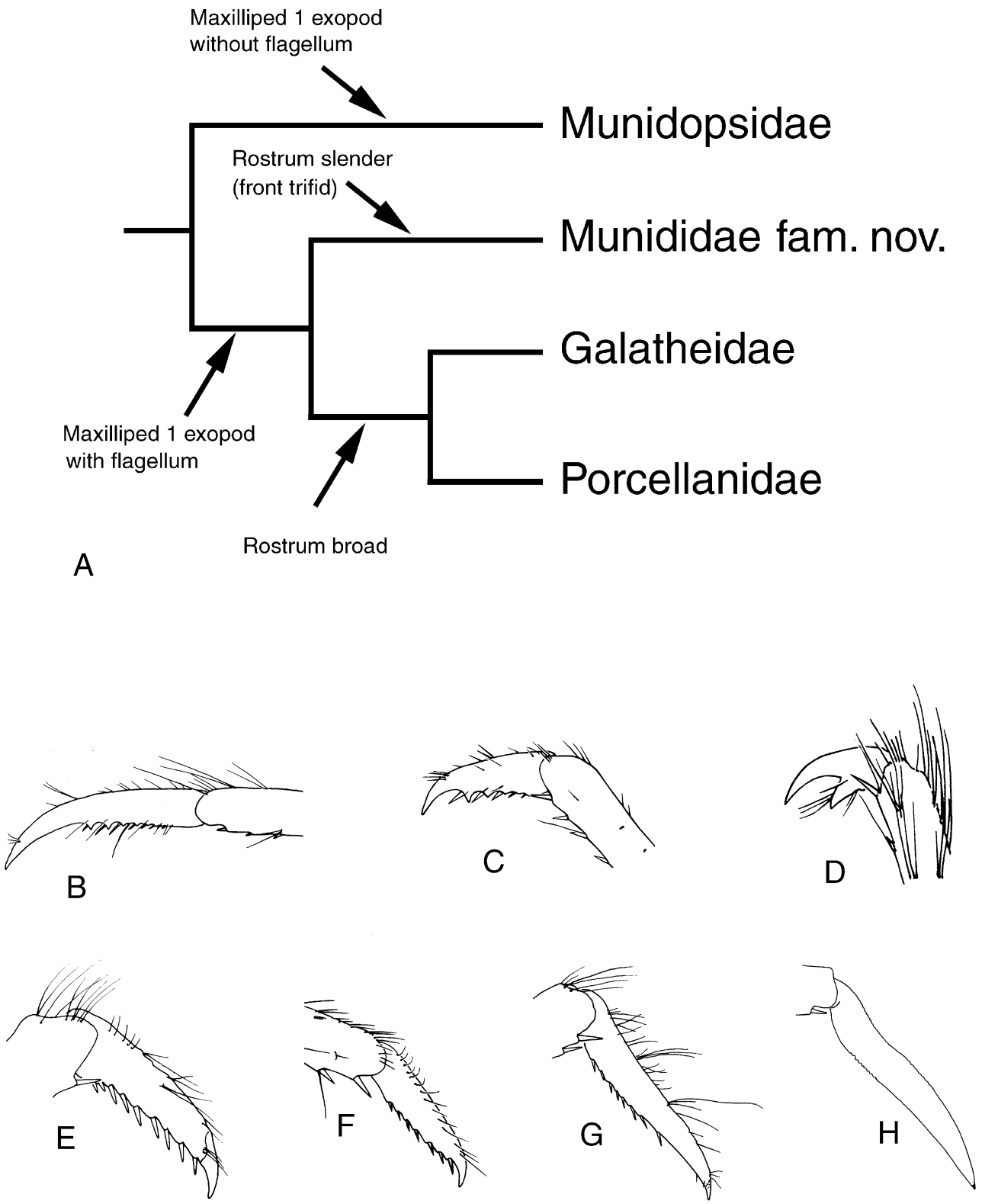

FIGURE 1. A, Phylogenetic relationships of the families of the Galatheoidea based on Ahyong *et al.* (2009) and Schnabel *et al.* (in press). B–H, walking leg dactyli of selected Galatheoidea. Galatheidae: B, *Allomunida magnicheles* Baba, 1988; C, *Galathea tropis* Baba, 2005; D, *Lauriea gardineri* (Laurie, 1926); E, *Phylladiorhynchus* cf. *pusillus* (Henderson, 1885); F, *Alainius crosnieri* Baba, 1991. Munididae **fam. nov.**: G, *Munida exilis* Ahyong, 2007; H, *Agononida eminens* (Baba, 1988). Figure sources: B (Baba 1988); C (Baba 2005); D (Baba 1994); E, G (Ahyong 2007); F (Baba 1991); H (Baba *et al.* 2008).

