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First notice of the Chirostylidae (Decapoda) in the fossil record and new Tertiary Galatheidae (Decapoda) from the Americas

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Abstract

Two new species from Alaska and Washington, USA, *Munida konara* sp. nov., and *Munida quadroblonga* sp. nov., comprise the first occurrence of the Galatheinae (Galatheidae) in western North America and only the third confirmed fossil occurrence of the family and subfamily from the North Pacific Ocean. A new genus and species from Patagonia, *Austromunida casadioi*, documents the first occurrence of the Galatheinae (Galatheidae) from that region. The Galatheinae appear to have evolved in the North Atlantic or Europe and subsequently dispersed to the Pacific and South Atlantic oceans via a polar route and/or Atlantic ocean currents. The Munidopsinae appear to have evolved in the North Atlantic region during the Jurassic and subsequently dispersed to the southern hemisphere by Cretaceous time, as documented by occurrences of the subfamily in Cretaceous rocks of Antarctica. A new Cretaceous genus and species, *Pristinaspina gelasina* from Alaska, USA, consitutes the earliest known occurrence of the Chirostylidae. That new taxon, in addition to two fossil species herein reassigned to *Eumunida, E. pentacantha* (Müller and Collins, 1991) and *E. nishioi* (Karasawa, 1993), constitute the first notice of the Chirostylidae in the fossil record. A key to the fossil Galatheoidea demonstrates that arrangement of genera within the Galatheidae, based solely upon characters of the dorsal carapace, generally conforms with subfamilial taxa defined on biological criteria; however, the Chirostylidae are not adequately constrained. *Rugafarius* Bishop, 1985, previously assigned to the Galatheidae, is herein placed within the Prosopidae von Meyer, 1860.

Key words: Galatheidae, Chirostylidae, Prosopidae, Decapoda, Cretaceous, Tertiary

Introduction

The record for many decapod families previously unknown as fossils has been recently extended into the Tertiary. For example, a fossil member of the Cheiragonidae was recently reported for the first time (Schweitzer and Salva, 2000), extending the record of that family into the Eocene. The geologic ranges of the Cyclodorippidae, Cancridae, Geryonidae, and Asthenognathinae (Pinnotheridae) have also been extended into the Eocene (Schweitzer and Feldmann, 2000, 2 in press; Schweitzer, in press) and the range of the Portunidae has been extended into the early Paleocene (Danian) (Schweitzer and Feldmann, 2000).

The Galatheidae has long been known to have a modest fossil record (Glaessner, 1969), and this report documents new occurrences and range extensions for the galatheine genus *Munida*. A new galatheine genus is described from

Patagonia, which is the first fossil occurrence for the subfamily in that region. More importantly, new material from the Cretaceous of Alaska and reassignment of fossil species previously assigned to the Galatheidae constitute the first reports of the Chirostylidae in the fossil record. The Alaskan material, *Pristinaspina* gen. nov., is the earliest known member of the Chirostylidae. The new genus differs from other chirostylids in its dimpled carapace ornamentation and well-developed marginal spines; this suggests that large spines and subdued carapace ornamentation may be primitive features within the group. Extant species possess either smooth dorsal carapaces or transverse ridges. *Pristinaspina* was recovered from siliciclastic deposits associated with thallassinoid ghost shrimp. Most modern chirostylids engage in commensal relationships with octocorals in deep water habitats (Baba, 1973). The lack of coralline fossils associated with *Pristinaspina* suggests that the genus may have been a free-living form and that the commensal habitat developed at a later time.

In addition to the new genus, two Tertiary species previously assigned to genera within the Galatheinae Samouelle, 1819, have been placed within the chirostylid genus *Eumunida*. These newly reported occurrences suggest that the genus evolved within the Tethys and subsequently dispersed to the Indo-Pacific region, where it is currently most speciose.

Systematic Paleontology

Infraorder Anomura MacLeay, 1838

Superfamily Galatheoidea Samouelle, 1819

Key to fossil Galatheoidea: In order to distinguish among described fossil galatheoid genera, a dichotomous key has been constructed (Appendix 1). Because of the bases of preservation, the key characters used are entirely features of the dorsal carapace. Biological keys to extant representatives of the superfamily (see Baba, 1988, for

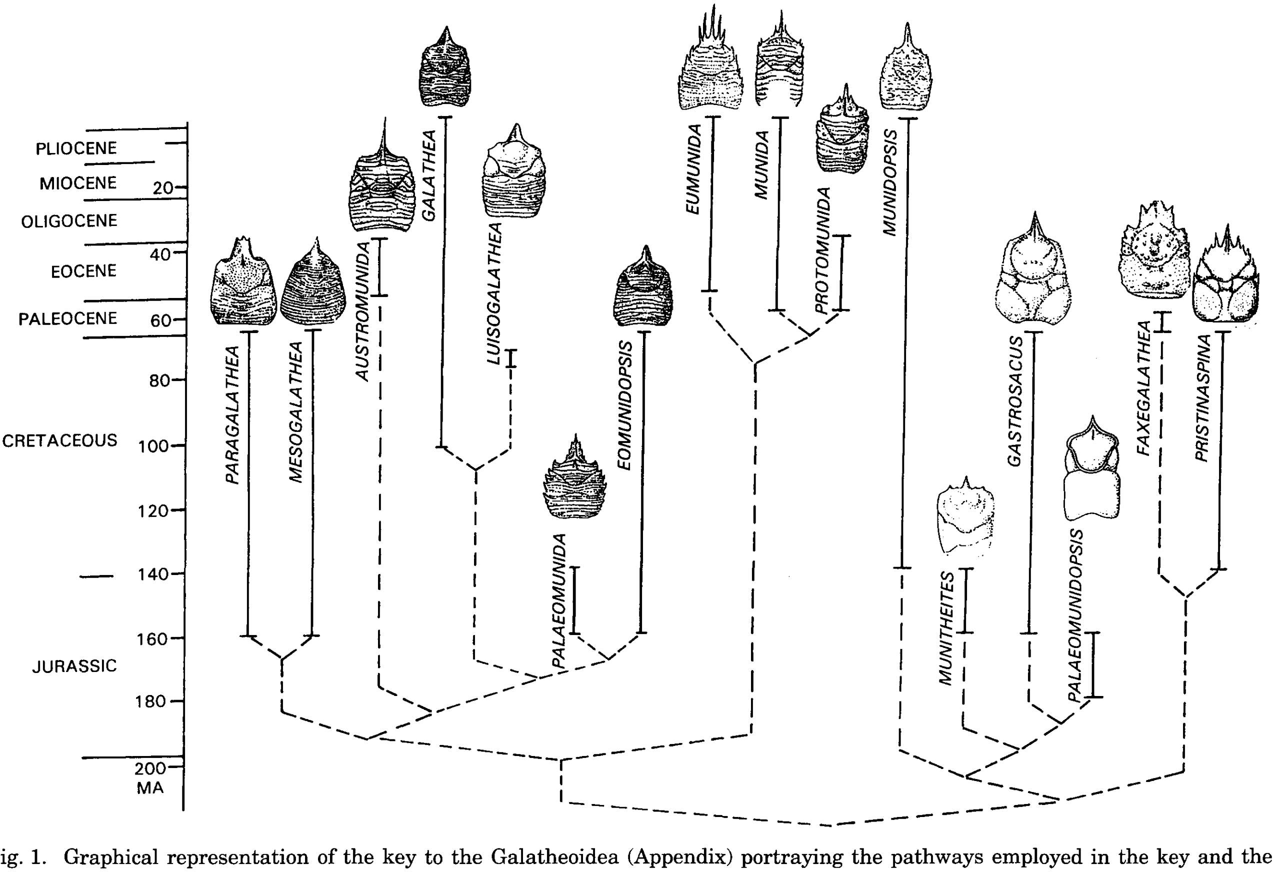

Fig. 1. Graphical representation of the key to the Galatheoidea (Appendix) portraying the pathways employed in the key and the stratigraphic distribution of the species embraced within the genera. Because the key characters have not been tested for phylogenetic significance, the branching pattern cannot be considered to represent phylogeny.

example) rely heavily upon characters such as eye and eyestalk development, nature of the exopod of the first maxilliped, antennal morphology, details of the pereiopods, sternal architecture, and development of uropods. None of these characters is commonly preserved in the fossil record and, therefore, none is useful in identification of fossils. It is not surprising that the results of the two approaches yield somewhat different groupings. The family and subfamily subdivisions recognized in the biological literature are, without question, based upon more fundamental characters than some of those characters preserved on the dorsal carapace. Thus, it is clearly reasonable to adopt the biologically based suprageneric classification. It is equally reasonable to utilize an artificial key to hard part characters in order to classify fossil forms. As an aside, this may well indicate that application of cladistic procedures to deduce phylogenies based upon fossils is difficult.

