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Systematics of 12 Jurassic, Cretaceous, and Paleogene squat lobster taxa (Galatheoidea)

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Abstract.—Squat lobsters within Galatheoidea are very diverse with over 1,300 extant species that live in all marine ecosystems, but their fossil record, starting in the Middle Jurassic, consists of only ~200 species. Consequently, much remains to be learned about their biodiversity, phylogeny, and paleobiogeography. We describe five new species (*Galatheites sforum* n. sp., Kimmeridgian, Late Jurassic, Germany; *Vasconilia zapotitlanensis* n. sp., Barremian, Early Cretaceous, Mexico; *Eomunidopsis texcalaensis* n. sp., Barremian, Early Cretaceous, Mexico; *Protomunida benickei* n. sp., Danian, Paleocene, Denmark; and *Protomunida eurekantha* n. sp., Danian, Paleocene, Denmark) and one new genus (*Tethysgalathea* n. gen., Ypresian, Eocene, Italy). We further reassign *Munida cretacea* (Albian, Early Cretaceous, Texas, USA) to *Galathea?*, return *Eomunidopsis? cobbani* (Campanian, Late Cretaceous, Colorado, USA) to its original genus, report on the second occurrence of *Vetoplautus latimarginus* Robins et al., 2013 (Tithonian, Late Jurassic, Czech Republic), and reinstate *Palaeomunidopsis moutieri* (middle Bathonian, Middle Jurassic, France) as the oldest galatheoid known to date. The five new species, all found in limestones containing corals, increase galatheoid diversity in the fossil record by 2.5%. Finally, the common yet hitherto unrecognized *Protomunida eurekantha* was discovered by making casts of external molds, revealing distinct spines on the posterior margin that are more difficult to see in internal molds and specimens with cuticle due to breakage. Collecting and studying the external molds for galatheoids and other fossil decapods could yield additional cryptic species.

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Introduction

Galatheoidea and Chirostyloidea are, together, known as squat lobsters (e.g., Schnabel, 2020). Galatheoidea is the most diverse clade of squat lobsters in modern oceans, consisting of over 1,300 species (e.g., Baba, 2005; Baba et al., 2009; Macpherson and Robainas-Barcia, 2015; Rodríguez-Flores et al., 2019, 2021; WoRMS, 2021), comprising Galatheidae (259 species), Munidae (470 species), Munidopsidae (301 species), and Porcellanidae (305 species). From the fossil record, two additional families are known from the Mesozoic, Paragalatheidae and Catillogalatheidae (Robins et al., 2016). The number of fossil Galatheoidea is limited (~200 species) compared with today, but it has grown substantially during the past 20 years (e.g., De Angeli and Garassino, 2002; Klompmaker et al., 2012; Robins et al., 2013, 2016; Nyborg and Garassino, 2015; Beschin et al., 2016, 2019; Robins and Klompmaker, 2019), with most occurrences found in reef deposits from Europe.

The sparse fossil record of Galatheoidea suggests many more species remain to be discovered. New taxa and records

will help to advance the study of their phylogenetic relationships, paleobiogeography, biodiversity, and environmental preferences now and in the future. To this end, we here describe and reassess 12 Mesozoic to early Cenozoic taxa.

Materials and methods

The studied material comprises 78 specimens from various Jurassic, Cretaceous, and Paleogene localities in Europe and North America. Most specimens (64) originate from the Paleocene (Danian) of Denmark. For specifics per taxon, referral is made to the materials sections for each taxon. The specimens were prepared by using air scribes (Compressed Air Hammer HW 70 and PaleoTools) to remove the matrix around the specimens as needed. For some of the Danish material, a casting technique was used to obtain morphological details that could not be seen easily on internal molds. Low-viscose silicone rubber (Silastic RTV 9161) was put into external molds in a vacuum environment for about a minute, after which the casts were pulled from the external mold. We have indicated when casts were used.

For the higher classification of fossil galatheoid taxa, Robins et al. (2012, 2013, 2016) was followed. For muscle

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scar and pit terminology, we used Klompmaker et al. (2019, figs. 13 and 14).

Repositories and institutional abbreviations.—Type, figured, and other specimens examined in this study are deposited in the following institutions: Non-vertebrate Paleontology lab, Jackson School Museum of Earth History, University of Texas at Austin, Austin, Texas, USA (BEG/NPL); Colección Nacional de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México, Mexico City, Mexico (IGM); Natural History Museum of Denmark, Type and Illustrated Paleontology Collection, Copenhagen, Denmark (MMH); Naturhistorisches Museum Wien, Vienna, Austria (NHMW); Geomuseum Faxe, Faxe, Denmark (OESM); Staatliche Naturwissenschaftliche Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany (SNSB-BSPG); Florida Museum of Natural History (Invertebrate Paleontology), University of Florida, Gainesville, Florida, USA (UF); Smithsonian National Museum of Natural History, Washington, D.C., USA (USNM); Museo di Storia Naturale di Verona, Verona, Italy (VR).

Systematic paleontology

Superfamily Galattheoidea Samouelle, 1819
Family Catillogalatheidae Robins et al., 2016
Genus *Galatheites* Balss, 1913

Type species.—*Galathea zitteli* Moericke, 1889 (Late Jurassic [Tithonian]; Austria, Poland, Czech Republic), by original designation.

Other species.—*Galatheites aiola* Robins et al., 2016 (Late Jurassic [Tithonian]; Austria, Czech Republic); *Galatheites diasema* Robins et al., 2016 (Late Jurassic [Tithonian]; Austria); *Galatheites britmelanarum* Robins and Klompmaker,

2019 (Late Jurassic [Tithonian]; Austria); *Galatheites obtecta* Robins et al., 2016 (Late Jurassic [Tithonian]; Romania); *Galatheites? royo* Van Straelen, 1927 (Early Cretaceous [Aptian]; Spain); *Galatheites sforum* new species (Late Jurassic [Kimmeridgian]; Germany)

Galatheites sforum new species

Figure 1

Types.—Holotype: SNSB-BSPG 2014 I 49a; paratypes: SNSB-BSPG 2014 I 48 and SNSB-BSPG 2014 I 49b.

Diagnosis.—Carapace excluding rostrum about 10–20% longer than maximum width; widening posteriorly, maximum width in posterior third of carapace. Rostrum slightly downturned, moderately wide at base, 20–25% of maximum carapace length including rostrum, with axial keel; narrowing anteriorly and ending in three spines, middle spine longest. Cervical groove strong, U-shaped; curves transversely near lateral margin. Ornamentation consists of strong tubercles on anterior carapace and transversely elongated ovate tubercles to ridges on posterior carapace on internal mold.

Occurrence.—Saal near Kelheim, Germany (48.89°N, 11.94°E); coral limestone of the Massenkalk Formation, Upper Jurassic, upper Kimmeridgian: *Hybonoticerias beckeri* Zone, *Sutneria subeumela* or *Virgataxioceras setatum* subzones.

Description.—Carapace excluding rostrum about 10–20% longer than maximum width; weakly convex longitudinally, moderately convex transversely; widening posteriorly, maximum width in posterior third of carapace; lateral margins not rimmed. Rostrum slightly downturned, moderately wide at base, 20–25% of maximum length including rostrum, with axial keel; narrowing anteriorly and ending in three spines, middle spine longest; margins flared up somewhat; tubercles

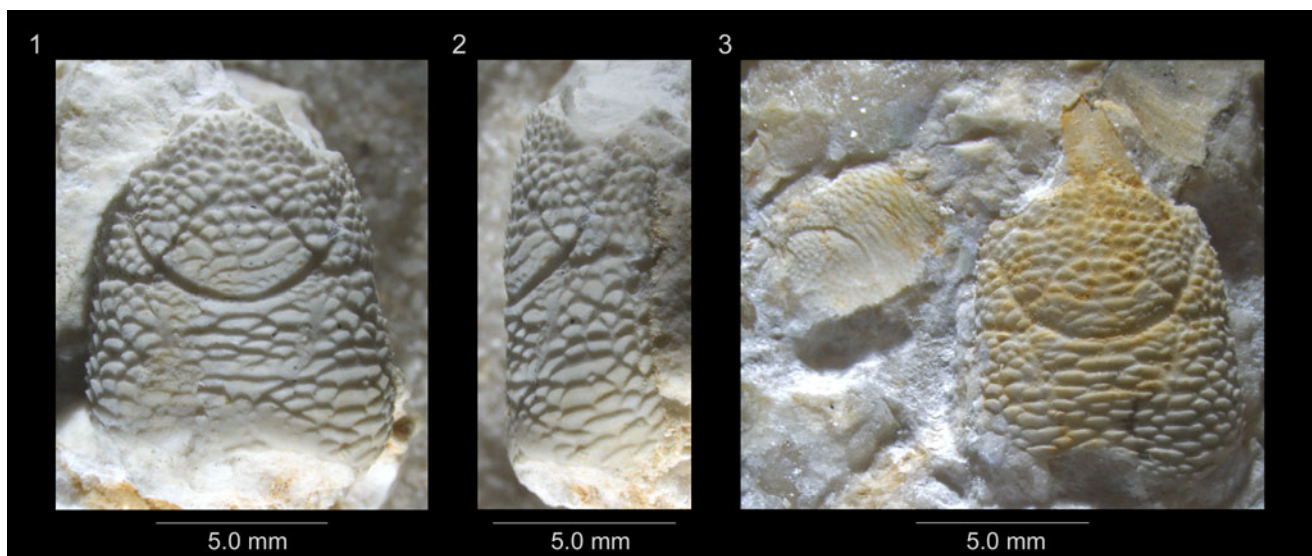


Figure 1. *Galatheites sforum* n. sp. from the Upper Jurassic (upper Kimmeridgian) Massenkalk Formation of Germany. (1, 2) Paratype SNSB-BSPG 2014 I 48, carapace: (1) dorsal view; (2) right lateral view. (3) Holotype SNSB-BSPG 2014 I 49a, carapace (right) in dorsal view, paratype SNSB-BSPG 2014 I 49b, carapace (left) in oblique view.

at base. Upper orbital margin directed forward, concave. Epigastric regions distinctly bordered anteriorly by inverse V-shaped rim with axial indent. Hepatic region small. Anterior part of gastric region with weak groove perpendicular to lateral margins and row of tubercles posterior to it. Mesogastric region well defined at posterior border, moderately so on lateral sides and at process. Cervical groove strong, U-shaped but curves transversely near lateral margin. Groove branching off cervical groove near posterolateral edges of mesogastric region laterally oriented, strong. Anterior branchial region triangular in dorsal view; posterior branchial region not subdivided. Cardiac region triangular, poorly defined anteriorly and posteriorly, with weak obliquely oriented lateral groove extending to groove branching off cervical groove. Intestinal region not defined by grooves, bears less ornamentation. Lateral margins ornamented with tubercles; spines do not appear to be present. Posterior margin rimmed, concave. Ornamentation consists of strong tubercles on anterior carapace and ovate tubercles to ridges on posterior carapace on internal mold. Ventral surface, abdomen, appendages, cuticle, and muscle scars unknown.

Etymology.—*sforum* is referring to the decapod paleontology team from Kent State University, Carrie Schweitzer (s) and Rodney Feldmann (f), for their enormous contributions to the taxonomy and systematics of fossil Decapoda in >150 joint scientific papers.

Measurements.—Holotype SNSB-BSPG 2014 I 49a: length excluding rostrum (L) = ~8.9 mm, maximum width (W) = 7.8 mm; paratype SNSB-BSPG 2014 I 48: L = 10.2 mm, W = 8.7 mm; paratype SNSB-BSPG 2014 I 49b: L = ~5.2 mm, W = ~4.4 mm.

Remarks.—Intraspecific variation appears limited, but only three specimens are known. We cannot determine the degree of ontogenetic variation with only a single, incomplete smaller specimen available.

Compared with the type species, *G. zitteli*, the new species exhibits coarser ornamentation in general. The elongated ornamentation on the cardiac region, the middle part of the mesogastric region, and the lateral parts of the branchial region in dorsal

view is more interrupted in *G. sforum* n. sp. Relative to *G. aiola*, *Galathea sforum* has a more U-shaped cervical groove, the transverse groove in the gastric region is less obvious, and it bears coarser ornamentation. The new species is close to *G. britmelanarum*, but the ornamentation of the new species is coarser, and more elongated ridges are present at the base of the mesogastric region and in the posterior carapace. The ornamentation of the new species is coarser and has diverging lateral margins toward the posterior carapace, whereas it is straight in *G. diasema*. Also compared with *G. obtecta*, the ornamentation of the new species is coarser. In addition, the lateral margins of the rostrum are straight, but they are slightly concave in *G. obtecta*. The ornamentation is weaker in *G. ? royoi*. The use of ornamentation to differentiate this new species from congeners is warranted because ornamentation shows limited intraspecific variation in general and does not differ substantially depending on the presence or absence of cuticle in galatheaids (e.g., Klompmaker et al., 2012; Robins et al., 2016).