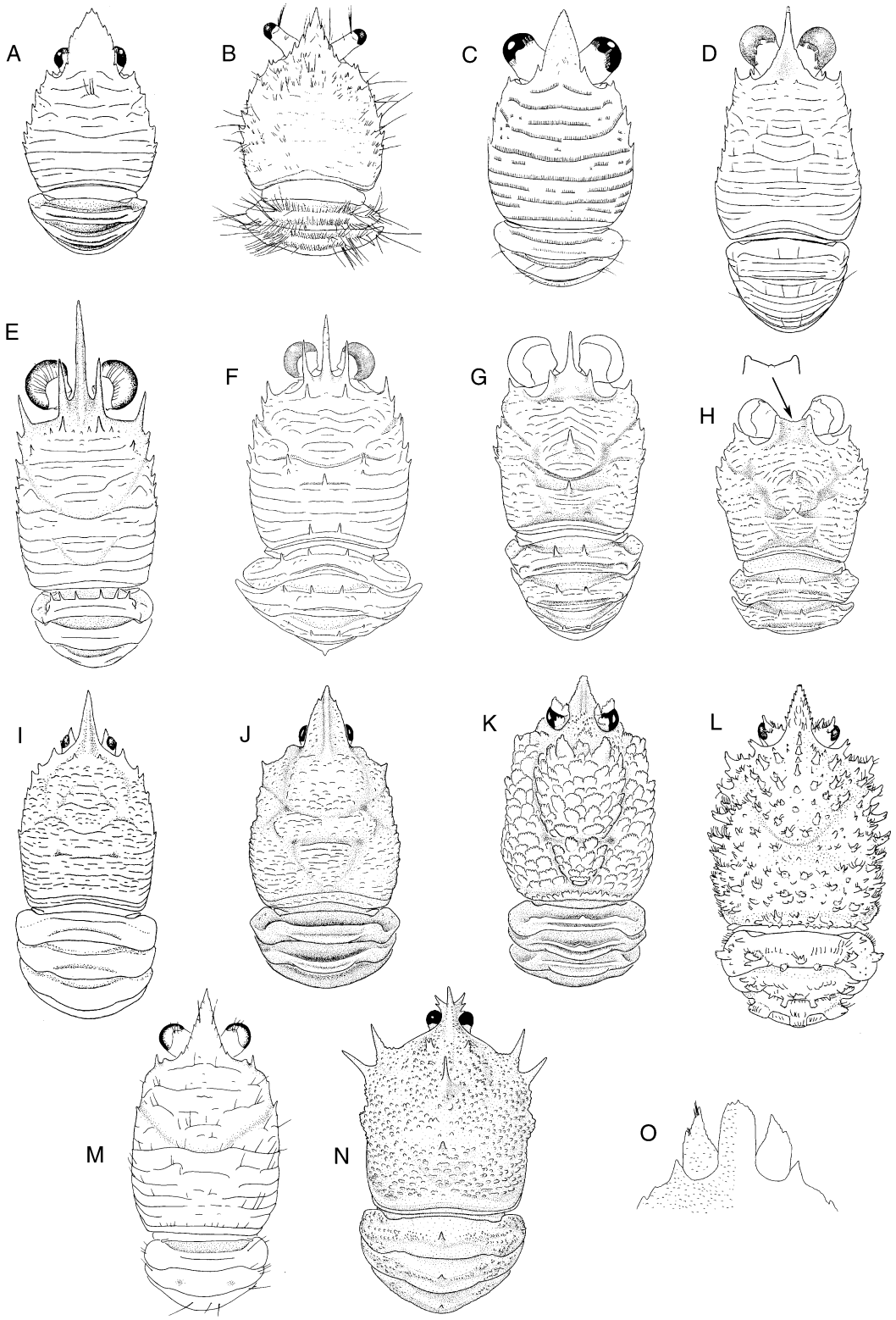

FIGURE 2. Carapace and abdomen (A–N) and anterior carapace (O) of selected Galatheoidea. Galatheidae: A, *Galathea tropis* Baba, 2005; B, *Lauriea siagiani* Baba, 1994; C, *Alainius crosneri* Baba, 1991; D, *Allomunida magnicheles* Baba, 1988. Munididae **fam. nov.**: E, *Munida exilis* Ahyong, 2007; F, *Agononida eminens* (Baba, 1988); G, *Bathymunida ocularis* Baba & de Saint Laurent, 1996; H, *B. frontis* Baba & de Saint Laurent, 1996; Munidopsidae: I, *Munidopsis pycnopoda* Baba, 2005; J, *M. norfanz* Ahyong, 2007; K, *M. bractea* Ahyong 2007; L, *M. laciniosa* Baba, 2005; M, *Leiogalathea laevirostris* (Balss, 1913); N, *Galacantha rostrata* A. Milne-Edwards, 1880; O, *Shinkaia crosnieri* Baba & Williams, 1998. Figure sources: A, I, L (Baba 2005); B (Baba 1994); C (Baba 1991); D (Baba 1988); E, J, K, M (Ahyong 2007); F, O (Baba *et al.* 2009); G, H (Baba & de Saint Laurent 1996); N (Baba & Poore 2002).

Type genus. *Munida* Leach, 1820.

Composition. Extant genera: *Agononida* Baba & de Saint Laurent, 1996, *Anomoeomunida* Baba, 1993; *Anoplonida* Baba & de Saint Laurent, 1996; *Babamunida* Cabezas, Macpherson & Machordom, 2008; *Bathymunida* Balss, 1914; *Cervimunida* Benedict, 1902; *Crosnierita* Macpherson, 1998; *Enriquea* Baba, 2005; *Heteronida* Baba & de Saint Laurent, 1996; *Sadayoshia* Baba, 1969; *Munida* Leach, 1820; *Neonida* Baba & de Saint Laurent, 1996; *Onconida* Baba & de Saint Laurent, 1996; *Paramunida* Baba, 1988; *Pleuroncodes* Stimpson, 1860; *Plesionida* Baba & de Saint Laurent, 1996; *Raymunida* Macpherson & Machordom, 2000; *Setanida* Macpherson, 2006; *Tasmanida* Ahyong, 2007; *Torbenella* Baba, 2008.

Fossil genera: *Protomunida* Beurlen, 1930 [Paleocene to Eocene]; *Cretagalathea* Garassino, De Angeli & Pasini, 2008 [Upper Cretaceous].