If the fossil organisms are arranged in the order in which they were distinguished in the key (Appendix 1) and are plotted against their geological range (Fig. 1), there is a remarkable general correspondence between the biological and paleontological arrangements within the Galatheidae. However, the chirostylids, *Eumunida* and *Pristinaspina* gen. nov., appear in quite different places on the array, based upon presence or absence of well-developed transverse ornamentation. Transverse ornamentation seems to be a reversable character state within the superfamily; thus, it cannot be used effectively to distinguish among galatheids and chirostylids in cladistic or other phylogenetic analyses.

Family Galatheidae Samouelle, 1819

Diagnosis: Carapace longer than wide, with or without transverse ornamentation, often with anterior gastric spines or other spinose or nodose ornamentation on dorsal carapace; rostrum well-developed, variable, may be needle-like, spatulate, keeled, or ornamented with small spines or serrations; typically one or more pairs of supraocular spines; cervical and branchiocardiac grooves always present, frequently deep and well-developed; lateral margins crenulate or ornamented with spines.

Discussion: Bishop (1985) described a new galatheid genus, *Rugafarius*, from the Cretaceous of South Dakota, although he noted that it differed considerably from all other galatheids and may in fact be a palinurid lobster. It appears likely that *Rugafarius* is allied either with the Middle Jurassic to Upper Cretaceous Prosopidae von Meyer, 1860 or the lower Jurassic Eocarcinidae Withers, 1932. *Rugafarius* is characterized by having a carapace that is much longer than wide; a very short, bifurcate rostrum; well-developed cervical and branchiocardiac grooves; coarse, rugose ornamentation; four anterolateral spines; a linear axial region, defined laterally by the branchiocardiac grooves; and inflated branchial regions. Members of the Prosopidae display all of these characteristics save one; most prosopids do not have numerous or well-developed anterolateral spines. *Eocarcinus* Withers, 1932, the sole genus within the Eocarcinidae, displays most of these characters; however, it lacks anterolateral spines and has a triangular rostrum. Thus, *Rugafarius* is placed within the Prosopidae.

Van Straelen (1924 [1925]) named *Charassocarcinus* as a member of the Homolodromiidae, and Glaessner (1933) subsequently referred it to the Galatheidae. It has since been referred to the Tanaidacea (Glaessner, 1969, p. R532, R628). Another genus, *Olinaecaris* Van Straelen, 1924 [1925], was originally considered to belong to the Erymidae Van Straelen, 1924 [1925], but was subsequently assigned to the Galatheidae (Glaessner, 1929). We concur with Van Straelen (1924 [1925]) that the taxon belongs within the Erymidae.

Subfamily Galatheinae Samouelle, 1819

Included solely fossil taxa: *Austromunida* gen. nov. Schweitzer and Feldmann, herein; *Eomunidopsis* Via Boada, 1981; *Luisogalathea* Karasawa and Hayakawa, 2000; *Mesogalathea* Houša, 1963; *Palaeomunida* Lőrenthey, 1902; *Paragalathea* Patrulius, 1960; *Protomunida* Beurlen, 1930.

Included fossil and recent genera: *Galathea* Fabricius, 1793; *Munida* Leach, 1820.

Included solely extant genera: *Agononida* Baba and Saint Laurent, 1996; *Alainius* Baba, 1991; *Allogalathea* Baba, 1969; *Allomunida* Baba, 1988; *Anomoeomunida* Baba, 1993; *Anoplonida* Baba and Saint Laurent, 1996; *Bathymunida* Balss, 1913; *Crosnierita* Macpherson, 1998; *Cervimunida* Benedict, 1902; *Coralliogalathea* Baba and Javed, 1974; *Fennerogalathea* Baba, 1988; *Heteronida* Baba and Saint Laurent, 1996; *Janetogalathea* Baba and

Wicksten, 1997; *Lauriea* Baba, 1971; *Liogalathea* Baba, 1969; *Nannogalathea* Tirmizi and Javed, 1980; *Neonida* Baba and Saint Laurent, 1996; *Onconida* Baba and Saint Laurent, 1996; *Paramunida* Baba, 1988; *Phylladiorhynchus* Baba, 1969; *Plesionida* Baba and Saint Laurent, 1996; *Pleuroncodes* Stimpson, 1860; *Raymunida* Macpherson and Machordom, 2000; *Sadayoshia* Baba, 1969.

Diagnosis: Carapace longer than wide, with transverse ornamentation, often with anterior gastric spines or other spinose or nodose ornamentation on dorsal carapace; rostrum well-developed, needle-like or ornamented with small spines or serrations; typically one or more pairs of supraocular spines; cervical and branchiocardiac grooves generally deep and well-developed but may be weakly developed in some genera; lateral margins crenulate or ornamented with spines; carapace regions usually poorly defined.

Discussion: Glaessner (1969) referred four genera known from the fossil record to the Galatheinae: *Galathea, Munida, Palaeomunida*, and *Protomunida*; we concur. Herein, four previously described fossil genera, *Eomunidopsis, Luisogalathea, Mesogalathea* and *Paragalathea*, and one new genus, *Austromunida*, are referred to the subfamily. *Eomunidopsis* was originally referred to the Munidopsinae (Via Boada, 1981; 1982); however, that genus lacks some of the key characters of the Munidopsinae including an ovate, inflated gastric region and a well-developed cardiac region. Additionally, *Eomunidopsis* possesses well-developed transverse ridges on the carapace, a type of ornamentation not seen in typical munidopsines. *Eomunidopsis* exhibits several characters typical of the Galatheinae, including transverse ornamentation, deep cervical and branchiocardiac grooves, and poorly developed carapace regions. Thus we have placed *Eomunidopsis* within the Galatheinae. *Mesogalathea* and *Paragalathea* each possess well-developed transverse ornamentation, deep cervical grooves, and poorly developed carapace regions; thus, they are also referred to the Galatheinae.

Müller and Collins (1991, p. 56) introduced *Acanthogalathea* as a subgenus of *Galathea* and, at the same time, ranked *Palaeomunida* as a subgenus of *Galathea*. The type species of the former, *G.* (*A.*) *parva* Müller and Collins, falls well within the definitional basis for the genus and, therefore we have not treated *Acanthogalathea* as a separate generic-level taxon. Without detailed evaluation of all species of *Galathea*, it would be unwise to judge on the subgeneric division of the genus. Certainly, many extant galatheids have strong spines developed in the branchial, cardiac, and gastric regions. With regard to their placement of *Palaeomunida* as a subgenus within *Galathea*, the possession of a keeled rostrum with a spinose tip separates *Palaeomunida* from *Galathea* as it is presently understood. Therefore, we continue to consider *Palaeomunida* a separate genus.

Karasawa and Hayakawa (2000) described a new genus and species of galatheid, *Luisogalathea tomitai*, and a new species of *Eomunidopsis, E. kojimai*, from Cretaceous rocks of Japan. *Luisogalathea* is differentiated from other galatheid genera in possessing a broad rostrum that lacks both lateral spines and a central keel. Examination of the illustrations of both *L. tomitai* and *E. kojimai* (Karasawa and Hayakawa, 2000, fig. 4) indicates that the specimens representing these two taxa in fact belong to the same taxon. The specimen referred to *Eomunidopsis kojimai* was differentiated from the specimen referred to *L. tomitai* because of its lack of lateral spines (p. 143). However, examination of the description and photographs of *E. kojimai* indicates that it does in fact have lateral spines (p. 144, Fig. 4.2). Comparison of the carapace regions and ornamentation of *E. kojimai* to those of *L. tomitai* suggests that the specimens are conspecific. Therefore, the specimens are referred to the new genus *Luisogalathea*, and *Eomunidopsis* thus remains unknown from deposits of Japan.