Genus *Vasconilia* Robins et al., 2016

Type species.—*Vasconilia ruizi* (Van Straelen, 1940) (Early Cretaceous [Albian]; Spain), as *Galathea*, by original designation.

Other species.—*Vasconilia? miyakoensis* (Takeda and Fujiyama, 1983) (Early Cretaceous [Aptian]; Japan), as *Paragalathea*; *Vasconilia straeleni* (Ruiz de Gaona, 1943; = *Galathea alsuasensis* Van Straelen, 1944) (Early Cretaceous [Albian]; Spain), as *Paragalathea*; *Vasconilia xystosa* Robins et al., 2016 (Late Jurassic [Tithonian]; Austria); *Vasconilia zapotitlanensis* n. sp. (Early Cretaceous [Barremian]; Mexico)

Vasconilia zapotitlanensis new species

Figure 2

2019 *Paragalathea ruizi* (Van Straelen, 1940); Vega et al., p. 3, fig. 4.1–4.6.

Types.—Holotype: IGM-11373; paratype: IGM-11372.

Diagnosis.—Carapace excluding rostrum about as wide as long; moderately convex longitudinally, strongly convex transversely;

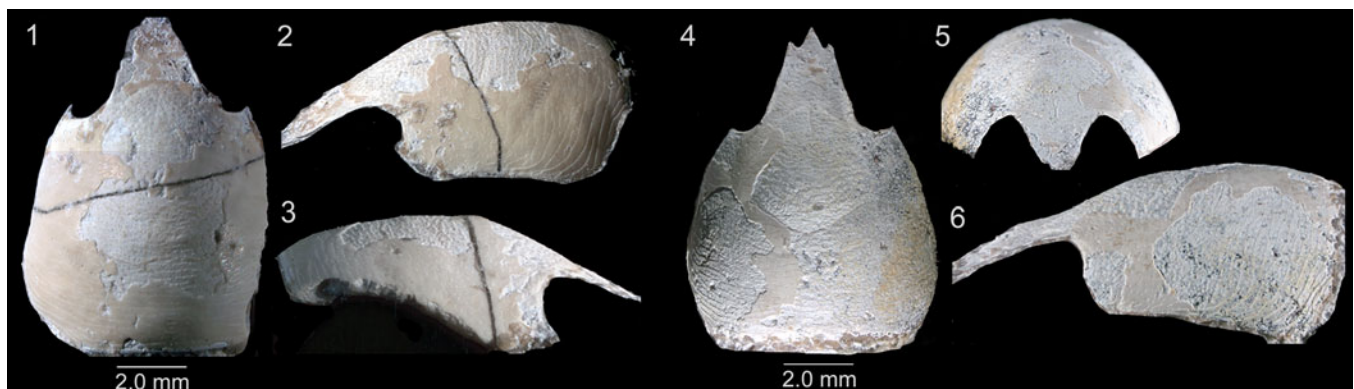


Figure 2. *Vasconilia zapotitlanensis* n. sp. from the Lower Cretaceous (upper Barremian) Zapotitlán Formation of Mexico. (1–3) Holotype IGM-11373, carapace: (1) dorsal view; (2) left lateral view; (3) right lateral view. (4–6) Paratype IGM-11372, carapace: (4) dorsal view; (5) frontal view; (6) left lateral view. Specimen images from Vega et al. (2019, fig. 4.1–4.6), reproduced with permission.

widening posteriorly. Rostrum downturned, moderately wide at base, narrowing anteriorly and ending in three spines. Cervical groove shallow, widely V-shaped but rounded at axis; no groove branching off cervical groove. Ornamentation consists of small tubercles on anterior carapace and long ridges on posterior carapace.

Occurrence.—El Ojito section, ~3 km NW of San Antonio Texcala, Puebla, Mexico (18.418°N, 97.459°W); coral limestone of the Zapotitlán Formation, Lower Cretaceous (upper Barremian).

Description.—Carapace excluding rostrum about as wide as long; moderately convex longitudinally, strongly convex transversely; widening posteriorly, maximum width in posterior third of carapace; lateral margins not rimmed. Rostrum downturned, moderately wide at base, approximately 25% of maximum length including rostrum; narrowing anteriorly and ending in three spines, middle spine longest; rostral surface appears flat. Upper orbital margin directed forward and concave, with possible spine at outer orbital margin. Epigastric regions distinctly bordered anteriorly by inverse V-shaped rim. Protogastric, hepatic, and mesogastric regions not delimited, except for tip of mesogastric process. Cervical groove shallow, widely V-shaped but rounded at axis, appears to disappear at lateral third of dorsal carapace; no groove branching off cervical groove. Branchial, cardiac, and intestinal regions not clearly defined. Posterior margin nearly straight, may be rimmed. Ornamentation consists of small tubercles on anterior carapace and long ridges on posterior carapace that bend forward on flanks, on both cuticular layers visible. Muscle scar impressions may be discernable at base of mesogastric region (posterior gastric muscles) and adjacent to approximate position of cardiac region. Ventral surface, abdomen, and appendages unknown.

Etymology.—Named after the Zapotitlán Formation, in which specimens were found.

Measurements.—Holotype IGM-11373: L = 8.0 mm, W = 8.0 mm; paratype IGM-11372: L = –, W = 7.8 mm.

Remarks.—Although *Paragalathea ruizi* was assigned as the type species of *Vasconilia* by Robins et al. (2016), Vega et al. (2019) assigned two specimens to *P. ruizi*. The specimens from Mexico are separated geographically from the specimens from Spain by ~9,000 km today. In addition, a long temporal gap exists between the late Albian specimens from Spain and the late Barremian specimens from Mexico (ca. 25 million years). Although long stratigraphic ranges have been reported for fossil decapods (see Klompmaker et al., 2012, p. 792–793, for references), such ranges are rare. Above all, the specimens differ morphologically from *Vasconilia ruizi* in that the carapace of the new species widens much more toward the posterior carapace, the rostrum is more downturned, and the flanks appear to be longer, giving the carapace a more convex appearance transversally. The latter characters are similar to *Mesogalathea* Houša, 1963 (see Robins et al., 2016, fig. 5), but the anterior carapace with the anterior portion of the

epigastric regions and the tip of the mesogastric region clearly defined, in addition to the narrower rostrum, suggest this species does not fit *Mesogalathea*.

Compared with *V.?* *miyakoensis*, *Vasconilia zapotitlanensis* n. sp. does not possess a groove branching off the cervical groove and is wider posteriorly. *Vasconilia straeleni* bears more-distinct tubercles on the anterior carapace and has a higher length–width ratio (~1.15 [see Vía Boada, 1982; Klompmaker et al., 2012; Robins et al., 2016] versus ~1.00 for IGM-11372). *Vasconilia xystosa* does not exhibit transverse ridges on the posterior carapace as in the new species, and the cervical groove appears less V-shaped axially. The use of ornamentation to differentiate species can be problematic for brachyurans as the cuticular layers and internal mold may show different ornamentation (summarized by Klompmaker et al., 2015), but this possible issue does not appear to exist for galatheoids (summarized by Robins et al., 2016).

The two specimens are nearly identical, but the paratype does not show an equally expressed cervical groove as seen in the holotype, although it is present (Vega et al., 2019, fig. 4.1, right of axis). Whether this is a matter of preservation or intra-specific variation cannot be determined at this stage.

Muscle scars are not often reported for squat lobsters, but some have been recorded at the base of the mesogastric region (Klompmaker et al., 2019). Such posterior gastric muscle scars are also present in the new species, but another set lateral to the approximate position of the cardiac region (branchial muscles, see Figure 2.2) has not been recorded in the literature from fossil galatheoids thus far.

Family Galatheidae Samouelle, 1819

Included genera (*F* = fossil, *R* = recent).—*Acanthogalathea* Müller and Collins, 1991 (F); *Alainius* Baba, 1991 (R); *Allogalathea* Baba, 1969 (R); *Allomunida* Baba, 1988 (R); *Bolcagalathea* Beschin et al., 2016 (F); *Coralliogalathea* Baba and Javed, 1974 (R); *Eomunidopsis* Vía Boada, 1981 (F); *Fennerogalathea* Baba, 1988 (R); *Galathea* Fabricius, 1793 (F, R); *Janetogalathea* Baba and Wicksten, 1997 (R); *Lauriea* Baba, 1971 (R); *Lessinigalathea* De Angeli and Garassino, 2002 (F); *Luisogalathea* Karasawa and Hayakawa, 2000 (F); *Macrothea* Macpherson and Cleva, 2010 (R); *Nanogalathea* Tirmizi and Javed, 1980 (R); *Palaemunida* Lörenthey, 1902 (F); *Phylladorhynchus* Baba, 1969 (R); *Tethysgalathea* new genus (F); *Triodonthea* Macpherson and Robainas-Barcia, 2013 (R).

Genus *Tethysgalathea* new genus

Type species.—*Tethysgalathea prealpina* (Beschin et al., 2016) (Eocene [Ypresian]; Italy), as *Eomunidopsis* (Figure 3).

Diagnosis.—Carapace with a length–width ratio (excluding rostrum) of 1.2–1.3, ratio of length of base rostrum to axis cervical groove to length of base rostrum to posterior margin is ~0.6, rostrum triangular without lateral spines and without a distinct keel from base to tip, lateral margins of carapace subparallel to slightly narrowing toward posterior carapace, strong cervical groove, triangular cardiac region well defined,

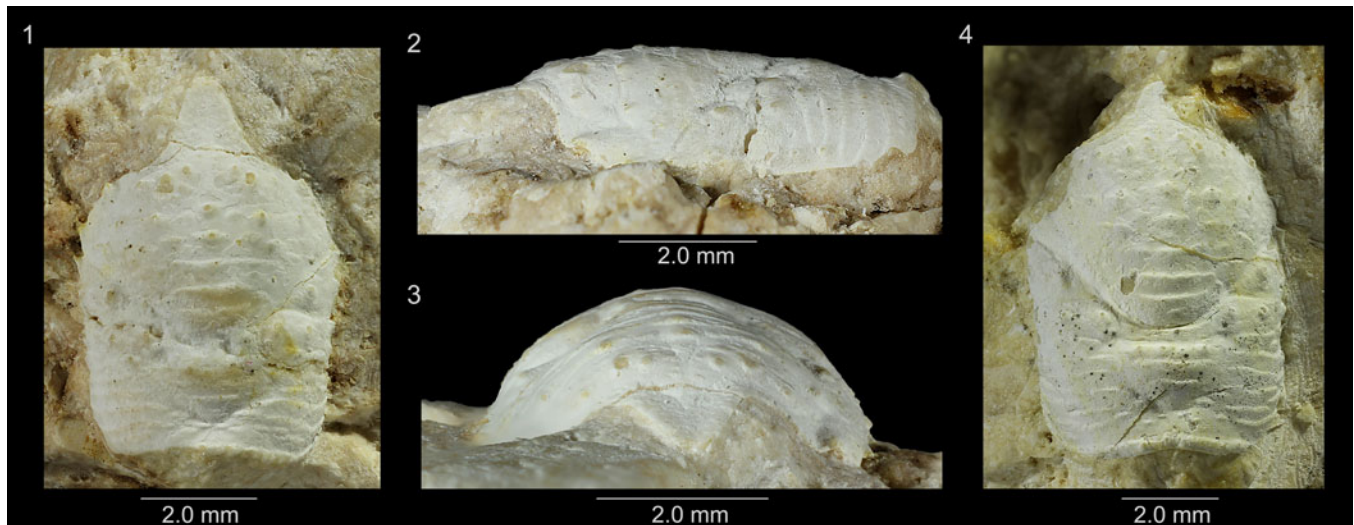


Figure 3. *Tethysgalathea prealpina* (Beschin et al., 2016) from a lower Eocene (Ypresian) coral limestone of Italy. (1–3) Holotype VR 93884, carapace: (1) dorsal view; (2) left lateral view; (3) frontal view. (4) Paratype VR 93886, carapace in dorsal view. Reproduced from Beschin et al. (2016, pls. 3.4, 4.1), with permission. Courtesy of Ministero della Cultura (MiC) of Italy—Soprintendenza Archeologia Belle Arti e Paesaggio per le province di Verona, Rovigo e Vicenza.

ornamentation with spines mostly on anterior carapace and transverse ridges mostly on posterior carapace, depression present posterior to cardiac region.