Remarks. The family Munididae fam. nov. includes those genera formerly in the Galatheidae having a trifid frontal margin of the carapace, usually in the form of a spiniform rostrum flanked on either side by supraorbital spines. In some genera, however, particularly those allied to *Bathymunida* (see Baba & de Saint Laurent 1996), the rostrum and supraorbital spines may be variously reduced, sometimes present as small points or tubercles along the protruding front (compare Fig. 2G, H). As such, these taxa may appear to have a truncated, subquadrate or subtrapezoid rostrum, although careful examination will reveal the three anterior points, homologous with the rostral and supraorbital spines of other munidids.

Although the family Munididae is formally erected here, it should be noted that Dana (1852: 478) used the Latin construction, *Munidae* (as well as *Munida*) in comparisons with *Galathea* and the invalid *Grimothea* (= *Munida*). *Munidae* was clearly used by Dana only as a plural noun referring to species of *Munida*, rather than as a new suprageneric taxon, and as such is not an available family-group name (ICZN Article 11.7.1.2).

Munididae **fam. nov.** is the most diverse family of the galatheoids with 20 extant and two fossil genera, and more than 350 species. The Cretaceous *Cretagalathea* is regarded as a munidid. The rostrum of the only known specimen is not preserved, but its long, slender pereopods closely resemble those of many munidids, especially species of *Munida*. Schweitzer *et al.* (2010) listed the Middle Eocene *Austromunida* Schweitzer & Feldmann, 2000, as a valid genus, although we follow Garassino & De Angeli (2003) and Casadío *et al.* (2004) in treating it as a junior synonym of *Munida*.