The fossil record for the Galatheinae extends into the Jurassic (Glaessner, 1969) (Table 1). Jurassic occurrences are known from Europe, and the subfamily is reported from Cretaceous rocks of Europe, Texas, and Japan; Paleocene rocks of Denmark and Greenland; and post-Paleocene rocks of Europe, North America, and questionably from Australia and New Zealand (Table 1). The Cretaceous *Galathea cretacea* Stenzel, 1945, which as illustrated by Glaessner (1969) appears to have a smooth rostrum, does in fact possess the diagnostic small spines on the rostrum and is thus a member of *Galathea* (Fig. 2).

The report herein of two new species of *Munida* from the west coast of North America constitutes the first notice of the subfamily from that region. One species of

Table 1. Geologic and geographic range of genera of the Galatheidae and Chirostylidae known from the fossil record.

Family	Subfamily	Genus	Geologic Range	Occurrence in Fossil Record
Galatheidae	Galatheinae	*Galathea*	Upper Cretaceous-Recent	Europe, Greenland, Japan, Gulf Coastal USA, ?New Zealand
		Austromunida gen. nov.	Cretaceous	southern Argentina
		Eomunidopsis	Upper Jurassic-Upper Cretaceous	Europe, USA
		Luisogalathea	Cretaceous	Japan
		Mesogalathea	Upper Jurassic-Cretaceous	Europe
		Munida	Danian-Recent	Europe, North America, ?Australia
		Palaeomunida	Upper Jurassic-Eocene	Europe
		Paragalathea	Upper Jurassic-Cretaceous	Europe
		Protomunida	Paleocene-Eocene	Europe
		Mesogalathea	Upper Jurassic-Cretaceous	Europe
	Munidopsinae	*Munidopsis*	Cretaceous-Recent	Antarctica
		Faxegalathea	Lower Paleocene	Europe
		Gastrosacus	Upper Jurassic-Cretaceous	Europe
		Munitheites	Upper Jurassic	Europe
		Palaeomunidopsis	Middle Jurassic	Europe
Chirostylidae		*Eumunida*	Eocene-Miocene	Europe, Japan
		Pristinaspina gen. nov.	Cretaceous	western North America

Luisogalathea from Cretaceous rocks and one species of *Galathea* from the Miocene of Japan comprise the only other confirmed fossil occurrences of the subfamily in the North Pacific Ocean in the fossil record. Two South Pacific occurrences are reported but they are poorly documented. Feldmann and Maxwell (1990) and Feldmann and Keyes (1992) listed an undescribed species of *Galathea* from the Pliocene of New Zealand, and Jenkins (1977) reported a species of *Munida* from the Paleogene of Australia. The occurrence of the new genus *Austromunida* in Eocene rocks of Argentina constitutes the first unequivocal notice of the subfamily in that area. The family appears to have evolved in Europe, and subsequently achieved a broad northern hemisphere distribution by the Cretaceous and a nearly cosmopolitan distribution by the middle Tertiary, perhaps because of the pelagic habit of members of the group.

Genus *Austromunida* gen. nov.

Type species: *Austromunida casadioi* sp. nov., by original designation.

Diagnosis: as for species.

Etymology: The name is taken from the Latin word "*austro*," meaning southern, and the genus name *Munida*, the taxon to which the new genus appears to be most closely related.

Discussion: A small number of galatheine genera have been reported from the fossil record, and comparison of

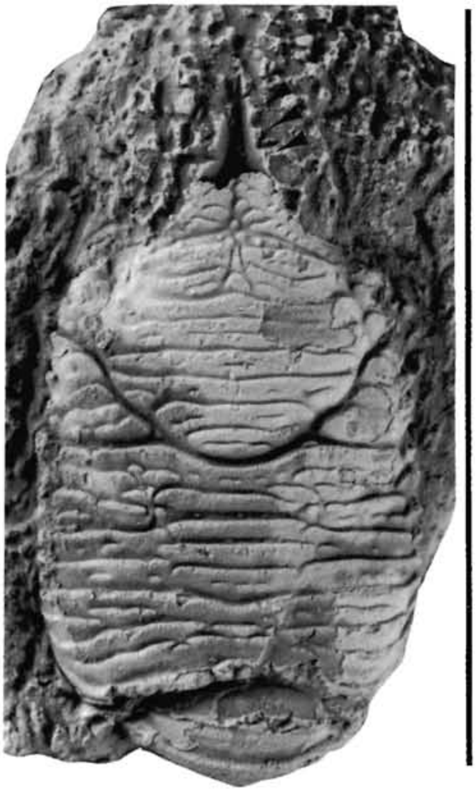

Fig. 2. *Galathea cretacea* Stenzel, 1945, holotype, BEG 21118, Texas Memorial Museum, University of Texas at Austin. Arrows indicate positions of tiny spines on rostrum. Scale bar equal to 1 cm.

the new Eocene material from Argentina with both fossil and Recent galatheines suggests that it represents a new genus. The new material is differentiated from all other known fossil galatheids in possessing a narrow, needle-like rostrum; transverse ridges; and numerous lateral spines. No other fossil galatheine displays this combination of characters.

The argentine material is superficially similar to some genera within the Galatheinae, especially *Munida*, and has a cervical and branchiocardiac groove configuration and carapace ornamentation that is nearly identical to that seen in species of *Munida, Galathea,* and other members of the Galatheinae. The new genus may be differentiated from *Munida* based upon several differences. The new material has no supraorbital spines; species of *Munida* have one pair of supraorbital spines. Species of *Munida* regularly possess anterior gastric spines ornamenting the carapace while the new material lacks spinose or nodose ornamentation in that region. Species of *Munida* typically have a rather well-developed spine on the distal corner of the frontal margin; the new material lacks such a spine. Species of *Munida* typically have poorly developed carapace regions and do not have defined axial regions, while the new taxon has faintly but clearly marked regions. Most species of *Munida* have nearly straight or weakly convex lateral margins; the new taxon has markedly convex lateral margins.

The new genus differs from *Paragalathea, Luisogalathea, Galathea*, and *Mesogalathea* because *Austromunida* has a keel on the rostrum while the others do not. *Austromunida* differs from *Palaeomunida* because *Palaeomunida* has spines or serrations on the rostrum, which *Austromunida* lacks. *Protomunida* has one pair of supraocular spines which *Austromunida* lacks.

Austromunida casadioi sp. nov.

(Figs. 3.1, 3.2, 4)

Diagnosis: Carapace about 1.5 times as long as wide; rostrum long, needle-like; anterolateral and lateral margins with several small spines; cervical and branchiocardiac grooves deep; carapace ornamented by continuous and discontinuous ridges; carapace regions moderately well-defined.

Etymology: The species is named for Dr. Silvio Casadıo, Universidad Nacional de La Pampa, Santa Rosa, Argentina, who assisted in field work resulting in collection of the material and who has been an invaluable colleague and friend.

Description: Carapace longer than wide, about 1.5 times as long as wide (length including rostrum), widest about three-quarters the distance posteriorly on carapace, oblong in shape; weakly vaulted longitudinally; moderately vaulted transversely; ornamented with transverse ridges, ridges smooth, some continuous across carapace, others discontinuous.