Occurrence.—The single species currently within this genus occurs within lower Eocene (Ypresian) coral limestones in Rama and Monte di Malo (Rossi quarry) in Italy (Beschin et al., 2016, 2017).

Etymology.—*Tethysgalathea* is a merger of *Tethys* and *Galathea*. The specimens of the genus known so far inhabited the western part of the Tethys during the early Eocene. Gender is feminine.

Remarks.—The type species was originally placed in *Eomunidopsis*, but members of this genus do not bear strong spines on the anterior part of the dorsal carapace. Moreover, the axial point of the cervical groove is located more posteriorly (see Table 1). The taxon also superficially resembles *Acanthogalathea*, but *Acanthogalathea* bears two distinct spines at the base of the rostrum, which *Tethysgalathea* n. gen. lacks. A further difference separating this from *Acanthogalathea* is a higher length–width ratio (see Table 1). Of the other fossil galatheid genera, *Bolcagalathea*, *Lessinigalathea*, and *Palaeomunida* bear prominent spines on the lateral margins of the rostrum, which are absent in the new genus. Moreover, *Palaeomunida* bears a keel on the rostral axis from the base to tip, whereas such a keel is not present in the new genus. Unlike *Tethysgalathea*, *Luisogalathea* does not exhibit distinct spines on the anterior carapace.

All galatheid genera with modern representatives can also be distinguished from the new genus. *Alainius* bears no spines on the anterior carapace, has indistinct grooves, and bears two small accessory spines adjacent to the central rostral spine. *Allogalathea* exhibits a longer rostrum with small spines along the rostral margins and more rounded lateral carapace margins. *Allomunida* possesses an indistinct cervical groove, the cardiac region is poorly delineated, and the carapace is widening posteriorly.

Coralliogalathea has wide-based rostrum with distinct lateral spines and a poorly delineated cardiac region. *Fennerogalathea* exhibits a narrower, spine-like rostrum and a less-defined cardiac region. *Galathea* and *Janetogalathea* both have a rostrum with distinct lateral spines and a less-spinose anterior carapace. *Lauriea* has poorly defined regions and a rostrum with distinct lateral spines. *Macrothea* exhibits a longer carapace that is widening posteriorly, and the rostrum bears spines on its lateral margins. *Nanogalathea* possesses more-rounded lateral margins of the carapace and bears fewer spines on the anterior carapace. *Phylladiorhynchus* has a less-defined cardiac region and a lateral margin with at least two prominent spines. Finally, *Triodonthea* possesses a rostrum with distinct lateral spines and bears no transverse ridges on its carapace.

We also considered placing *Acanthogalathea paucispinosa* Beschin et al., 2016, in the new genus because this species is proportionally longer than other species within *Acanthogalathea*, but this taxon bears two distinct spines at the base of the rostrum not figured previously (Fig. 4) and is proportionally not as long as *Tethysgalathea prealpina*.

Genus *Eomunidopsis* Vía Boada, 1981

Type species.—*Eomunidopsis orobensis* (Ruiz de Gaona, 1943) (Early Cretaceous [Albian]; Spain), as *Galathea*, by original designation.

Other species.—*Eomunidopsis aldoirarensis* Klomp maker et al., 2012 (Early Cretaceous [Albian]; Spain); *E.?* *cobbani* Bishop, 1985 (Late Cretaceous [Campanian]; USA); *E. kinokunika* Karasawa et al., 2008 (Early Cretaceous [Barremian]; Japan); *E.?* *kojimai* Karasawa and Hayakawa, 2000 (Late Cretaceous [Santonian]; Japan); *E. limonitica* (Stenzel, 1945) (Early Cretaceous [Albian]; USA), as *Galathea?*; *E. meerssensensis* Collins et al., 1995 (Late Cretaceous [Maastrichtian]; The Netherlands); *E. navarrensis* (Van Straelen, 1940) (Early Cretaceous [Albian]; Spain), as

Table 1. Comparisons of carapace ratios of specimens of *Eomunidopsis* Vía Boada, 1981, *Tethysgalathea* n. gen., and *Acanthogalathea* Müller and Collins, 1991.

Taxon	Ratio length base rostrum to axis cervical groove / length base rostrum to posterior margin	Ratio length along axis (excluding rostrum) and maximum width (excluding spines)	Reference image, for similar-sized specimens
<i>Eomunidopsis aldoirarensis</i>	0.53	1.19	Klompemaker et al. (2012, fig. 3B)
<i>E. aldoirarensis</i>	0.54	1.29	Klompemaker et al. (2012, fig. 3C)
<i>E. kinokunika</i>	0.54	1.12	Karasawa et al. (2008, fig. 2.5)
<i>E. limonitica</i>	0.55	1.09	Franțescu (2014, fig. 4A)
<i>E. meersensis</i>	—	—	Collins et al. (1995, fig. 4I)
<i>E. navarrensis</i>	0.51	1.09	Klompemaker et al. (2012, fig. 4D)
<i>E. navarrensis</i>	0.52	1.06	Klompemaker et al. (2012, fig. 4E)
<i>E. orobensis</i>	0.51	1.30	Klompemaker et al. (2012, fig. 5C)
<i>E. orobensis</i>	0.51	1.28	Klompemaker et al. (2012, fig. 5E)
<i>E. orobensis</i>	0.53	1.25	Klompemaker et al. (2012, fig. 5F)
<i>E. texcalaensis</i> n. sp.	0.48	1.05	Vega et al. (2019, fig. 3.1), Figure 6
<i>Tethysgalathea prealpina</i>	0.61	1.24	Beschin et al. (2016, pl. 3.4)
<i>T. prealpina</i>	0.63	1.29	Beschin et al. (2016, pl. 4.1)
<i>Acanthogalathea broglioi</i> Beschin et al., 2016	0.61	1.00	Beschin et al. (2016, pl. 1.2)
<i>A. devechii</i> Beschin et al., 2016	0.56	0.98	Beschin et al. (2016, pl. 1.3)
<i>A. devechii</i>	0.57	1.09	Beschin et al. (2016, pl. 1.4)
<i>A. devechii</i>	0.57	1.03	Beschin et al. (2007, pl. 1.5, as <i>A. squamosa</i>)
<i>A. feldmanni</i>	0.59	1.02	De Angeli and Garassino (2002, pl. 3.3)
<i>A. feldmanni</i>	0.61	1.06	De Angeli and Garassino (2002, pl. 3.4)
<i>A. feldmanni</i>	0.61	1.04	Beschin et al. (2019, fig. 13)
<i>A. parva</i> Müller and Collins, 1991	0.56	0.98	Müller and Collins (1991, pl. 2.3)
<i>A. parva</i>	0.57	1.05	De Angeli and Garassino (2002, pl. 2.4)
<i>A. parva</i>	0.55	0.98	De Angeli and Garassino (2002, pl. 3.1)
<i>A. parva</i>	0.59	1.03	De Angeli and Garassino (2002, pl. 3.2)
<i>A. parva</i>	0.59	—	Beschin et al. (2019, fig. 12)
<i>A. paucispinosa</i> Beschin et al., 2016	0.60	1.17	Beschin et al. (2016, pl. 1.5)
<i>A. squamosa</i> Beschin et al., 2007	0.64	1.10	De Angeli and Cecon (2016, pl. 1.2)
<i>A. squamosa</i>	0.61	1.08	De Angeli and Cecon (2016, pl. 1.3)
<i>A. squamosa</i>	0.62	1.04	De Angeli and Cecon (2016, pl. 1.4)

Galathea; *Eomunidopsis texcalaensis* new species (Early Cretaceous [Barremian]; Mexico)



Figure 4. Paratype VR 93798 of *Acanthogalathea paucispinosa* Beschin et al., 2016, from a lower Eocene (Ypresian) coral limestone of Italy in dorsal view. Note the broken spine on the left margin of the rostrum. Precise scale unknown.

Emended diagnosis.—Carapace without rostrum somewhat longer than wide. Rostrum long, triangular, ending in one or, usually, three spines, with median keel. Cervical groove strong, U-shaped. Transverse groove branching off cervical groove present. Tip of mesogastric process and epigastric regions well defined. Ornamentation consists of transverse ridges that are variously interrupted, without large spines dorsally. Lateral margins of carapace usually lined with row of tubercles/spines.

Remarks.—Some disagreement over the family placement of *Eomunidopsis* has arisen within the recent literature. Ah Yong et al. (2010) and Beschin et al. (2016) placed this genus in Munidopsidae, whereas Klompemaker et al. (2012) favored placement in Galatheidae. Robins et al. (2013) pointed out that this genus does not belong to Munidopsidae. Ah Yong et al. (2010) placed *Eomunidopsis* within the Munidopsidae, as well as pointing out similarities between *Calteagalathea*, *Paragalathea*, and *Munidopsis*. Although *Calteagalathea* is a munidopsid, the species of *Paragalathea* and *Eomunidopsis* they examined have mostly been reassigned from *Eomunidopsis* and *Paragalathea* to other genera in new families by Robins et al. (2016). The type species of *Eomunidopsis* does not possess a circumgastric groove and has transverse ornamentation, which are far more common in Galatheidae than in Munidopsidae. The paper by Beschin et al. (2016), who put *Eomunidopsis* in Munidopsidae, was

published at a similar time to Robins et al. (2016), and thus did not consider the new generic placements in their work.

The galatheid *Eomunidopsis limonitica* was placed in this genus by Schweitzer et al. (2010), Klompmaker et al. (2012), and Vega et al. (2019), but Franțescu (2014) moved it to a different genus and family (*Munida* Leach, 1820, and Munididae, resp.). This change was based primarily on similarities in the sternum of *Eomunidopsis limonitica* with *Munida*, but a comparison with venters of Galatheidae was not provided. Munididae are diagnosed by a trifold frontal margin with a central rostral spine and one or two pairs of supraorbital spines close to the axis (Ahyong et al., 2010; Robins et al., 2012). *Eomunidopsis limonitica* bears a single triangular rostrum. All other characters match *Eomunidopsis* and Galatheidae, which is why we maintain placement within that genus and family.

Vía Boada (1981) assigned *Eomunidopsis orobensis* as the type species upon the erection of the genus but incorrectly (International Commission for Zoological Nomenclature, 1999, article 70.2) listed *E. navarrensis* as the type species in Vía Boada (1982), in which he provided a diagnosis of the genus. The suggested change may relate to not having a specimen of *E. orobensis* with a complete rostrum available, nor did Ruiz de Gaona (1943) and Bataller (1950). Vía Boada (1982, p. 13) provided a diagnosis of the genus, indicating that rostra would have a tridentate tip. However, Klompmaker et al. (2012, fig. 5E) showed a specimen of *E. orobensis* that seems to have only a single spine at the tip. As multiple taxa were ascribed to and removed from *Eomunidopsis* since 1982, we provide a new genus diagnosis.

Eomunidopsis? *cobbani* Bishop, 1985

Figure 5

- v 1985 *Eomunidopsis cobbani* Bishop, p. 602, figs. 1–3.
- v 1986 *Eomunidopsis cobbani*; Bishop, fig. 6f.
- 1995 *Eomunidopsis cobbani*; Collins et al., p. 176.
- 2000 *Luisogalatheia cobbani*; Karasawa and Hayakawa, p. 143.
- 2010 *Luisogalatheia cobbani*; Schweitzer et al., p. 49.
- 2014 *Munida cobbani*; Franțescu, p. 223.
- 2015 *Munida cobbani*; Nyborg and Garassino, p. 96.
- 2015 *Munida cobbani*; Feldmann et al., p. 87.
- 2019 *Eomunidopsis cobbani*; Vega et al., p. 3.
- 2019 *Luisogalatheia cobbani*; Vega et al., p. 3.

Types.—Holotype: USNM PAL 370191; paratypes: USNM PAL 370192–370196.

Occurrence.—Localities in Larimer County, Colorado, USA; *Baculites reesidei* Elias, 1933, and *B. jenseni* Cobban, 1962, ammonite biozones of the Larimer and Richard Sandstones, Pierre Shale, Upper Cretaceous (upper Campanian) (for stratigraphy, see Landman et al., 2018).