Machordom & Macpherson (2004) studied the phylogenetic relationships of a large suite of primarily munidids and recovered three main clades, one containing *Agononida*, *Bathymunida*, *Paramunida* and allies (sharing the loss of pleopod 1 in males and absence of pereopodal epipods), one containing *Munida*, *Cervimunida*, *Pleuroncodes* and allies (sharing the presence of pleopod 1 in males and the absence of pereopodal epipods), and a third containing *Raymunida* and *Alainius* (sharing the presence of pleopod 1 in males and the presence of pereopodal epipods). The *Raymunida* + *Alainius* clade was sister to other munidids, but the position of *Alainius* is anomalous under the present concept of the family. *Alainius* corresponds more closely to the Galatheidae than Munididae **fam. nov.** by its broad triangular rostrum, and apart from the presence of epipods, is dissimilar to *Raymunida*. The presence of pereopodal epipods is not unique to *Alainius* and *Raymunida*, being present, or even variable in several other galatheid genera (Baba 2005). Schnabel *et al.* (in press) also found a similar position for *Alainius* as sister to the clade of munidids. The nodal support for the position of *Alainius* recovered by both Machordom & Macpherson (2004) and Schnabel *et al.* (in press) is not universally high, so its position may represent an analytical artefact. Conversely, the position may be correct; although *Alainius* has a galatheid-like rostrum, it also has well-developed supraocular spines (Fig. 2C) that are also present in munidids; similarly for *Phylladiorhynchus*. Also, the morphology of the walking-leg dactyli of *Alainius* and *Phylladiorhynchus* might support a close relationship to munidids. In most Galatheidae, the flexor margin of the dactylus of each walking leg is either biunguiculate or evenly toothed, with each tooth usually bearing a small movable spine at its base (Fig. 1B–D). These flexor marginal teeth range from obtusely to acutely triangular. In Munididae **fam. nov.**, the walking leg dactylus also usually has small movable spines, but the flexor margin itself is not toothed, instead being smooth, crenulated or stepped (Fig. 1G, H). Of the genera presently assigned to the Galatheidae, the walking leg dactyli of *Alainius* and *Phylladiorhynchus* correspond to the munidid form (Fig. 1E, F), and in the case of *Alainius*, corroborates its position in current phylogenetic analyses. Unfortunately, the polarity of evolution of the walking leg dactylus

armature is not clear because all of the states found in galatheids and munidids are also present in munidopsids. Thus, whether or not these features of dactylar morphology reflect fundamental phylogenetic differences remains to be determined and more detailed analyses of the relationships within the Munididae **fam. nov.** are currently underway in collaboration with N. Andreakis. It is conceivable that even further subdivision of the galatheoid families may eventually be warranted, but at present, *Alainius* and *Phylladiorhynchus* are retained in the Galatheidae.

Members of the Munididae **fam. nov.** usually occur at outer shelf or slope depths, although some species may enter shallow water (Baba *et al.* 2008).

Munidopsidae Ortmann, 1898
(Fig. 2I–O)

Munidopsinae Ortmann, 1898: 1151.
Shinkaiinae Baba & Williams, 1998: 152, 155.

Diagnosis. Rostrum well developed, subtriangular or spiniform; supraocular spines absent. Carapace (excluding rostrum) longer than wide; dorsum variously ornamented, smooth, tuberculate, spinose or with transverse striae. Tailfan well developed, not folded against preceding somite; telson distinctly or indistinctly subdivided into multiple plates. Eyes reduced or with well-developed cornea. Antennal peduncle directed anteriorly or anterolaterally. Maxilliped 1 exopod flagellum absent or reduced. Maxilliped 3 pediform; ischium and merus elongate, not expanded mesially; epipod present. Chelipeds subcylindical to ovate in cross-section.

Type genus. *Munidopsis* Whiteaves, 1874.

Composition. Extant genera: *Galacantha* A. Milne-Edwards, 1880; *Leiogalathea* Baba, 1969; *Munidopsis* Whiteaves, 1874; *Shinkaia* Baba & Williams, 1998.

Fossil genera: *Brazilomunida* Martins-Neto, 2001 [Upper Cretaceous]; *Calteagalathea* De Angeli & Garassino, 2006 [Upper Cretaceous]; *Eomunidopsis* Vía Boada, 1981 [Upper Jurassic to Upper Cretaceous]; *Faxegalathea* Jakobsen & Collins, 1997 [Lower Paleocene]; *Gastrosacus* von Meyer, 1851 [Upper Jurassic to Cretaceous]; *Munitheities* Lőrenthey *in* Lőrenthey & Beurlen, 1929 [Upper Jurassic]; *Palaeomunidopsis* Van Straelen, 1925 [Middle Jurassic]; *Paragalathea* Patrulius, 1960 [Upper Jurassic to Cretaceous].