Rostrum very long; needle-like; one-third total length of carapace; broadened at base; with central keel extending onto anterior gastric region. Frontal margin arcuate, entire, sloping posteriorly, about 70 percent maximum carapace width. Anterolateral margin with two or three small spines anterior to intersection of cervical groove with lateral margin, spines directed anterolaterally; at least four small spines on lateral margin posterior to cervical groove, triangular, directed forward; remainder of

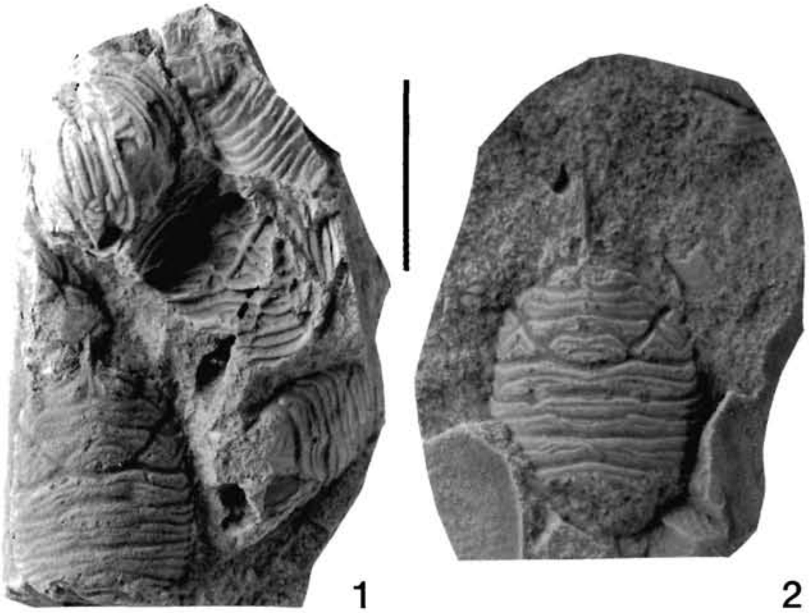

Fig. 3. *Austromunida casadioi* gen. et sp. nov. 1, dorsal view of nearly complete carapace and fragments of carapaces of several other individuals in a single concretion, holotype, GHUNLPam 16832. 2, latex cast of dorsal view of carapace of paratype, GHUNLPam 16833. Scale bar equal to 1 cm.

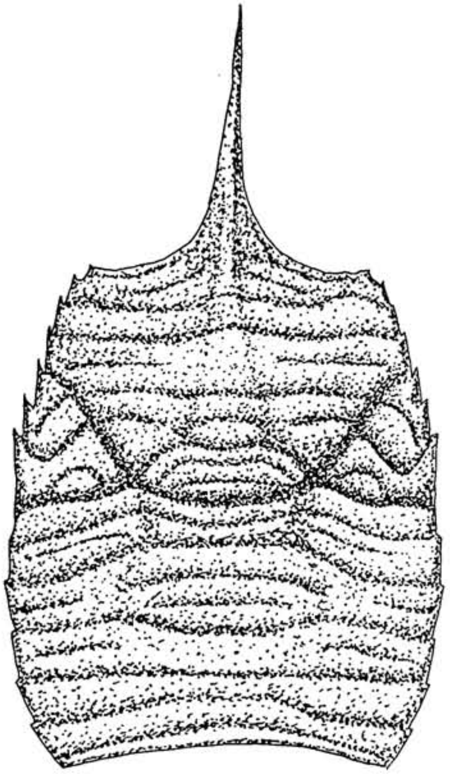

Fig. 4. Line drawing reconstruction of *Austromunida casadioi* sp. nov. showing details of definition of regions and ornamentation of dorsal carapace.

lateral margin crenulate due to intersection of transverse ridges with margin. Posterior margin concave, rimmed.

Cervical groove deep, broad, concave forward, slightly sinuous; extending posteriorly on carapace from margin just posterior to second or third anterolateral spine. Branchiocardiac groove deep, broad. Carapace regions moderately defined. Protogastric regions triangular, with anterior gastric swellings at base of rostrum, ornamented with continuous and discontinuous transverse ridges. Hepatic region small, with short, oblique, scabrous ridges. Mesogastric region weakly but clearly delineated, with long anterior process, widening distally, lateral margins concave, posterior margin weakly convex. Urogastric region oblong transversely, constricted centrally. Cardiac region bluntly triangular, apex directed posteriorly. Epibranchial regions bounded by cervical and branchiocardiac grooves, ornamented with oblique ridges. Mesobranchial and metabranchial regions not differentiated, weakly inflated, ornamented with continuous and discontinuous transverse grooves.

Venter and appendages unknown.

Types: The holotype, GHUNLPam 16832, and paratypes, GHUNLPam 16833 and 16834, are deposited in the Geological Museum, Universidad Nacional de La Pampa, Santa Rosa, La Pampa, Argentina.

Measurements: Measurements (in mm) taken on the dorsal carapace of three specimens of *Austromunida casadioi* new species: GHUNLPam 16832 (holotype): maximum length (excluding rostrum) = 11.3, maximum width = 8.4, length to cervical groove = 4.8. GHUNLPam 16833: maximum length (including rostrum) = 17.3, length of rostrum > 5.7, maximum width = 11.6, length to cervical groove = 5.9. GHUNLPam 16834: maximum length (excluding rostrum) = 11.4, maximum width = 8.7, length to cervical groove = 5.9.

Occurrence: The material was collected from the middle Eocene Centinela Formation on Estancia 25 de Mayo, Calafate, Santa Cruz, Argentina, at Lat. 50° 27.5' South, Long. 72° 12' West.

Discussion: The new species is represented by several incomplete dorsal carapaces and numerous unidentifiable fragments of carapace. Most specimens retain some cuticular material, and many are molds of the interior. The specimens are often preserved as aggregates of individuals, suggesting that the animals were gregarious or lived in swarms of individuals as is common for living galatheids. The material was associated with several other decapod taxa, including portunids, geryonids, cancrids, and pinnotherids (Schweitzer and Feldmann 2000, 2 in press) as well as a diverse molluscan, brachiopod and bryozoan assemblage.

Genus *Munida* Leach, 1820

Type species: Pagurus rugosus Fabricius, 1775.

Fossil species: *Munida konara* sp. nov.; *M. primaeva* Segerberg, 1900; *M. quadroblonga* sp. nov.

Diagnosis: Carapace rectangular or ovoid, longer than wide, rostrum flanked by one pair of supraorbital spines; two or three anterolateral spines; several small, lateral spines posterior to intersection of cervical groove with lateral margin; deep, arcuate cervical groove; transverse carapace ridges that range from simple and parallel to complex and bifurcating; and linear array of gastric spines paralleling frontal margin of carapace.

Discussion: Two taxa are referred to this genus herein; *Munida quadroblonga* sp. nov. exhibits all of these characters and is referred to the genus with confidence. *Munida konara* sp. nov. is represented by two incomplete and poorly preserved specimens; however, its observable features make it most prudent to assign the material to *Munida* until more completely preserved material is recovered.

Munida has a cosmopolitan distribution in Recent oceans, and the genus is quite speciose (see Baba, 1988; Macpherson, 1993, 1994, 1996a, 1996b; Macpherson and Baba, 1993, for example). Fossil occurrences are limited to *M. primaeva* described from Danian rocks of Denmark (Segerberg, 1900) and the two new species described here. The temporal and geographic pattern of these occurrences suggests that the genus may have arisen in the North Atlantic region during the Paleocene and subsequently dispersed westward to the Pacific Ocean, either via a North Polar route or across the Atlantic Ocean to the Pacific Ocean through the open Central American Seaway. Each of these dispersal patterns is well-documented for Tertiary decapods (Schweitzer and Salva, 2000; Schweitzer and Feldmann, 2000; Schweitzer, in press, in revision), and each pathway is equally likely based upon the available evidence.

Munida quadroblonga sp. nov.
(Figs. 5.1, 5.2, 6)

Munida sp., Feldmann, Tucker, and Berglund, 1991, p. 357.

Diagnosis: Carapace longer than wide, maintaining nearly uniform width along entire length; oblong in shape, narrowing slightly anteriorly; ornamented with transverse ridges, ridges mostly simple and parallel, ridge edges granular; central rostral spine long, needle-like;

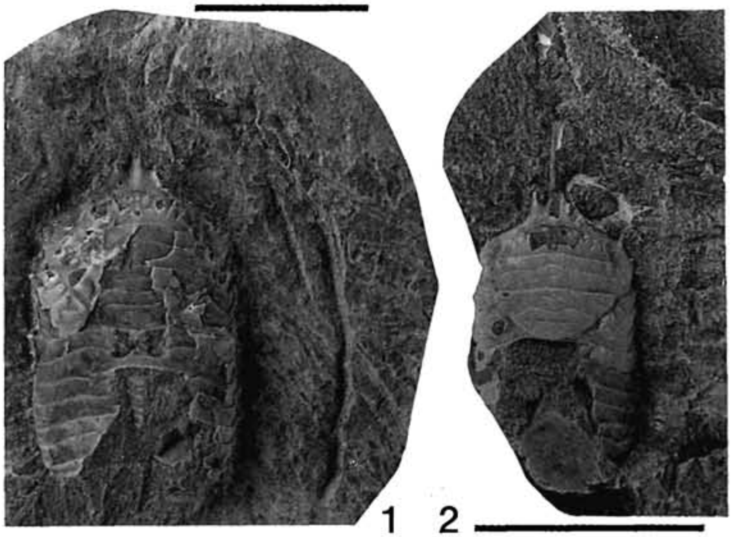

Fig. 5. *Munida quadroblonga* sp. nov. 1, dorsal view of carapace of holotype, USNM 490442. 2, dorsal view of paratype, USNM 490443. Scale bars equal to 1 cm.

supraorbital spines short, needle-like; three short anterolateral spines; several small posterolateral spines; cervical groove deep, smooth; anterior gastric spines linearly arranged transversely.