Remarks.—The holotype and one of the paratype carapaces have been figured in dorsal view. We here also provide new figures of the holotype from different angles.

The species has been placed in three genera (see synonymy list), so the taxon merits further discussion. Karasawa and Hayakawa (2000) transferred the species to *Luisogalatheia* on the basis of several characters, including the lack of a median rostral ridge. However, the figured type material has only a small part of the base of the rostrum preserved, and Bishop (1985, p. 602) expressed doubt about the presence or absence of a ridge on the rostrum (“unridged (?)”). The impression of the lower side of the rostrum with the medial groove of the holotype (Fig. 5)

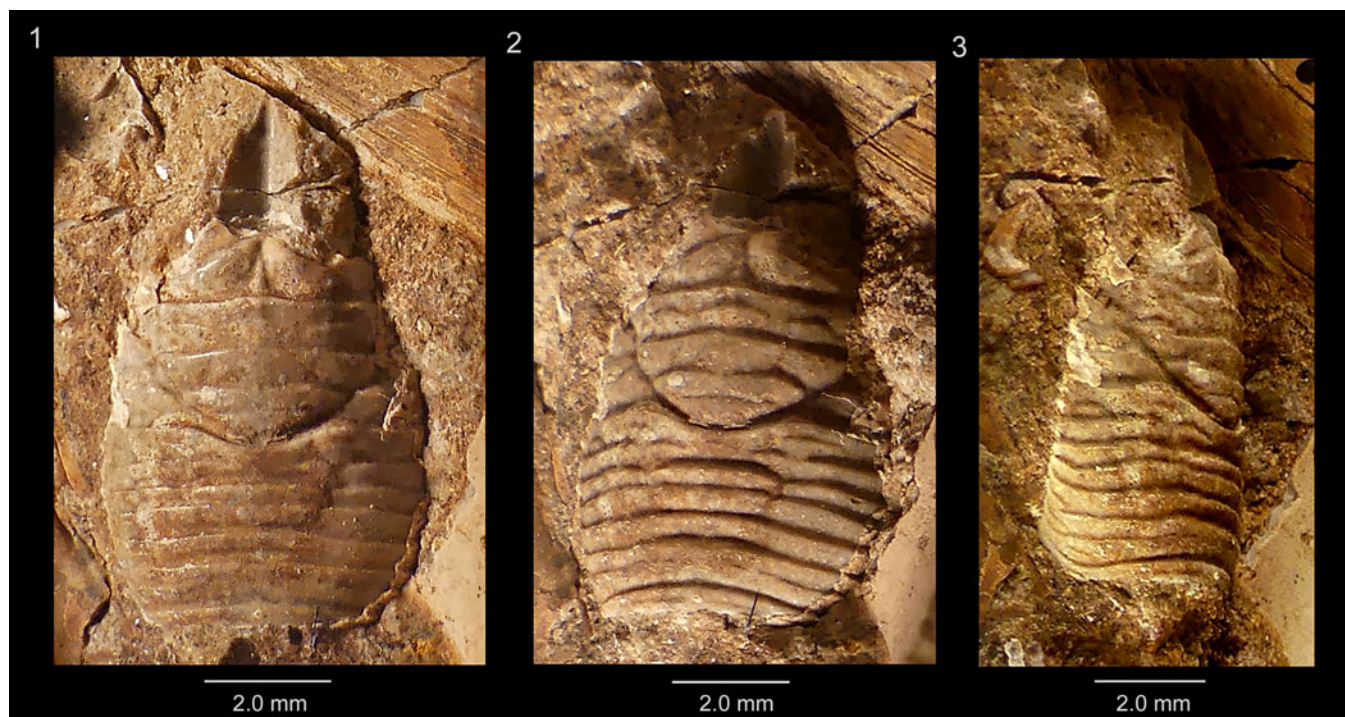


Figure 5. *Eomunidopsis?* *cobbani* Bishop, 1985, from the Upper Cretaceous (upper Campanian) Pierre Shale of the USA, holotype USNM PAL 370191, carapace: (1) dorsal view; (2) oblique view; (3) left lateral view.

cannot serve as a reliable proxy for the morphology of the upper side (see Klompmaker et al., 2012, fig. 5D, 5E). Frăntescu (2014) placed this species in *Munida* without further explanation. Subsequently, Nyborg and Garassino (2015) and Feldmann et al. (2015) noted that this species lacks the supra-orbital (= supraocular) spines. The latter authors also suggested a reevaluation and expressed that placement within Galatheidae might be possible on the basis of the wide rostrum and ornamentation. Munididae are characterized by supraorbital spines, so placement in *Munida* is not tenable. We questionably place the species in its original genus within Galatheidae because the preserved characters match the original (Vía Boada, 1982, p. 13) and emended diagnoses of *Eomunidopsis* herein. New material with a complete rostrum is needed to further evaluate this species.

Eomunidopsis texcalaensis new species

Figure 6

2019 *Luisogalatea cretacea* (Stenzel, 1945); Vega et al., p. 2, fig. 3.1–3.4.

Holotype.—IGM-11362.

Diagnosis.—Carapace excluding rostrum ~10% longer than wide, weakly convex longitudinally, moderately convex transversely; widening posteriorly. Rostrum triangular and sharp, slightly downturned, with strong median ridge.

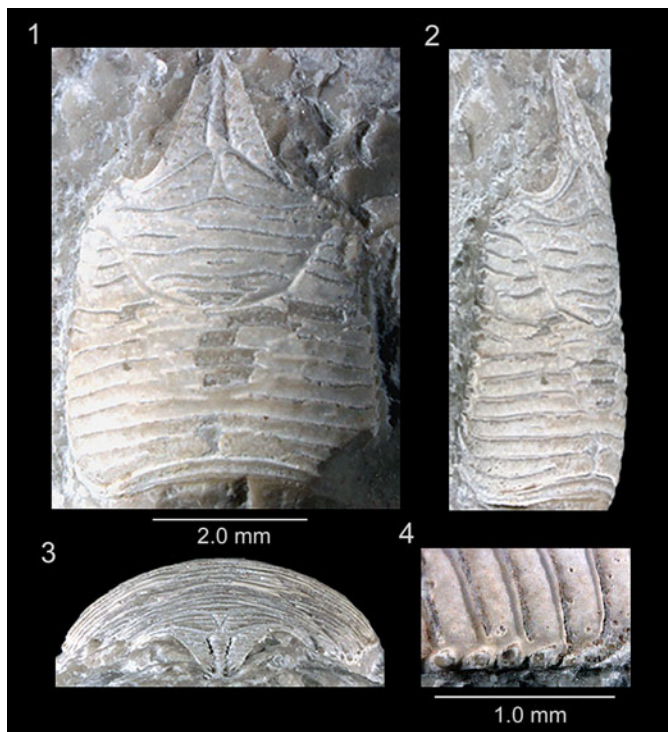


Figure 6. *Eomunidopsis texcalaensis* n. sp. from the Lower Cretaceous (upper Barremian) Zapotitlán Formation of Mexico, holotype IGM-11362, carapace: (1) dorsal view; (2) left lateral view; (3) frontal view; (4) closeup of spines on the left lateral margin. Scale bar for 1 applies also to 2 and 3. Specimen images from Vega et al. (2019, fig. 3.1–3.4), reproduced with permission.

Mesogastric region poorly delimited, except for sharp tip of mesogastric process. Cardiac region appears straight at anterior border and rounded posterior to it. Lateral margins of carapace with spines on anterior three-quarters. Ornamentation consists of continuous ridges on posterior carapace; ridges more interrupted on anterior carapace.

Occurrence.—El Ojito section, ~3 km NW of San Antonio Texcala, Puebla, Mexico (18.418°N, 97.459°W); coral limestone of the Zapotitlán Formation, Lower Cretaceous (upper Barremian).

Description.—Carapace excluding rostrum ~10% longer than wide; weakly convex longitudinally, moderately convex transversely; widening posteriorly, maximum width in posterior third of carapace. Rostrum triangular and sharp, slightly downturned, with strong median ridge, with tubercles on surface, tip appears incomplete. Upper orbital margin concave. Epigastric regions distinctly bordered anteriorly by inverse V-shaped rim. Protogastric, hepatic, and mesogastric regions not to poorly delimited, except for sharp tip of mesogastric process. Cervical groove broadly U-shaped and distinct, curves more laterally near lateral margins. Groove branching off cervical groove transversally not very distinct, separating anterior and posterior branchial regions. Cardiac region appears straight at anterior border and rounded posterior to it. Intestinal region not clearly defined. Lateral margins with spines on anterior three-quarters. Posterior margin slightly concave, rimmed. Ornamentation consists of continuous ridges on posterior carapace, more interrupted on anterior carapace; appears similar on cuticle and internal mold, as preserved. No muscle scar impressions discernable. Ventral surface, abdomen, and appendages unknown.

Etymology.—Named after the town of San Antonio Texcala, Puebla, Mexico.

Measurements.—Holotype IGM-11362: L = 4.4 mm, W = 4.0 mm.

Remarks.—Vega et al. (2019) presented two specimens they ascribed to *Luisogalatea cretacea* (Stenzel, 1945). Although this species is known from a not-too-distant region (Texas, USA), there is a substantial temporal gap of ca. 25 million years between the specimens, warranting a reassessment. Specimen IGM-11362 (Vega et al., 2019, fig. 3.1–3.4) does not represent *L. cretacea* because of the ridge on the axis of the rostrum, whereas *L. cretacea* has a groove here as described and figured by Stenzel (1945, p. 430–431, pl. 43.3) and Schweitzer and Feldmann (2000, fig. 2) and further implied by Frăntescu (2014, fig. 3). This specimen does not fit the diagnosis of *Luisogalatea* (see Karasawa and Hayakawa, 2000) because the rostrum bears an axial ridge and shows lateral spines near the tip. Instead, this specimen has many similarities to specimens of the late Albian species *Eomunidopsis navarrensis* (Van Straelen, 1940) found in Spain (see Klompmaker et al., 2012, fig. 4). The substantial temporal gap alone already may argue against conspecificity, which is confirmed by a morphological difference. The

cardiac region is consistently rectangular in *E. navarrensis* (Vía Boada, 1982 [non pl. 2.5]; Klompmaker et al., 2012, 2014), but the posterior margin of this region is more rounded in IGM-11362, and the anterior margin of the cardiac region of IGM-11362 appears less well defined. *Eomunidopsis aldoirarensis* bears more-frequently interrupted ridges than the new species, has fewer spines in the posterior part of the lateral margin, and the tip of the mesogastric process is wider. Compared with *E.? cobbani*, the new species has less-curved posterolateral margins. Karasawa et al. (2008) mentioned that the lateral margins of *E. kinokunika* do not show spines and that the rostral surface is smooth, both of which are not the case for *E. texcalaensis* n. sp. *Eomunidopsis? kojimai* does not widen comparably to the posterior carapace, and the transverse ridges are less continuous than in the new species. *Eomunidopsis limonitica* has its mesogastric region well delimited on all sides, unlike the new species, in which the lateral sides are not well defined. *Eomunidopsis meerssens* is not well preserved, but the lateral margins are parallel to nearly so, whereas they diverge toward the posterior carapace in the new species. The type species of *Eomunidopsis*, *E. orobensis*, bears small tubercles on the middle part of the carapace, and its lateral margins parallel each other, which is not the case in *E. texcalaensis*.

Eomunidopsis sp(p).

2019 *Luisogalatea cretacea* (Stenzel, 1945); Vega et al., p. 2, fig. 3.5–3.7.

2019 *Eomunidopsis limonitica* (Stenzel, 1945); Vega et al., p. 3, fig. 3.11–3.21.

Remarks.—The second of the two specimens of *Luisogalatea cretacea* (IMG-11363) presented by Vega et al. (2019) appears to be not conspecific to *L. cretacea* either, once again because of the presence of a ridge on the axis of the rostrum. Moreover, the mesogastric region is clearly defined on all sides, which is not the case for *L. cretacea* (Stenzel, 1945, pl 43.3; Schweitzer and Feldmann, 2000, fig. 2; Franțescu, 2014, fig. 3).