Remarks. The family Munidopsidae is united by the reduced or absent flagellum on maxilliped 1, and includes the genera formerly comprising the Munidopsinae and Shinkaiinae, and the former galatheid, *Leiogalathea*. Although Ortmann (1898) formalized the name Munidopsinae, A. Milne-Edwards & Bouvier (1894) had earlier recognized the characteristic synapomorphy of the group through the informal label, "Les Galathéens Non Flagellés". Other more general distinguishing features of munidopsids include (usually) reduced eyes of most species and dorsal carapace ornamentation. Munidids and galatheids almost always have long, distinct, transverse striae (or minute spinules in *Fennerogalathea* and *Paramunida*) whereas munidopsids generally have short or few striae, and are more commonly tuberculate or squamate.

Four extant and eight extinct genera are included in the Munidopsidae. Although the Mesozoic *Eomunidopsis* and *Paragalathea* have been considered to be galatheines (now galatheid) (Schweitzer & Feldmann 2000), we follow Collins *et al.* (1995) in a munidopsid alignment. Similarly, *Calteagalathea* is also regarded as a munidopsid. *Calteagalathea, Eomunidopsis* and *Paragalathea* resemble many species of *Munidopsis,* especially in the squamate, tuberculate or rippled carapace surface, and elongate, distally dentate rostrum with a median ridge. Moreover, *Calteagalathea, Eomunidopsis* and *Paragalathea* are readily accommodated within the current concept of *Munidopsis*, indicating that further refinement of the generic classification is required to harmonize neontological and palaeontological taxonomies.

Leiogalathea (Fig. 2M) was regarded as a galatheid on the basis of its general *Galathea*-like habitus, small size and well-developed eyes, although maxilliped 1 has a reduced flagellum. However, molecular phylogenetic analyses (Ahyong *et al.* 2009) found strong support for a close relationship between *Leiogalathea* and a clade containing *Munidopsis*, *Galacantha* and *Shinkaia*. Additionally, sternite 4 of

Leiogalathea is narrowly triangular with a narrow point of contact with sternite 3, which is more typical of *Munidopsis* and *Galacantha* than Galatheidae, in which sternite 3 is fully appressed to the anterior margin of sternite 4.

Shinkaia (Fig. 2O) was originally assigned to its own subfamily alongside the Munidopsinae and Galatheinae (Baba & Williams 1998). *Shinkaia* shares the suppression of the flagellum of the maxilliped 1 exopod with other munidopsids, but differs in numerous autapomorphies, such as the densely setose sternum and short rather than elongated epipods on the pereopods (Baba & Williams 1998). Ahyong *et al.* (2009) found a paraphyletic relationship between *Shinkaia* and other munidopsids, and as such did not support separate subfamily status for the former. Although the Shinkaiinae may yet prove to be valid after more extensive analysis of the munidopsid genera is completed (in collaboration with J. Taylor and N. Andreakis), it is presently regarded as a junior synonym of Munidopsidae.

The Munidopsidae include the deepest dwelling galatheoids, usually occupying slope to abyssal depths, although one species, *M. polymorpha,* lives as shallow as 2 m in submarine caves (Baba *et al.* 2008). The majority of munidopsids have reduced or degenerate eyes, reflecting their deep bathymetric preference (Alcock 1902).

Porcellanidae Haworth, 1825

Porcellanidae Haworth, 1825: 184.

Diagnosis. Rostrum well developed to obsolete, if well-developed, broad, subtriangular, flattened. Supraocular spines present or absent. Carapace (excluding rostrum) longer than wide to wider than long; dorsal surface smooth or variously ornamented with faint striae or tubercles. Tailfan well developed, folded against preceding somite, telson distinctly subdivided into 5 or 7 plates. Eyes with well-developed cornea. Antennal peduncle directed laterally or posteriorly. Maxilliped 1 exopod flagellum well developed. Maxilliped 3 operculiform; ischium and merus elongate, broad, expanded mesially; epipod absent. Chelipeds flattened.

Remarks. De Grave *et al.* (2009) provide a checklist of extant and fossil porcellanid genera and Osawa & McLaughlin (2010) list the extant porcellanid species.

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