Etymology: The trivial name is derived from the Latin *"quadruus,"* meaning fourfold, and *"oblongus,"* meaning oblong, referring to the rectangular shape of the carapace.

Description: Carapace longer than wide, about 1.5 times as wide as long measured from base of longest rostral spine to position of posterior margin, narrowing slightly anteriorly; oblong in shape; ornamented with transverse ridges; smooth except along edges of transverse ridges which are lined with small granules; highly vaulted transversely and weakly vaulted longitudinally.

Rostrum long, at least one-quarter maximum carapace width including rostrum, slender, needle-like, extending onto anterior gastric area as smooth keel; long rostral spine flanked by smaller, needle-like supraorbital spines. Frontal margin with narrow rim; sloping posteriorly to terminate in small, sharp, needle-like anterolateral spine; frontal margin width about 85 percent maximum carapace width. Anterolateral margin with three small, needle-like spines; first spine largest, directed weakly anterolaterally; second and third spines directed anterolaterally. Lateral margin posterior to cervical groove with three or four small spines; spines extending from transverse carapace ridges, directed anterolaterally; remainder of lateral margin crenulate due to intersection of transverse ridges with carapace margin. Posterior margin not known.

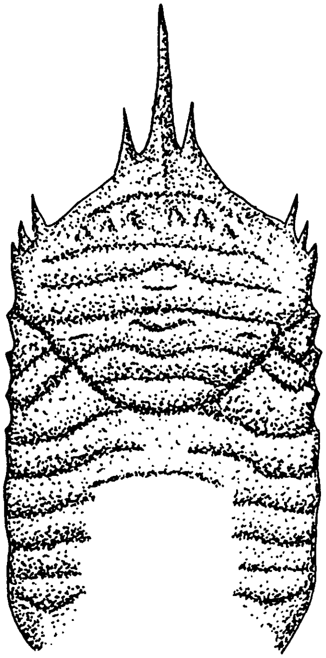

Fig. 6. Line drawing reconstruction of *Munida quadroblonga* sp. nov. showing details of definition of regions and ornamentation of dorsal carapace.

Cervical groove deep, smooth; concave forward; extending posteriorly on carapace from just posterior to last anterolateral spines and curving across axial region. Carapace regions moderately defined. Gastric region large; with several anterior gastric spines arranged in transverse linear array, spines directed forward; ornamented with about 5 transverse ridges extending entire width of region and sometimes alternating with short transverse ridges limited to axial area; ridges range from nearly straight to sinuous. Hepatic region not well-defined; ornamented with diffuse inflated areas and short, scabrous ridges. Metagastric region transversely elongate, weakly constricted axially, ornamented with a few transverse ridges. Cardiac region not known. Epibranchial region triangular, with several transverse ridges. Branchial regions elongate longitudinally, with several transverse ridges.

Venter and appendages unknown or insufficiently preserved to permit description.

Types: The holotype, USNM 490442, and paratype, USNM 490443, are deposited in the U. S. National Museum of Natural History, Washington, D. C.

Measurements: Measurements (in mm) taken on dorsal carapace of two specimens of taxon. USNM 490442 (holotype): maximum length (not including rostrum) > 16.8, maximum width = 11.3, frontal width measured between tips of first anterolateral spines = 9.6, length to cervical groove (not including rostrum) = 8.9. USNM 490443 (paratype): maximum length (not including rostrum) > 13.2, maximum width = 7.8, frontal width = 6.7, length to cervical groove (not including rostrum) = 6.2, length of rostrum = 4.3.

Occurrence: The two specimens referred to *Munida quadroblonga* were collected at RB33 of the locality register of Ross E. Berglund, Bainbridge Island, WA. Locality RB33 is located in the W1/2, N1/2, Sec. 4, T33N, R15W, Cape Flattery Quadrangle, 15 minute series, Clallam County, WA, near West Kydikabbit.

Discussion: *Munida quadroblonga* displays all of the typical characters of species of *Munida* and is therefore referred to the genus with confidence. *Munida quadroblonga* differs from *M. primaeva* because *M. primaeva* has more convex lateral margins, deeper grooves, better defined carapace regions, and more closely spaced transverse ridges than does *M. quadroblonga*. The axial keel of *M. primaeva* extends nearly to the cervical groove while that of *M. quadroblonga* extends from the rostrum to the anterior gastric region.

Munida konara sp. nov.

(Figs. 7.1, 7.2)

Diagnosis: Carapace cordate, with inflated branchial regions; transverse carapace ridges separated by deep furrows, ridge edges ornamented with large granules, ridges arranged parallel to one another anteriorly and becoming complex and bifurcating posteriorly; rostrum with three spines; anterolateral margin with three spines; cervical groove deeply incised, arcuate.

Etymology: The trivial name is derived from the Greek "*konaros*," meaning fat, referring to the inflated branchial regions.

Description: Carapace cordate in shape, about as wide as long; regions moderately well-defined; ornamented with transverse ridges, ridges relatively simple and parallel anteriorly and more complex and bifurcating posteriorly, edges of ridges ornamented with large granules, ridges high and separated by deep furrows; moderately vaulted transversely and weakly vaulted longitudinally.

Rostrum not well known, broad at base, appearing to have a pair of supraorbital and larger central rostral spine. Frontal margin appearing to be arcuate. Anterolateral margin with three spines; first spine small, directed forward; second spine long, needle-like, directed forward; third spine smallest, needle-like, directed forward. Lateral margins posterior to cervical groove with at least two small spines; convex; crenulated due to intersection of transverse ridges with lateral margins. Posterior margin concave, with granular rim.

Cervical groove very deep, arcuate, concave anteriorly. Protogastric regions ornamented with simple, parallel, transverse ridges; perhaps with several small anterior gastric spines arranged linearly anterior to first transverse ridge. Mesogastric region with long, narrow, poorly