Mexican specimens identified as *Eomunidopsis limonitica* by Vega et al. (2019) are ca. 25 million years older than the specimens from the United States (Texas) (Stenzel, 1945; Franțescu, 2014). Although the Mexican specimens are close to this species morphologically, there are some differences compared with the two figured specimens from the United States. One specimen (Vega et al., 2019, fig. 3.16, 3.17) is much more tubercular on the anterior carapace. Others show more ridges with granules on that region (Vega et al., 2019, fig. 3.13, 3.18, 3.19), which may or may not be influenced by preservation, the method of photography, and/or intraspecific variation. One difference that appears to be consistent is the short groove running from the anterolateral corners of the cardiac region to the groove branching off the cervical groove, which is present in the Mexican specimens but apparently absent in the *E. limonitica* from the United States (Franțescu, 2014, fig. 4). Such a groove is present in the type species of *Eomunidopsis*, *E. orobensis*, from the late Albian of Spain (Vía Boada, 1982, pl. 2.8, 2.9; Klompmaker et al., 2012, fig. 5). Our

comparisons between the Mexican and US specimens are complicated by the fact that the Mexican specimens are smaller (2–4 mm wide) than the two US specimens (5–6 mm wide), implying that ontogenetic change is more difficult to consider. We conclude that the specimens are highly unlikely to represent *L. cretacea* or *E. limonitica* and refer them to open nomenclature within *Eomunidopsis*. More complete, well-preserved specimens are needed to determine the range of intraspecific variation to determine whether there is one new species with variable ornamentation (compare Vega et al., 2019, fig. 3.5–3.17) or multiple species.

Genus *Galathea* Fabricius, 1793

Type species.—*Galathea strigosa* (Linnaeus, 1761) (extant; NE Atlantic, Mediterranean Sea, Red Sea), as *Cancer*, by original designation.

Galathea? cretacea Stenzel, 1945

Figure 7

v 1945 *Galathea cretacea* Stenzel, p. 430, pl. 43.3.

v 1969 *Galathea cretacea*; Glaessner, p. R482, fig. 290.4.

1985 *Eomunidopsis cretacea*; Bishop, p. 603.

2000 *Luisogalatea cretacea*; Karasawa and Hayakawa, p. 143.

v 2000 *Galathea cretacea*; Schweitzer and Feldmann, p. 150, fig. 2.

2002 *Galathea cretacea*; Schweitzer et al., p. 37.

2010 *Luisogalatea cretacea*; Schweitzer et al., p. 50.

2014 *Munida cretacea*; Franțescu, p. 225, fig. 3.

2015 *Munida cretacea*; Nyborg and Garassino, p. 96.

2015 *Munida cretacea*; Feldmann et al., p. 86, 87, 90.

Holotype.—BEG0002118.000.

Remarks.—*Galathea cretacea* from the Early Cretaceous (Albian) of Texas, USA, has been placed in a variety of genera since its description (see preceding synonymy list). Feldmann et al. (2015) called for a reevaluation of the placement of the species in *Munida*. The reassignment to a different family (Munididae) by Franțescu (2014) was based primarily on similarities in the sternum of *Galathea cretacea* with *Munida*, but a differentiation to venters of Galatheaidea was not provided. Moreover, Munididae are diagnosed by a trifid frontal margin with a central rostral spine and one or two pairs of supraorbital spines close to the axis (Ahyong et al., 2010; Robins et al., 2012), but *G. cretacea* bears a single triangular rostrum without adjacent spines. Thus, placement of *G. cretacea* in *Munida* is not tenable. *Luisogalatea* was defined as possessing no lateral spines on the rostrum, but Schweitzer and Feldmann (2000) noted small spines on this margin, more consistent with *Galathea*. The medial groove on the rostrum is also in agreement with the type species of *Galathea*, extant *G. strigosa*. *Eomunidopsis* bears a rostrum with a median keel. Additional specimens of *G. cretacea* with complete rostra are required to further assess its generic placement. For now, we questionably assign it *Galathea*.

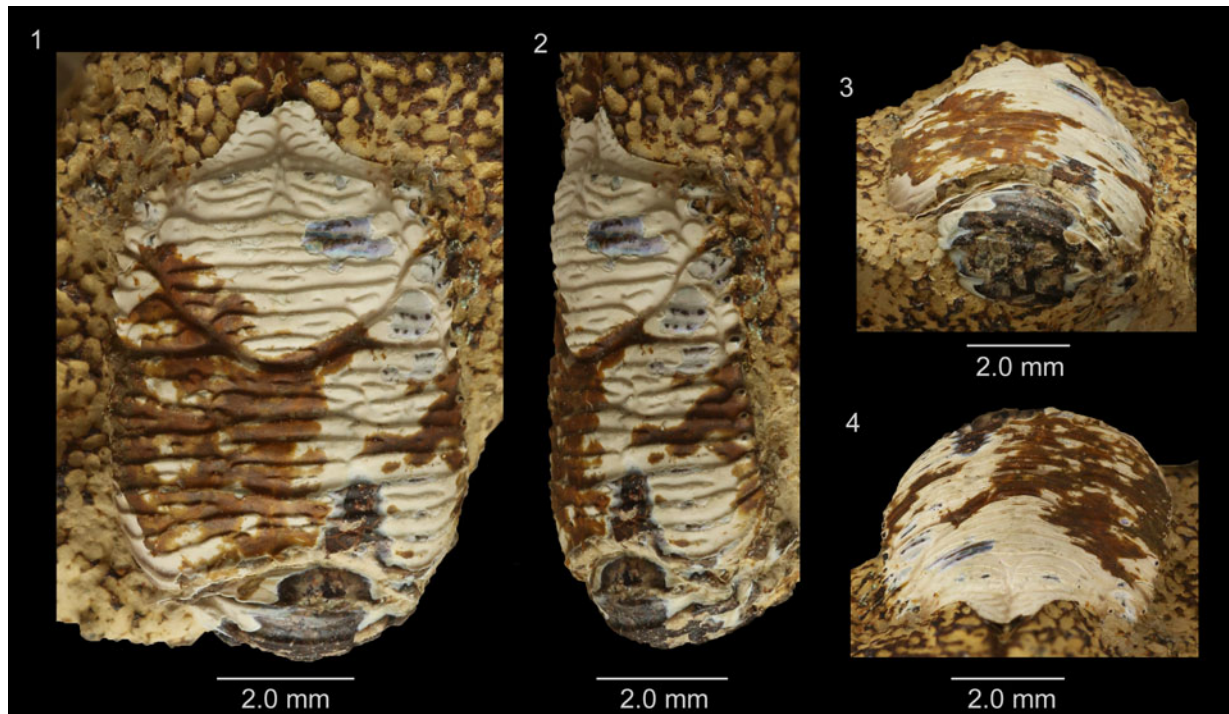


Figure 7. *Galathea? cretacea* Stenzel, 1945, from the Lower Cretaceous (upper Albian) Pawpaw Shale of Texas, USA, holotype BEG0002118.000, carapace: (1) dorsal view; (2) right lateral view; (3) posterior view; (4) frontal view.

The species has been described first from the upper Albian Pawpaw Formation in Texas, USA (Stenzel, 1945; Franțescu, 2014). A specimen ascribed to *G. cretacea* from the Santonian of Texas was figured by McCall et al. (2012, fig. 4-U1) and is

refigured herein (Fig. 8). This specimen is ca. 15 million years younger than the holotype, which is why we restudied it. Unfortunately, the rostrum is not preserved, and the ventral side is not as well preserved as those in Franțescu (2014). The dorsal side is

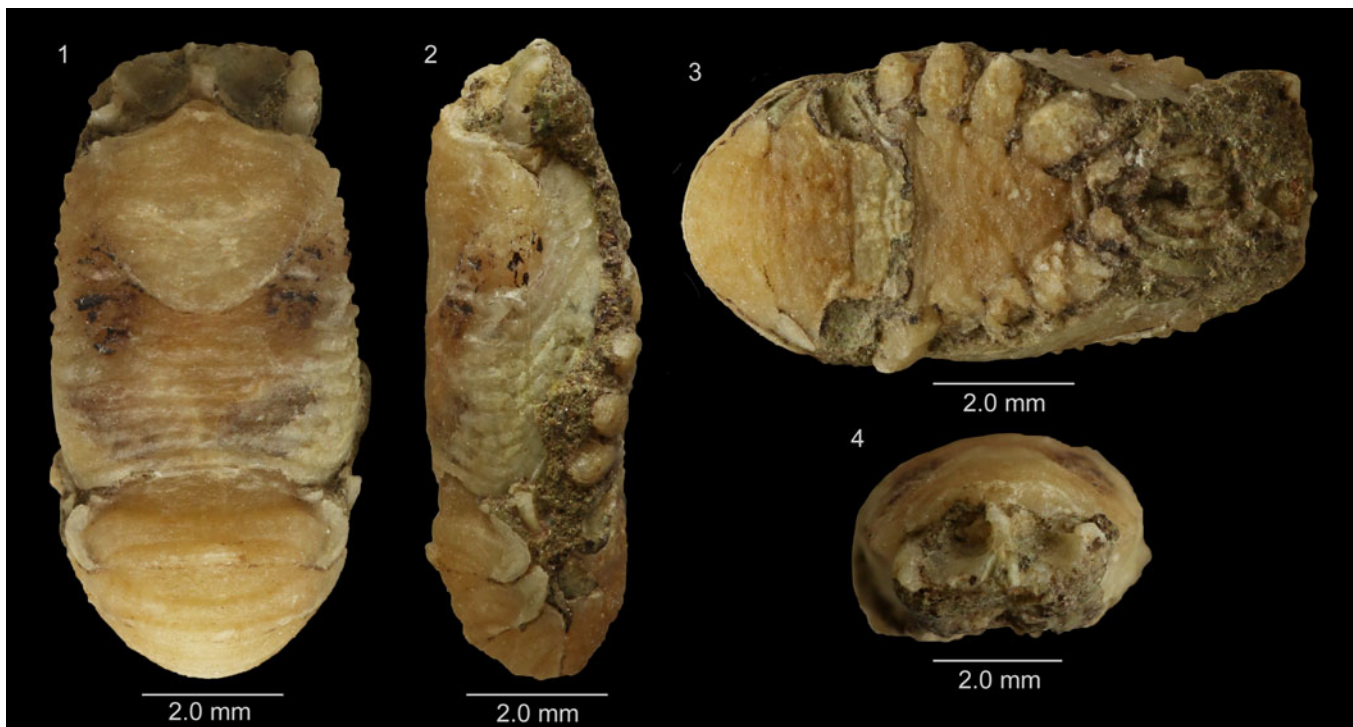


Figure 8. Galatheaidae indet. from the Upper Cretaceous (Santonian) “Pyroclastic Zone” of the Austin Group of Texas, USA, NPL00049997.000, carapace: (1) dorsal view; (2) right lateral view; (3) ventral view; (4) frontal view.

comparable to the holotype, but the rostrum is a key feature. It is difficult to ascertain whether the rostrum is truly narrow or whether it was wider, but breakage caused it to appear narrower. We did not observe obvious bases of supraocular spines as in Munididae, which suggests placement in Galatheaidea is most likely. Specimens with complete rostra are necessary to determine the species.

Family Munididae Ahyong et al., 2010
Genus *Protomunida* Beurlen, 1930

Type species.—*Protomunida munidoides* (Segerberg, 1900) (Paleocene [Danian]; Denmark), as *Galathea*, by original designation.

Other species.—*Protomunida bennickei* n. sp. (Paleocene [Danian]; Denmark); *P. eurekantha* n. sp. (Paleocene [Danian]; Denmark); *P. ? pentaspinosa* Beschin et al., 2016 (Eocene [Ypresian]; Italy); *P. primaeva* (Segerberg, 1900) (Paleocene [Danian]; Denmark), as *Munida*; *P. spitzbergica* (Gripp, 1927) (late Paleocene; Spitsbergen), as *Galathea*.

Emended diagnosis.—Carapace excluding rostrum longer than wide, subrectangular. Three-pronged rostrum, with one major, moderately narrow spine on axis and two smaller accessory spines. Forwardly directed spine at outer orbital angle; row of spines or tubercles on epigastric regions; epibranchial regions with tubercles dorsally and spines laterally; other ornamentation consists of transverse ridges; fairly smooth, nondepressed area posterior to cardiac region (modified from Hryniewicz et al., 2019, p. 124).

Remarks.—The species accommodated in this genus were discussed recently by Hryniewicz et al. (2019) on the basis of a species from Spitsbergen. Here, we describe four species from Denmark in detail and have updated the genus diagnosis consequently. *Protomunida* spp. are known only from the Paleogene of Europe thus far.