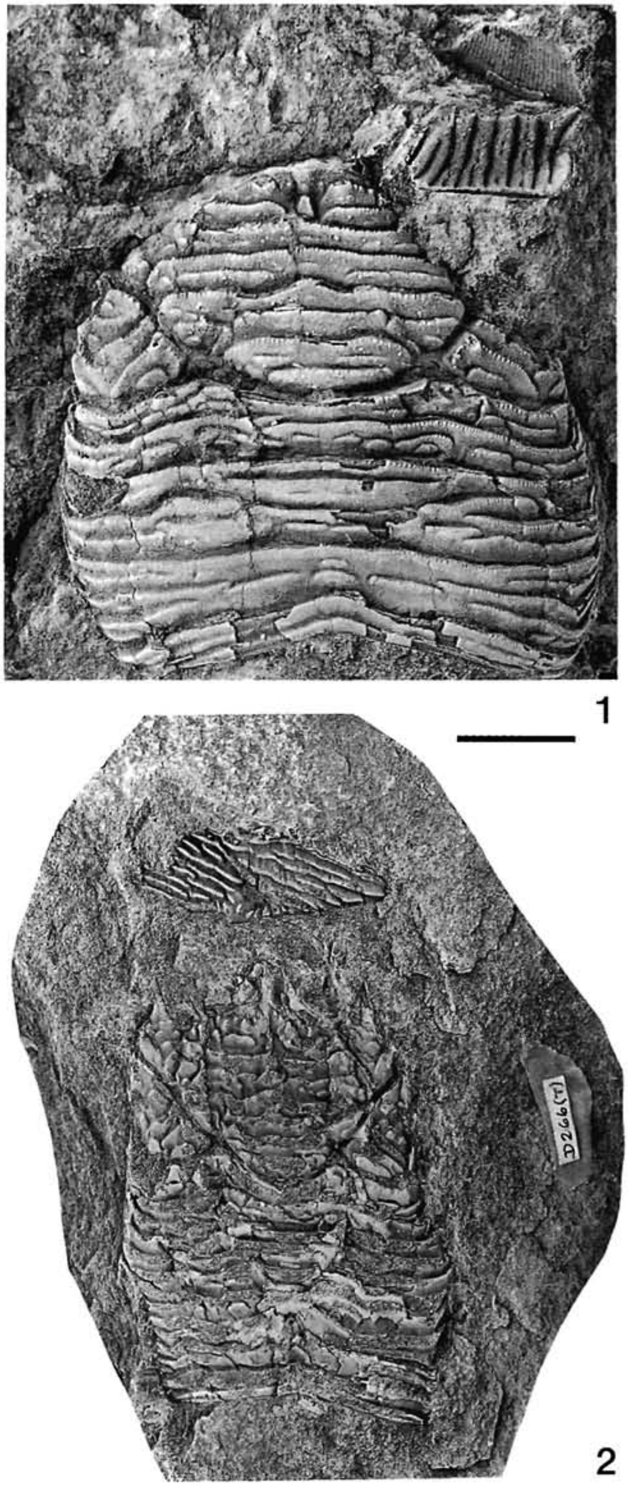

Fig. 7. *Munida konara* sp. nov. 1, dorsal view of carapace of holotype, UCMP 154104. 2, dorsal view of carapace of paratype, UCMP 154106. This specimen has been somewhat distorted by compaction or tectonism. Scale bar equal to 1 cm.

defined anterior process; anterior gastric spine near base of rostrum; posterior portion of region broad, with straight lateral margins and convex posterior margin; ornamented with transverse ridges. Metagastric region transversely elongate, weakly constricted centrally, bounded posteriorly by deep, smooth groove, ornamented with bifurcating transverse ridges. Cardiac region broadly triangular, apex directed posteriorly, ornamented with bifurcating ridges. Hepatic regions with short, oblique, scabrous ridges. Epibranchial regions triangular, with discontinuous transverse and oblique ridges, well defined by deep cervical and branchiocardiac grooves. Branchial regions broad, moderately inflated, ornamented with bifurcating transverse ridges.

Venter and appendages unknown.

Types: The holotype, UCMP 154104, and one paratype, UCMP 154105, collected from locality SM 134G-70, and three paratypes, UCMP 154106-154108, collected from locality D266(T), are deposited in the Museum of Paleontology, University of California at Berkeley, Berkeley, California.

Occurrence: The holotype, UCMP 154104, and one paratype, UCMP 154105, were collected at locality SM 134G-70 from rocks of the late Oligocene to early Miocene Poul Creek Formation, 492 feet above the base of the North Yakataga Ridge section, Secs. 2, 3, and 11, T21S, R14E, Bering Glacier (A-4) Quadrangle, Yakataga District, south-central Alaska, interpreted as having been deposited in an inner neritic, warm temperate environment (Scott McCoy, field notes for Phillips Petroleum, 1970). Three paratypes, UCMP 154106-154108, were collected at locality D266 (T) just south of Lituya Bay, Alaska, at Lat. 58° 36' North, Long. 137° 39' West. The locality is either in the late Miocene Yakataga Formation or the early to middle Miocene Topsy Formation, Lituya District, Gulf of Alaska Tertiary Province, Alaska.

Discussion: Five specimens of the new species have been recovered; one is well-preserved but only retains the posterior two-thirds of the carapace. Another retains most of the dorsal carapace but has been badly sheared, making it difficult to determine the original shape of the carapace. However, the presence of a rostrum and one pair of supraocular spines; a small number of anterolateral spines; a deeply incised, arcuate cervical groove; well-developed transverse ridges; and the apparent oblong shape of the carapace make it most prudent to assign the new taxon to *Munida* until better-preserved material is recovered. *Munida konara* differs from all other species in the fossil record because of its inflated branchial regions and very deeply incised furrows separating the transverse ridges.

Interestingly, the pattern of complexity of transverse ridges in *Munida konara* is similar to that observed in some species of the brachyuran genus *Lophoranina* Fabiani, 1910, of the Raninidae de Haan, 1841. Both *Munida* and *Lophoranina* display transverse ridges on the dorsal carapace. In some species of each genus, the ridges are simple and are arranged parallel to one another on the anterior portion of the dorsal carapace and become complex, bifurcating, and parallel or oblique on the posterior portion of the carapace. The transverse ridges of species of *Lophoranina* are ornamented with tiny spines that are directed forward (Beschin et al., 1988; Feldmann et al., 1996; Vega et al., in review), an adaptation that Feldmann et al. (1996) suggested served to anchor the carapace into debris or organic material in shallow marine settings. However, most galatheids are known to be pelagic, so the function of the transverse ridges in *Munida* is probably not analagous to their function in *Lophoranina*. The transverse ridges may be used to strengthen or streamline the carapace. Alternatively, transverse ridges are often the site of setal hair attachments as they are in albuneids (Glaessner, 1969) which may have been used for tactile purposes or stabilization in the water column.

Subfamily Munidopsinae Ortmann, 1898

Included solely fossil genera: *Faxegalathea* Jakobsen and Collins, 1997; *Gastrosacus* von Meyer, 1851 (= *Galatheites* Balss, 1913); *Munitheites* Lőrenthey in Lőrenthey and Beurlen, 1929; *Palaeomunidopsis* Van Straelen, 1924 [1925].

Included fossil and living genus: *Munidopsis* Whiteaves, 1874.

Diagnosis: Carapace widening distally; ornamented with short, discontinuous scabrous ridges or oblong nodes; rostrum needle-like, keeled, keel often extending onto anterior gastric region; lacking supraorbital spines; usually with smooth front but sometimes with frontal spine or projection; lateral margins with or without spines; gastric region circular; cardiac and branchial regions well-defined; cervical groove well-developed.

Discussion: The diagnosis above is derived in part upon the work of Chace (1942), Ambler (1980), and Baba (1988) and is based upon the sole Recent genus, *Munidopsis* which is highly variable and speciose. Attempts to subdivide *Munidopsis* into several genera or subgenera have generally failed (Chace, 1942); the species varies in carapace ornamentation, the development of the rostrum, the number and development of lateral spines, and the development of regions. The four fossil genera referred to the subfamily share the diagnostic characters listed above and are thus referred to it.

The Munidopsinae has a limited fossil record and occurrences of the subfamily range from the Jurassic to Recent. Glaessner (1969) listed no fossil genera of the Munidopsinae and referred four galatheoid genera to an uncertain subfamily. Since then, *Munidopsis* has been reported from the Cretaceous and Eocene rocks of Antarctica (Feldmann and Wilson, 1988; Feldmann et al., 1993), and two of Glaessner's (1969) uncertain taxa are herein referred to the Munidopsinae. Via Boada (1982) referred *Paragalathea, Eomunidopsis*, and *Gastrosacus* to the Munidopsinae based upon possession of a singular, triangular rostrum. We have referred *Paragalathea* and *Eomunidopsis* to the Galatheinae as discussed above. Van Straelen (1923) had previously suggested placing *Gastrosacus* within the Munidopsinae. *Gastrosacus* is characterized by possession of a circular gastric region, well-developed branchial and cardiac regions, and a singular rostrum and absence of transverse ornamentation; thus, it is referred to the Munidopsinae. *Munitheites* has a circular gastric region and lacks transverse ornamentation and is therefore referrable to the Munidopsinae. *Palaeomunidopsis* is poorly illustrated but has a singular rostrum, a deeply incised cervical groove, and a circular gastric region; therefore, it is referred herein to the Munidopsinae. *Faxegalathea* is an unusual form, but the singular rostrum, trapezoidal shape, small anterolateral spines, circular gastric region, and lack of transverse ornamentation suggest that it is most closely allied with the Munidopsinae. However, the nodose ornamentation and swollen protogastric regions of that genus suggest that an alternative placement may be possible in the future.

The Munidopsinae appear to have evolved in the region of Europe and the Tethys during the Jurassic. The subfamily apparently then dispersed to the southern hemisphere by the Cretaceous, as documented by Cretaceous and Eocene occurrences in Antarctica and the Eocene occurrence of the new genus described below in Patagonia. *Munidopsis* has a cosmopolitan distribution in modern oceans (Baba, 1988). The subfamily would appear to be waning in that only *Munidopsis* has persisted to the present day.

Subfamily Shinkaiinae Baba and Williams, 1998

Included genus: *Shinkaia* Baba and Williams, 1998.

Diagnosis: "Carapace slightly convex, without grooves on dorsal surface, lateral margins smoothly convex, slightly upturned and bearing many forward trending spines in adults." (Baba and Williams, 1998, p. 148).

Discussion: Baba and Williams (1998) erected the monotypic subfamily Shinkaiinae to accommodate their new genus *Shinkaia* which they reported to be similar to *Munidopsis*, but sufficiently different to require its own subfamily. There are no known members of the Shinkaiinae in the fossil record.

Family Chirostylidae Ortmann, 1892

Included solely fossil genus: *Pristinaspina* gen. nov. Schweitzer and Feldmann, herein.

Included fossil and living genus: *Eumunida* Smith, 1883.

Included solely extant genera: *Chirostylus* Ortmann, 1892; *Gastroptychus* Caullery, 1896; *Pseudomunida* Haig, 1979; *Uroptychus* Henderson, 1888.

Discussion: The Chirostylidae has heretofore been unknown from the fossil record. Recent members of the family are generally tiny commensals with octocorallian corals in deep-water settings (Baba, 1973). Members of the family superficially resemble the Galatheidae but are differentiated based upon characters of the sternum and antennae. These features are rarely preserved in fossils. All chirostylids are united in lacking the last thoracic somite and having an antennal peduncle with five segments and an antennal scale (Baba, 1989). Additionally, members of the family possess a triangular carapace which achieves maximum width about three-quarters the distance posteriorly on the carapace and a narrow frontal area that rapidly diverges posteriorly. However, genera within the Chirostylidae display one of two different carapace forms. Some genera, including *Chirostylus, Uroptychus*, and *Gastroptychus*, exhibit relatively smooth carapaces, few lateral spines, a simple rostrum with no supraocular spines, and a narrow frontal area that diverges posteriorly. Members of *Eumunida* and *Pseudomunida* are characterized by transverse ridges on the dorsal carapace, a rostrum with one or two pairs of supraocular spines, numerous lateral spines, and several delineated carapace grooves and regions. The new genus to be described below is clearly allied with *Eumunida* and *Pseudomunida* in possessing a rostrum with one pair of supraocular spines, numerous lateral spines, and several well-defined carapace regions. It also displays the general characteristics of the dorsal carapace of members of the family.

Two previously described fossil species are referrable to *Eumunida*. Müller and Collins (1991) described *Protomunida pentacantha* from Eocene coral-rich rocks of Hungary. The species was described as possessing five rostral spines, differentiating it from other species of *Protomunida*. In fact, the species is referrable to *Eumunida*, the only galatheoid genus characterized by five frontal spines (a rostrum and two pairs of supraorbital spines). The association of the fossils with corals indicates that the chirostylid commensal relationship with corals may have begun at least as early as the Eocene. Karasawa (1993) described *Munida nishioi* from Miocene rocks of Japan, a taxon which Imaizumi (1971) had questionably referred to *Eumunida*. Kato (1996) illustrated material he tentatively referred to *M. nishioi*; however, the rostrum was missing on that specimen also. *Munida nishioi* displays well-developed regions, numerous lateral spines, and a carapace that is widest about three-quarters the distance posteriorly, all typical of *Eumunida*. The front is missing, making it impossible to determine whether it possessed a rostrum and two pairs of supraorbital spines, diagnostic for *Eumunida*. Because species of *Munida* do not have well-developed carapace regions, lack numerous lateral spines, and have a rectangular carapace, *Munida nishioi* is best referred to *Eumunida*.

Eumunida is cosmopolitan in Recent oceans, but seems to be most speciose in the Indo-Pacific region. The Eocene appearance of *Eumunida* in the Tethyan region of Europe followed by a Miocene occurrence in Japan suggests that the genus arose in the Tethys and dispersed eastward through the Tethys to the Indo-Pacific.

The reassignment of two species of *Eumunida* and recognition of the new genus to be described below constitute the first notices of the Chirostylidae in the fossil record. The geological range of the family is herein extended into the Cretaceous, which is not surprising because the range of the closely related Galatheidae extends into the Jurassic (Glaessner, 1969). The dimpled carapace surface and the well-developed carapace grooves and regions of the new genus from the Cretaceous of Alaska suggest that these characters may be primitive within the family. Additionally, the Cretaceous specimens were not associated with corals but were recovered from siliciclastic deposits. This suggests that the family was originally composed of free-living animals, such as those that comprise the Galatheidae, and that the development of commensal relationships may have been a geologically younger event.

Genus *Pristinaspina* gen. nov.

Type species: *Pristinaspina gelasina* sp. nov., original designation.

Diagnosis: As for species.

Etymology: The generic name is derived from the Latin roots "*pristinus*," meaning early or primitive, and "*spina*," meaning thorn, in reference to the Cretaceous occurrence of the genus and the spiny carapace margins.

Discussion: The new genus is referrable to the Chirostylidae as discussed above. It superficially resembles members of the Galatheidae but may be differentiated from members of that family. Members of the Galatheinae are typified by a carapace with transverse ridges, poorly delineated carapace regions, few carapace grooves, a rectangular carapace that achieves its maximum width about half the distance posteriorly on the carapace or maintains a uniform width along the entire length of the carapace, a simple rostrum sometimes with one pair of supraocular spines, and a frontal margin that is nearly straight transversely or diverges weakly posteriorly. The Munidopsinae are characterized by a simple rostrum with no supraocular spines, weakly developed and often discontinuous transverse ridges, a rectangular or trapezoidal carapace, a straight front, and few lateral spines. Members of the Shinkaiinae exhibit a smooth carapace without well-developed carapace grooves and upturned lateral margins. Based upon the characters listed for it above, the new genus is not referrable to any of the subfamilies of the Galatheidae.

Pristinaspina is most similar to *Eumunida* and *Pseudomunida* but differs from those genera in several ways. All three genera have several well-delineated carapace regions, including protogastric, mesogastric, metagastric, hepatic, branchial, and cardiac regions, differentiating them from all other galatheoid taxa. The development of the carapace regions varies among the three genera; the regions are best delineated in the new genus and most poorly delineated in *Pseudomunida*. Both *Eumunida* and *Pseudomunida* have transverse ridges on the dorsal carapace while *Pristinaspina* has a dimpled carapace surface. The new genus has a narrow keel extending from the anterior gastric region onto the rostrum, which *Eumunida* and *Pseudomunida* lack. The rostrum and postocular spines are needle-like in *Eumunida* and *Pseudomunida* but are flattened in *Pristinaspina*. The posterior margin of *Pristinaspina* is nearly straight while those of *Eumunida* and *Pseudomunida* are concave. Based upon these numerous differences, the designation of a new genus seems well-justified; however, the numerous similarities clearly indicate that the new material is referrable to the Chirostylidae.

The earliest occurrence of the Chirostylidae along the North Pacific Rim suggests that the family may in fact have evolved in that region, a pattern documented for other decapod families and subfamilies (Schweitzer, in revision). The occurrence in the Cretaceous contributions to the growing number of families whose origin seems to be at least as early as the Cretaceous.

Pristinaspina gelasina sp. nov.

(Figs. 8, 9)

Diagnosis: Carapace longer than wide, widest about two-thirds the distance anteriorly on carapace; surface dimpled, dimples most pronounced posteriorly; rostrum long, triangular, flattened; postocular spines triangular, attenuated, narrower than rostrum; lateral margins with six forward-directed spines; carapace regions well-defined by grooves; carapace grooves well-developed, cervical and branchiocardiac grooves prominent.

Etymology: The trivial name is derived from the Latin word "*gelasinus*," meaning dimple, in reference to the dimpling on the dorsal carapace.