Protomunida munidoides (Segerberg, 1900)
Figure 9

v 1900 *Galathea munidoides* Segerberg, p. 353, pl. 7.5.

v 1994 *Protomunida munidoides*; Collins and Jakobsen, pl. 10.1.

v 1997 *Protomunida munidoides*; Jakobsen and Collins, pl. 2.10.

Lectotype.—MMH 248.

Diagnosis.—Carapace excluding rostrum ~15–25% longer than wide; maximum width about mid-length. Rostrum with narrow, sharp, triangular central rostral spine; fairly flat but with faint keel on axis to about mid-length. Lateral margins of carapace with spines on anterior two-thirds. Posterior margin slightly concave, rimmed, without spines. Spines absent just posterior to transverse groove branching off cervical groove.

Occurrence.—Faxe Quarry, Denmark (55.26°N, 12.13°E); coral-bryozoan limestone of the Faxe Formation, Paleocene (middle Danian) (Lauridsen et al., 2012; Lauridsen and

Bjerager, 2021). The Faxe Formation is dated as nannofossil zone NNTp2G-3 (Bjerager et al., 2018) using the zonation of Varol (1998), which is equivalent to lower Zone NP3 (Martini, 1971).

Description.—Carapace excluding rostrum ~15–25% longer than wide, up to ~8 mm wide; weakly convex longitudinally, moderately convex transversely, maximum width about mid-length. Rostrum with narrow, sharp, triangular central rostral spine; fairly flat but with faint keel on axis to about mid-length; slightly downturned at distal half; one spine at base rostrum on either side of central rostral spine. Upper orbital margin concave. Forward spine at anterolateral angle. Epigastric regions distinctly bordered, triangular, with row of spines near anterior border. Hepatic regions small, weakly delimited. Protogastric and mesogastric regions not or poorly delimited, except for sharp tip of mesogastric process, which may show a tubercle. Cervical groove broadly U-shaped and distinct, somewhat sinuous more laterally, intersects with lateral margin posterior to hepatic region. Transverse grooves branching off cervical groove distinct, separating anterior and posterior branchial regions. Cardiac region appears straight at anterior border and straight to rounded posterior to it. Intestinal region not clearly defined. Lateral margins with spines on anterior two-thirds. Posterior margin slightly concave, rimmed, without spines. Ornamentation consists of fairly continuous, transverse ridges on most of carapace; tubercles/spines on epibranchial regions and near anterior margin; ornamentation appears similar on internal molds and casts. Spines absent just posterior to transverse groove branching off cervical groove. Muscle scar impressions generally not discernable, except posterior gastric muscles in OESM 11189. Posterior gastric pits within cervical groove expressed as slits. Ventral surface, abdomen, and appendages unknown.

Materials.—Lectotype MMH 248, OESM 11187, OESM 11189, OESM 11191, OESM 11193–11198, OESM 11204 (cast), OESM 11205 (cast), OESM 11227, OESM 11229, OESM 11230, OESM 11234, OESM 11241, OESM 11242, and OESM 11256 (cast + external mold).

Measurements (mm).—OESM 11205: L = 4.5, W = 3.8; lectotype MMH 248: L = 5.1, W = 4.1; OESM 11189: L = 4.8, W = 4.1; OESM 11193: L = 3.2, W = 2.7; OESM 11204: L = 4.8, W = 3.9; OESM 11234: L = –, W = 7.0; OESM 11194: L = 6.2, W = 5.2.

Remarks.—Despite this species being commonly cited in the literature (see synonymy lists), no specimens from the previous literature other than the type specimen can be confidently attributed to this species. The posterior margin of the lectotype is incompletely preserved, but it is preserved to the extent that we can confirm the absence of a tubercle/spine or a base thereof. This statement is supported by visual inspection combined with a quantitative comparison with the position of spines on this margin for *Protomunida eurekantha* n. sp. (Fig. 9.6; Table 2). No obvious ontogenetic variations are observed within *P. munidoides*. In terms of intraspecific variation, the number of

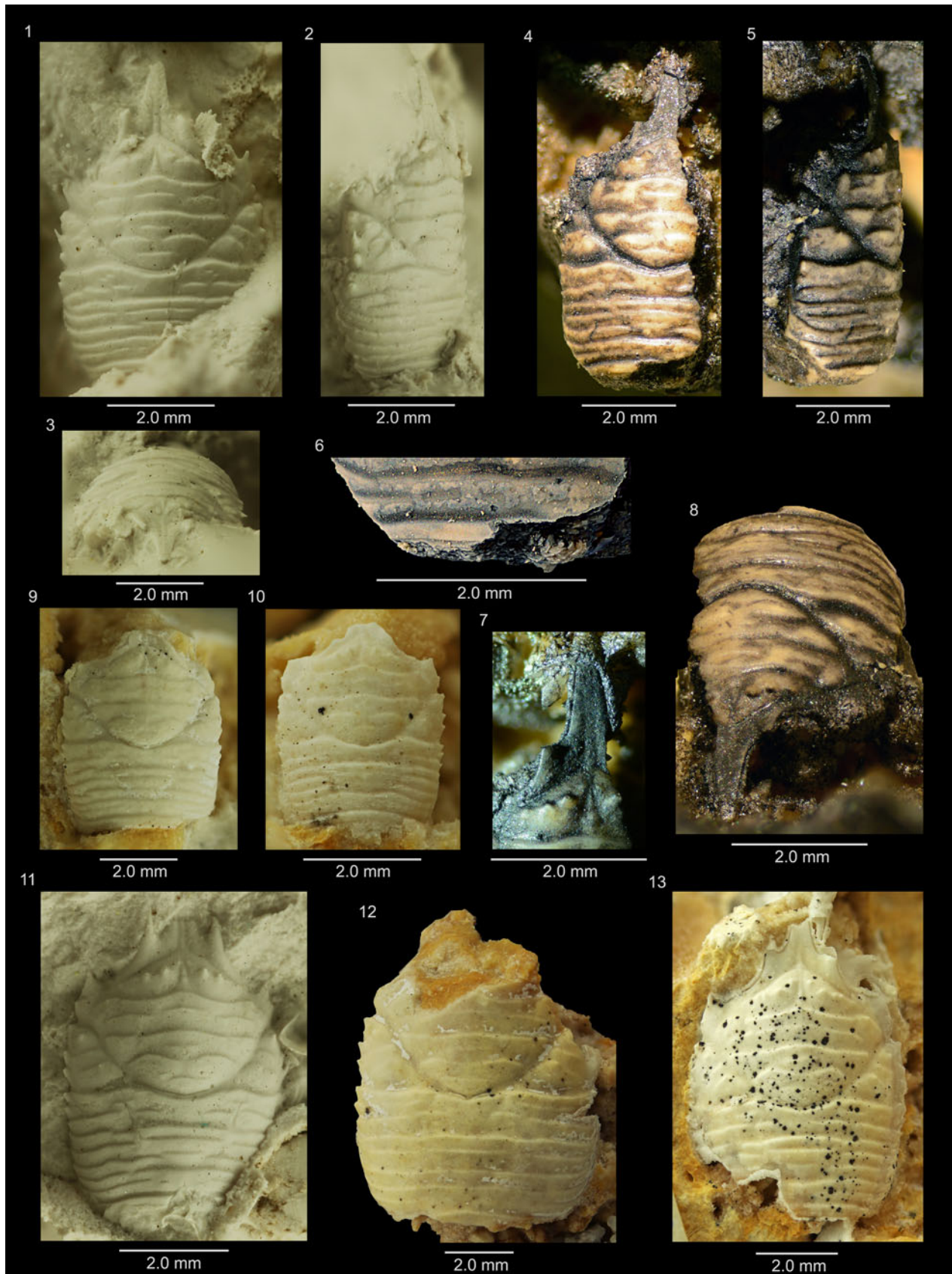


Figure 9. *Protomunida munidoides* (Segerberg, 1900) from the Paleocene (middle Danian) Faxe Formation of Denmark. (1–3) OESM 11205 (cast), carapace: (1) dorsal view; (2) left lateral view; (3) frontal view. (4–8) Lectotype MMH 248, carapace: (4) dorsal view; (5) left lateral view; (6) posterior margin; (7) rostral view; (8) frontal view. (9–13) Carapaces in dorsal view: (9) OESM 11189 (cast); (10) OESM 11193 (cast); (11) OESM 11204 (cast); (12) OESM 11234; (13) OESM 11194.

Table 2. Relative position of the spines on the posterior margin for *Protomunida eurekantha* n. sp. For the lectotype of *Protomunida munidoidea* (Segerberg, 1900) (MMH 248), 0.83 of the left half of the posterior margin is preserved without any signs of a spine, implying this specimen did not have spines on the posterior margin.

Specimen	Width from lateral margin to which spine occurs/width from lateral margin to longitudinal axis
<i>Protomunida eurekantha</i> n. sp. (OESM 11181)	0.77
<i>P. eurekantha</i> (OESM 11180)	0.73
<i>P. eurekantha</i> (OESM 11192)	0.75
<i>P. eurekantha</i> (OESM 11185)	0.72
Paratype <i>P. eurekantha</i> (OESM 11176)	0.70
<i>P. eurekantha</i> (OESM 11173)	0.73
<i>P. eurekantha</i> (OESM 11175)	0.68
Paratype <i>P. eurekantha</i> (OESM 11172)	0.73
Paratype <i>P. eurekantha</i> (OESM 11184)	0.71

spines marking the anterior border of the epigastric regions appears to vary from two to five and the number of spines on the epibranchial regions varies from two to three. However, taphonomy may have affected the preservation of these spines.

Because this species is diagnosed and described anew here, a comparison with congenetics is necessary. Differences between *P. munidoidea* and the new species are described in the remarks sections of those taxa. The central part of the rostrum of *P. ? pentaspinosa* appears to be wider at its base, and the spines on the lateral margins appear to extend more posteriorly. *Protomunida primaeva* does possess spines just posterior to the transverse groove branching off the cervical groove, unlike *P. munidoidea*. In addition, the base of the rostrum has a shorter keel in *P. primaeva*. *Protomunida spitzbergica* bears transverse ridges that are more interrupted than in *P. munidoidea*.

Protomunida primaeva (Segerberg, 1900)

Figure 10

- v 1900 *Munida primaeva* Segerberg, p. 353, pl. 7.6.
- ? 1901 *Galathea munidoidea*; Woodward, p. 489, pl. 12.8.
- ? 1969 *Protomunida munidoidea*; Glaessner, p. R482, fig. 290.1.
- v 1994 *Munida primaeva*; Collins and Jakobsen, pl. 10.2.
- v 1997 *Munida primaeva*; Jakobsen and Collins, pl. 2.8.
- ? 2010 *Munida primaeva*; Damholt et al., fig. on p. 22.
- ? 2011 *Munida primaeva*; Rasmussen et al., fig. on p. 83.
- ? 2015 *Munida primaeva*; Klompmaker and Boxshall, fig. 1d.

Lectotype.—MMH 249.

Diagnosis.—Carapace excluding rostrum ~15–25% longer than wide; maximum width about mid-length. Rostrum with narrow, sharp, triangular central rostral spine; fairly flat but with faint keel on axis only at base rostrum. Lateral margins of carapace with spines on anterior two-thirds. Posterior margin slightly concave, rimmed, without spines. Spines present just posterior to transverse groove branching off cervical groove.

Occurrence.—Faxe Quarry, Denmark (55.26°N, 12.13°E); coral-bryozoan limestone of the Faxe Formation, Paleocene (middle Danian) (Lauridsen et al., 2012; Lauridsen and Bjerager, 2021). The Faxe Formation is dated as nanofossil zone NNTp2G-3 (Bjerager et al., 2018) using the zonation of Varol (1998), which is equivalent to lower Zone NP3 (Martini, 1971).

Description.—Carapace excluding rostrum ~15–25% longer than wide, up to ~6 mm wide; weakly convex longitudinally, moderately convex transversely, maximum width about mid-length. Rostrum with narrow, sharp, triangular central rostral spine; fairly flat but with faint keel on axis only at base rostrum; slightly downturned at distal half; one spine at base rostrum on either side of central rostral spine. Upper orbital margin concave. Forward spine at anterolateral angle. Epigastric regions distinctly bordered, triangular, with row of spines near anterior border. Hepatic regions small, weakly delimited. Protogastric and mesogastric regions not or poorly delimited, except for sharp tip of mesogastric process that may show two small tubercles. Cervical groove broadly U-shaped and distinct, somewhat sinuous more laterally, intersects with lateral margin posterior to hepatic region. Transverse grooves branching off cervical groove distinct, separating anterior and posterior branchial regions. Cardiac region appears straight at anterior border and straight to rounded posterior to it. Intestinal region not clearly defined. Lateral margins with spines on anterior two-thirds. Posterior margin slightly concave, rimmed, without spines. Ornamentation consists of fairly continuous, transverse ridges on most of carapace; tubercles/spines on epibranchial regions and near anterior margin; ornamentation appears similar on internal molds and casts. Spines present just posterior to transverse groove branching off cervical groove. Muscle scar impressions generally not discernable, except for posterior gastric muscles in some specimens (MMH 249, OESM 11199). Posterior gastric pits within cervical groove expressed as slits. Ventral surface, abdomen, and appendages unknown.