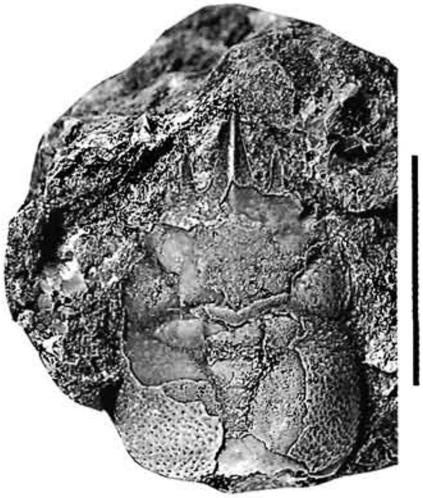

Fig. 8. Dorsal view of carapace of *Pristinaspina gelasina* gen. et sp. nov., holotype UAM-2571. Scale bar equal to 1 cm.

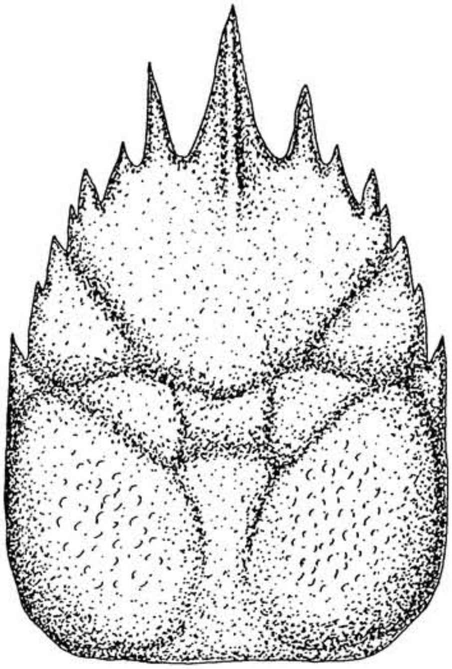

Fig. 9. Line drawing reconstruction of *Pristinaspina gelasina* gen. et sp. nov. showing details of definition of regions and ornamentation of dorsal carapace

Description: Carapace small, longer than wide, widest about two-thirds the distance posteriorly on carapace; surface dimpled; moderately vaulted transversely and weakly vaulted longitudinally.

Rostrum two-thirds as wide as long, triangular, acute, medial keel extending onto carapace. Postocular spines triangular, attenuated, narrower than rostrum, about half as long as rostrum. Lateral margins with six spines; first spine at base of postocular spines, directed forward, triangular; second spine long, needle-like, with third spine at its base, second and third spines directed forward; fourth and fifth spines small, triangular, directed forward; sixth spine needle-like, attenuated, directed weakly anterolaterally, positioned at about midlength. Remainder of lateral margins smooth, with broad, flat rim. Posterior margin appearing to be nearly straight.

Gastric and hepatic regions not well differentiated, dimpled. Metagastric region quadrate, upper margin concave, lower margin weakly concave, lateral margins concave. Cardiac region much longer than wide; triangular, apex directed posteriorly; merging posteriorly with ill-defined intestinal region. Epibranchial region wedge-shaped, surface dimpled. Cervical groove well-defined, extending adaxially from margin from between third and fourth lateral spines, extending posteriorly along margins of metagastric region, becoming shallow and less distinct across axial regions. Branchiocardiac groove distinct, curving arcuately from margin just anterior to sixth lateral spine to posterior margin. Mesobranchial region triangular, situated on either side of metagastric region. Metabranchial region large, dimpled, inflated, bordered by well-developed, flattened rim.

Types: The holotype, UAM-2571, and two paratypes UAM-2572 and UAM-2573, are deposited in the University of Alaska Museum, Fairbanks, Alaska.

Measurements: Measurements taken on UAM-2571: maximum width = 10.6; maximum length = 16.7; length excluding rostrum = 12.8.

Occurrence: The specimens were collected as talus, probably from the Cretaceous Matanuska Formation, which is part of the Peninsular Terrane of the Wrangellia composite terrane, south central Alaska (Plafker and Berg, 1994). The field position of the talus indicates that it could be Cenomanian to Maastrichtian in age (R. Gangloff, pers. commun.). The Matanuska Formation is composed of gray marine siltstone, sandstone, claystone, and small amounts of conglomerate deposited in a forearc apron (Nokleberg, Plafker, and Wilson, 1994). Wrangellia was emplaced against North America by the middle Cretaceous, and perhaps as early as the middle Jurassic (Plafker and Berg, 1994), so the deposits of the Matanuska Formation were most likely deposited at the latitude at which they are now found. Thus, paleobiogeographic interpretations utilizing the occurrence of *Pristinaspina gelasina* at its collection locations are most likely valid.

Discussion: The specimens are preserved in silty shale and are associated with ghost shrimp fossils. Most of the decapod occurrences in the Pacific Northwest of North America are in deep water, continental slope deposits (Feldmann, Tucker, and Berglund, 1991; Tucker, 1998; Schweitzer and Feldmann, 1999), and the environment for *Pristinaspina gelasina* appears to be no exception. The occurrence of ghost shrimp in slope deposits is unusual, because most modern members live in intertidal or other near-shore environments. However, the ghost shrimp genus, *Callianopsis* de Saint Laurent, is known from continental slope settings in the fossil record and in Recent oceans (Schweitzer Hopkins and Feldmann, 1997). This genus, as well as numerous other callianassid taxa (Rathbun, 1926) are known from rocks well-constrained as having been deposited in continental slope settings on the Pacific Coast of North America (Schweitzer and Feldmann, 1999; Tucker, 1998). It is not known if the ghost shrimp occurrences are autocthonous or if they were transported to slope environments after death; however, the occurrence of the Recent *Callianopsis goniophthalma* in deep waters of coastal Alaska suggests that some may prefer deep water habitats.

Acknowledgments

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Appendix. Key to the genera of the Galatheoidea known from the fossil record. G = Galatheinae, M = Munidopsinae, C = Chirostylidae.

1. Carapace with transverse ridges ············ 2
1.' Carapace without transverse ridges but may have other ornamentation ············ 11
2. Carapace with rostrum and no supraorbital spines ············ 3
2.' Carapace with rostrum and 1 or 2 pairs of supraorbital spines ············ 9
3. Epibranchial regions not well-defined ············ 4
3.' Epibranchial regions well-defined ············ 5
4. Rostrum very broad, short, sulcate, with tridentate tip ············ *Paragalathea* (G)
4.' Rostrum smooth laterally ············ *Mesogalathea* (G)
5. Rostrum long, slender, needle-like ······ *Austromunida* (G)
5.' Rostrum not as above ············ 6
6. Rostrum without medial carina, laterally smooth or serrate, termination simple ············ 7
6.' Rostrum with medial carina, laterally spined or serrate, termination tridentate ············ 8
7. Rostrum laterally dentate or serrate ············ *Galathea* (G)
7.' Rostrum laterally smooth ············ *Luisogalathea* (G)
8. Rostrum with spined lateral margins ···*Palaeomunida* (G)

8.' Rostrum with smooth lateral margins ··· *Eomunidopsis* (M)

9. Carapace with two pairs supraorbital spines ··· *Eumunida* (C)

9.' Carapace with one pair supraorbital spines ··· 10

10. Anterior gastric spines well-developed, no swellings at base of rostrum ··· *Munida* (G)

10.' Anterior gastric spines lacking, pair of swellings at base of rostrum ··· *Protomunida* (G)

11. Rostrum singular, no supraorbital spines ··· 12

11.' 1 pair supraorbital spines ··· 15

12. Carapace without large gastric swellings ··· *Munidopsis* (M)

12.' Carapace with large gastric swellings ··· 13

13. Two pairs frontal spines and large, circular epigastric swellings ··· *Munitheites* (M)

13.' Frontal spines absent, entire gastric area swollen ··· 14

14. Gastric region circular, branchiocardiac groove well-developed ··· *Gastrosacus* (M)

14.' Gastric region not circular, branchiocardiac groove poorly developed ··· *Palaeomunidopsis* (M)

15. Carapace with large nodes, supraorbital spines projecting obliquely from base of rostrum ··· *Faxegalathea* (M)

15.' Carapace with dimples, supraorbital spines parallel and distinct from rostral base ··· *Pristinaspina* (C)