Materials.—Lectotype MMH 249, OESM 11199, OESM 11202 (cast + external mold), OESM 11228, OESM 11231, and OESM 11250 (cast + internal and external mold).

Measurements (mm).—OESM 11202: L = 6.4, W = 5.3; OESM 11199: L = 7.2, W = 6.1; lectotype MMH 249: L = 5.7, W = 4.7; OESM 11250: L = 3.6, W = 2.9; OESM 11231: L = 3.8, W = 3.1.

Remarks.—No specimens from the previous literature other than the type specimen can be attributed to this species with certainty. No obvious ontogenetic variations are observed within *P. primaeva*. In terms of intraspecific variation, the number of spines marking the anterior border of the epigastric regions appears to vary from four to five, and the number of obvious spines on the epibranchial regions varies from two to three. Taphonomic processes may have influenced the preservation of these spines.

A comparison with the two new species of *Protomunida* is provided in the following and a comparison with *P. munidoidea*



Figure 10. *Protomunida primaeva* (Segerberg, 1900) from the Paleocene (middle Danian) Faxø Formation of Denmark: (1, 2, 9) OESM 11202 (cast), carapace (1) dorsal view; (2) right lateral view; (9) frontal view. (3, 6, 8) Carapaces in dorsal view: (3) OESM 11199; (6) OESM 11250 (cast); (8) OESM 11231. (4, 5, 7) Lectotype MMH 249, carapace: (4) dorsal view; (5) left lateral view; (7) frontal view.

was given in the preceding. Compared with *P.?* *pentaspinosa*, the base of the central rostral spine appears narrower in *P. primaeva*, and the latter species bears spines just posterior to groove branching off cervical groove, which appear absent in *P.?* *pentaspinosa*. *Protomunida spitzbergica* bears transverse ridges that are much more interrupted than in *P. primaeva*.

Protomunida bennickei new species
Figure 11

2008 trolldhummer; Bonde et al., fig. on p. 69.

Types.—Holotype: OESM 11213; paratypes: OESM 11211, OESM 11246, and OESM 11248.

Diagnosis.—Carapace excluding rostrum ~5–15% longer than wide; maximum width in posterior half of carapace. Rostrum triangular and sharp, slightly downturned, with strong median ridge along entire axis. Lateral margins of carapace with spines on anterior half. Posterior margin slightly concave, rimmed, without spines. Spines absent just posterior to transverse groove branching off cervical groove.

Occurrence.—Glacial erratics, Hesnæs beach, Denmark (54.8314°N, 12.162°E); uppermost lower Paleocene (Danian); nannofossil subzone NNTp2C (Varol, 1998), equivalent to lower Zone NP2 (Martini, 1971).

Description.—Carapace excluding rostrum ~5–15% longer than wide, up to ~4 mm wide; weakly convex longitudinally, moderately convex transversely; somewhat widening posteriorly, maximum width in posterior half of carapace. Rostrum with narrow, sharp, triangular central rostral spine and strong median ridge along entire axis; slightly downturned at distal half; one spine at base rostrum on either side of central rostral spine. Upper orbital margin concave, rimmed. Forward spine at anterolateral angle. Epigastric regions distinctly bordered, triangular, with row of spines near anterior border. Hepatic regions small, weakly delimited. Protogastric and mesogastric regions not or poorly delimited, except for sharp tip of mesogastric process, which may show two small tubercles. Cervical groove broadly U-shaped and distinct, somewhat sinuous more laterally, intersects with lateral margin posterior to hepatic region. Transverse grooves branching off cervical groove distinct, separating anterior and posterior branchial regions. Cardiac region appears straight at anterior border and straight to rounded posterior to it. Intestinal region not clearly defined. Lateral margins with spines on anterior half. Posterior margin slightly concave, rimmed, without spines. Ornamentation consists of fairly continuous, transverse ridges on posterior carapace and on central gastric region; tubercles/spines on epibranchial regions and near anterior margin; ornamentation appears similar on internal molds and casts. Spines absent just posterior to transverse groove branching off cervical groove. Muscle scar impressions generally not discernable, except posterior gastric muscles in holotype. Posterior gastric pits within cervical groove expressed as slits. Ventral surface, abdomen, and appendages unknown.

Etymology.—Named after Peter Bennicke, sole collector of the specimens.

Materials.—Type material + OESM 11207–11209 (external molds and casts), OESM 11216–11218, and OESM 11247a+b (two specimens).

Measurements (mm).—Holotype OESM 11213: L = 3.8, W = 3.3; paratype OESM 11211: L = 4.4, W = 3.8; paratype OESM 11246: L = 3.3, W = 3.1; paratype OESM 11248: L = 2.6, W = 2.4.

Remarks.—The geographic origin of the glacial erratics remains unclear. It is possible they came from Danian layers at Limhamn near Malmö (Sweden) or from elsewhere in Denmark. Decapod taxa found in the same erratics include *Protomunida eurekantha* n. sp. (OESM 11258); *Caloxanthus ornatus* (von Fischer-Benzon, 1866) (on same rock as OESM 11218); *Dromiopsis rugosus* (von Schlotheim, 1820); *D. elegans* Reuss, 1859; *Latheticocarcinus spinigus* (Jakobsen and Collins, 1997); *L. affinis* (Jakobsen and Collins, 1997); and *Raniliformis baltica* (Segeberberg, 1900). All these species except *P. eurekantha* are known from the middle Danian Faxø Formation of Faxø, Denmark (nannofossil zone NNTp2G-3, ca. 64.5 Ma, see Hvid et al., 2021). One of us (E.S.) investigated the nannofossils assemblage preserved in the carbonates of the glacial erratics to determine the age. Stratigraphically important nannofossil taxa (for nannofossil taxonomy, see Young et al., 2021) include *Biantholithus sparsus* Bramlette and Martini, 1964; *Biscutum harrisonii* Varol, 1989; *Coccolithus pelagicus* (Wallich, 1877); *Cyclagelosphaera alta* Perch-Nielsen, 1979; *Neocrepidolithus cruciatus* (Perch-Nielsen, 1979); *Neocrepidolithus fossus* (Romein, 1977); and *Zeughrabdodus sigmoides* (Bramlette and Sullivan, 1961) (see Appendix 1 for all taxa), which assigns the sample to nannofossil subzone NNTp2C (uppermost lower Danian or ca. 65.5 Ma, see Hvid et al., 2021). This age is ca. 1 Myr older than the Faxø decapods, extending the stratigraphic range of many of these decapod taxa.

A principal difference between the new species and all other species of *Protomunida* is the strong keel present along the entire axis of the rostrum, a feature that is not seen to that extent in congeners. Some other differences include the following. *Protomunida?* *pentaspinosa* bears spines located more posteriorly on the lateral margins. *Protomunida spitzbergica* has transverse ridges that are more interrupted. Unlike *P. bennickei* n. sp., *P. primaeva* and *P. eurekantha* show spines just posterior to where the posterior cervical groove branches off the cervical groove. The carapace of *P. primaeva* appears proportionally longer. *Protomunida eurekantha* also exhibits spines on the posterior margin, absent in *P. bennickei*. The spines on the lateral margin appear to extend more posteriorly in *P. munioides*, and the carapace of *P. bennickei* appears proportionally wider than that of *P. eurekantha*. No obvious ontogenetic and intraspecific variations are observed within *P. bennickei*.

Protomunida eurekantha new species
Figure 12

1997 *Protomunida munioides* (Segeberberg, 1900); Jakobsen and Collins, pl. 2.11.

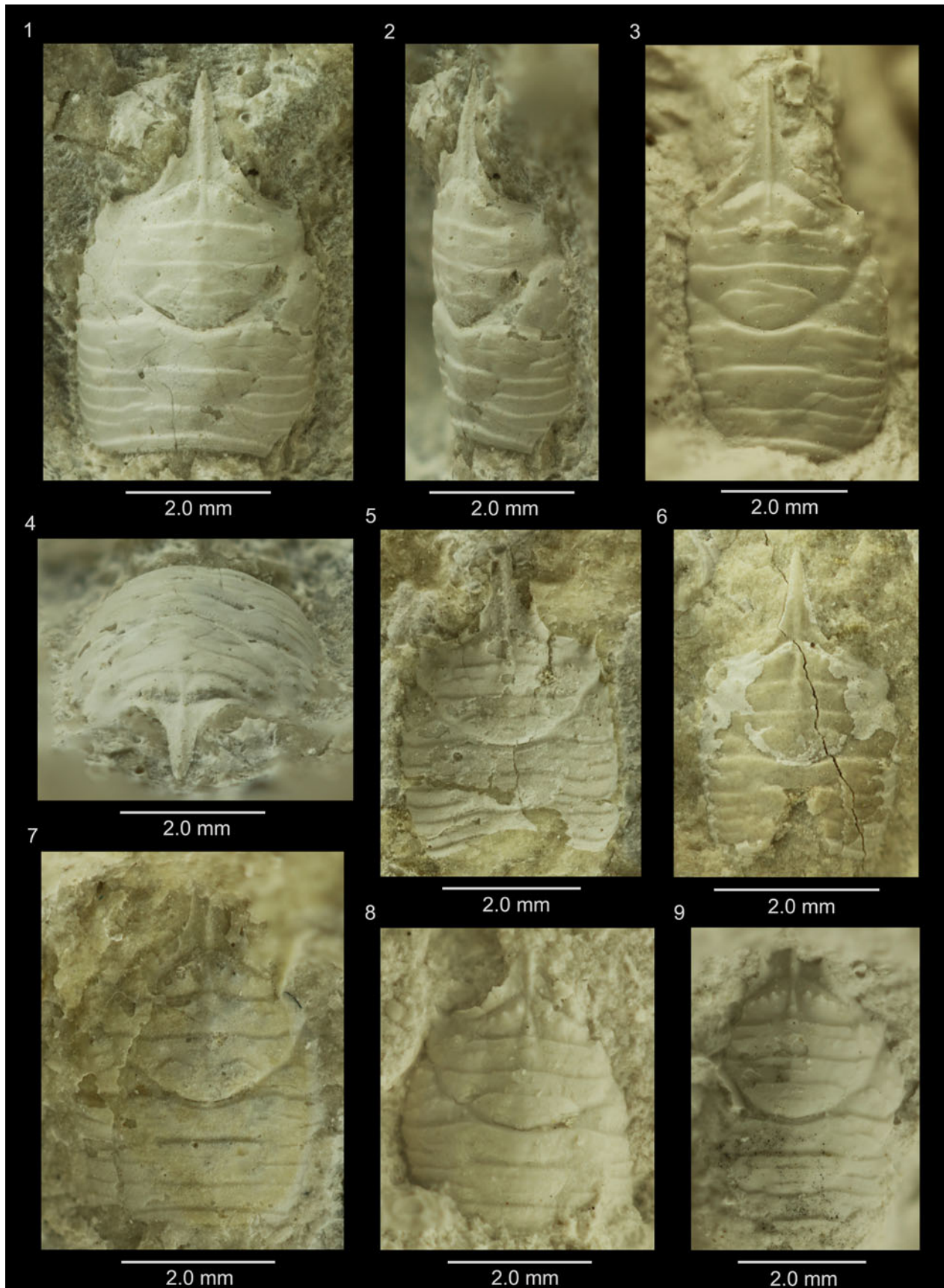


Figure 11. *Protomunida bennickei* n. sp. from the Paleocene (Danian) of Denmark. (1, 2, 4) Holotype OESM 11213, carapace: (1) dorsal view; (2) right lateral view; (4) frontal view. (3, 5–9) Carapaces in dorsal view: (3) paratype OESM 11211 (cast); (5) paratype OESM 11246; (6) paratype OESM 11248; (7) OESM 11247a; (8) OESM 11208 (cast); (9) OESM 11207 (cast).



Figure 12. *Protomunida eurekantha* n. sp. from the Paleocene (middle Danian) Faxø Formation of Denmark. (1, 2, 4) Holotype OESM 11255 (cast), carapace: (1) dorsal view; (2) right lateral view; (4) frontal view. (3, 5–9) Paratypes, carapaces in dorsal view: (3) OESM 11172; (5) OESM 11174; (6) OESM 11184; (7) OESM 11245; (8) OESM 11176; (9) OESM 11254.

- 2008 *Protomunida munidoides*; Wienberg Rasmussen et al., pl. 3.3.
 ? 2010 *Protomunida munidoides*; Damholt et al., fig. on p. 22.
 2014 *Protomunida munidoides*; Polkowsky, fig. 49, pl. 11.4.
 ? 2016 *Protomunida munidoides*; Klompmaker et al., fig. 3c.

Types.—Holotype: OESM 11255 (cast + external mold); paratypes: OESM 11172, OESM 11174, OESM 11176, OESM 11184, OESM 11245, and OESM 11254 (internal and external mold + cast).

Diagnosis.—Carapace excluding rostrum ~20–25% longer than wide; maximum width about mid-length. Rostrum with narrow, sharp, triangular central rostral spine; fairly flat but with faint keel on axis only at base rostrum. Lateral margins of carapace with spines on anterior two-thirds. Posterior margin slightly concave, rimmed, with spines. Spines present just posterior to transverse groove branching off cervical groove.

Occurrence.—Faxe Quarry, Denmark (55.26°N, 12.13°E); coral-bryozoan limestone of the Faxe Formation, Paleocene (middle Danian) (Lauridsen et al., 2012; Lauridsen and Bjerager, 2021). The Faxe Formation is dated as nannofossil zone NNTp2G-3 (Bjerager et al., 2018) using the zonation of Varol (1998), which is equivalent to lower Zone NP3 (Martini, 1971). In addition, ex situ specimens are found in Danian erratics from Zarrentin in northern Germany (Polkowsky, 2014) and erratics of Hesnæs beach (nannofossil subzone NNTp2C) in Denmark (OESM 11258) along with *Protomunida bennecke* n. sp.

Description.—Carapace excluding rostrum ~20–25% longer than wide, up to ~5 mm wide; weakly convex longitudinally, moderately convex transversely, maximum width about mid-length. Rostrum with very narrow, sharp, triangular central rostral spine; fairly flat but with faint keel on axis only at base rostrum; slightly downturned at distal half; one spine at base rostrum on either side of central rostral spine. Upper orbital margin concave. Forward spine at anterolateral angle. Epigastric regions distinctly bordered, triangular, with row of spines near anterior border. Hepatic regions small, weakly delimited. Protogastric and mesogastric regions not or poorly delimited, except for sharp tip of mesogastric process that may show a small tubercle. Cervical groove broadly U-shaped and distinct, somewhat sinuous more laterally, intersects with lateral margin posterior to hepatic region. Transverse grooves branching off cervical groove distinct, separating anterior and posterior branchial regions. Cardiac region appears straight at anterior border and straight to rounded posterior to it. Intestinal region not clearly defined. Lateral margins with spines on anterior two-thirds. Posterior margin slightly concave, rimmed, with at least two spines near position of lateral edges of cardiac region. Ornamentation consists of fairly continuous, transverse ridges on most of carapace; tubercles/spines on epibranchial regions and near anterior margin; ornamentation appears similar on internal molds and casts. Spines present just posterior to transverse groove

branching off cervical groove. Muscle scar impressions generally not discernable, except for posterior gastric muscles in OESM 11172. Posterior gastric pits within cervical groove expressed as slits. Ventral surface, abdomen, and appendages unknown.

Etymology.—The species name (*eurekantha*) is a merger of the Greek *Eureka* or εὕρηκα (*heúrēka*) meaning “I have found (it)” and the Greek ἀκανθα or *acantha* meaning spine. This name refers to the spines on the posterior margin of the carapace, which are diagnostic for this species and were first noted by one of us (S.L.J.) after casting external molds.

Materials.—Type specimens + OESM 11173, OESM 11175, OESM 11177, OESM 11179–11182, OESM 11185, OESM 11192, OESM 11220, OESM 11221, OESM 11223, OESM 11232, OESM 11235, OESM 11237, OESM 11244, OESM 11249 (cast + external mold), OESM 11252 (cast + external mold), OESM 11257 (cast, external mold, and internal mold + cuticle), and OESM 11258 (cast + external mold).

Measurements (mm).—OESM 11255: L = 4.6, W = 3.7; OESM 11172: L = 4.4, W = 3.7; OESM 11174: L = 3.6, W = 3.0; OESM 11184: L = 3.1, W = 2.5; OESM 11245: L = 5.3, W = 4.4; OESM 11176: L = 6.4, W = 5.3; OESM 11254: L = 4.4, W = 3.6.

Remarks.—No obvious ontogenetic variations are observed. In terms of intraspecific variation, the number of spines marking the anterior border of the epigastric regions appears to vary from two to five, the number of spines on the epibranchial regions varies from one to two, and the number of spines on the posterior margin varies from two to four. Taphonomic processes may have influenced the preservation of these spines.

Several specimens from the previous literature can be attributed to this new species with certainty because they bear spines on the posterior margin. Such spines were not previously recognized in galatheoids from Faxe, but spines at or near the posterior margin can be of prime taxonomic importance in distinguishing species in extant galatheoids (Macpherson, 2004, p. 249; Osawa and Takeda, 2007, p. 140; Macpherson et al., 2020, p. 24). The presence or absence of spines on the posterior margin is relatively constant in the same species in extant galatheoids (never zero to two or zero to four) (E. Macpherson, personal communication, 2021), and sexual dimorphism in spines on the dorsal carapace has not been observed (E. Macpherson, personal communication, 2020). When broken, the bases of these spines in fossil specimens can be observed after careful examination with a hand lens or microscope.

The main difference between all other species of *Protomunida* and *P. eurekantha* n. sp. is the presence of spines on the posterior margin, which are lacking in other species. Some additional differences per species are discussed briefly. A comparison with *P. bennecke* n. sp. was provided in the preceding. *Protomunida munidoides* and *P. ? pentaspinosa* lack the spines just posterior to the groove branching off the cervical groove, which are present in *P. eurekantha*. Moreover, *P. munidoides* bears a longer keel on the axis of the rostrum, and the base of

the central rostral spine appears wider in *P.?* *pentaspinosa*. Differences other than the presence/absence of spines on the posterior margin between *P. eurekantha* and *P. primaeva* are minimal. *Protomunida spitzbergica* bears more interrupted transverse ridges.

Family Munidopsidae Ortmann, 1892
Genus *Palaeomunidopsis* Van Straelen, 1925

Type and sole species.—*Palaeomunidopsis moutieri* Van Straelen, 1925 (Middle Jurassic [Bathonian]; France), by original designation.

Palaeomunidopsis moutieri Van Straelen, 1925

Figure 13

- 1923 *Gastrosacus moutieri* Van Straelen, p. 553.
1925 *Palaeomunidopsis moutieri* Van Straelen, p. 138, fig. 141, pl. 9.8.
1969 *Palaeomunidopsis moutieri*; Glaessner, p. R482–483, fig. 290.2.
2013 *Palaeomunidopsis moutieri*; Robins et al., fig. 6.16.
2019a *Palaeomunidopsis moutieri*; Fraaije et al., p. 291, 293.

Holotype.—Collection of Dr. Moutier from Caen. Carapace is presumed to be lost during World War II (Fraaije et al., 2019a).

Occurrence.—Giberville (Calvados), France; Calcaire de Caen Formation, Middle Jurassic (middle Bathonian).



Figure 13. The oldest galatheid known to date: *Palaeomunidopsis moutieri* Van Straelen, 1925, from the Middle Jurassic (middle Bathonian) Calcaire de Caen Formation of France. Carapace in dorsal view. Reproduced from Van Straelen (1925, pl. 9.8).

Description.—“The carapace is hardly wider behind than in front, its lateral margins are straight and almost parallel. The rostrum is very wide, appreciably triangular and appears to have been quite long, tending to be styliiform; it is a little depressed compared to the dorsal surface, at its base it has a small keel and its edges are marginalized. The antero-lateral angles of the carapace are rounded, they are attached to the rostrum by a smooth surface, limited on the internal side by a small groove. This surface corresponds to a small bead. The cervical groove is very deep, strongly concave towards the front, this depth is held in the antennal groove which follows it, this one is hardly marked. The gastric region is very prominent. The latero-posterior angles of the carapace are broadly rounded, projecting a little over the posterior marginal edge. Scaly tubercles, more or less arranged in rows, cover almost all parts of the cephalothorax. These tubercles have a tendency to become spiniform towards the lateral edges” (translated from Van Straelen, 1925, p. 308).

Remarks.—*Palaeomunidopsis moutieri* from the Middle Jurassic (middle Bathonian) of France was considered the oldest fossil representative of Galatheoidea, but Fraaije et al. (2019a) declared it a nomen dubium in the same paper in which they described a newly proposed oldest galatheid, *Gastrosacus raboeufi*, from the late Bathonian of France. We disagree with this nomen dubium as *P. moutieri* was published with a detailed description, a line drawing, and a photo. While the illustrations may not be the high quality preferred today, they fulfill the rules set within the ICZN (International Commission on Zoological Nomenclature, 1999, article 12). Although the holotype was presumed to be destroyed in World War II, it is clearly described by Van Straelen (1925). The line drawing is inaccurate because it does not match the photo closely (compare the course of the circumgastric groove for example), but the photo shows hallmark characters of a munidopsid: the strong circumgastric groove and the base of a wide rostrum accompanied by a medial keel. These characters were also described. Other characters described by Van Straelen (1925) such as the tubercular ornamentation, the well-defined gastric region, and lateral margins with spines are also mentioned in the diagnosis of Munidopsidae (Robins et al., 2013, p. 175). Van Straelen (1925) inferred the rostrum would be long, a character that is common in Jurassic Munidopsidae (Robins et al., 2013). A similar circumgastric groove would also be present in Gastrodoridae, Parapylochelidae, and Pylochelidae according to Fraaije et al. (2019a). However, the groove in the gastric region in Gastrodoridae is generally more V-shaped, more sinuous, and less circular than in *P. moutieri*, and gastrodorids do not have a wide rostral base (Van Bakel et al., 2008; Klomp maker et al., 2011; Fraaije et al., 2013; Krzemińska et al., 2020). Members of Parapylochelidae do not possess a circular groove in the gastric region and bear a short rostrum without a keel (Fraaije et al., 2012a, 2019b, 2020; Fraaije, 2014). Pylochelidae exhibit a gastric groove that is much more sinuous and V-shaped, and the rostrum appears short (Van Bakel et al., 2008; Fraaije et al., 2012b, 2019b; Fraaije, 2014). In conclusion, we reinstate *P. moutieri* as a munidopsid and oldest galatheid to date.

Gastrosacus raboeufi is only slightly younger than *P. moutieri* and is from the same region in France, warranting a further comparison between these two munidopsids. According to the photos available, some differences may be present. Van Straelen (1925) mentioned a wide rostrum, and it may indeed be wider than in *G. raboeufi*. Moreover, the tubercles of *P. moutieri* are said to have been arranged in rows, which is not obvious in *G. raboeufi*. Munidopsid specimens from the stratigraphic horizon in which *P. moutieri* was found and additional specimens of *G. raboeufi* would be most welcome for further comparisons and to evaluate the generic status of *Palaeomunidopsis* because the only specimen has many similarities to *Gastrosacus* von Meyer, 1851. For now, we keep the taxa separate within their respective genera.

Genus *Vetoplautus* Robins et al., 2013

Type and sole species.—*Vetoplautus latimarginus* Robins et al., 2013 (Late Jurassic [Tithonian]; Austria, Czech Republic), by original designation.

Vetoplautus latimarginus Robins et al., 2013

Figure 14

2013 *Vetoplautus latimarginus* Robins et al., 2013, p. 241, figs. 6.19, 15.3.

Holotype.—NHMW 2007z0149/0151.

Occurrence.—Holotype: reef limestone of the Ernstbrunn Limestone at the Ernstbrunn quarries, near Dörfles, Austria (Google Earth coordinates: ~48.55°N, ~16.35°E), Late Jurassic (middle–late Tithonian) (Zeiss, 2001). Additional specimen UF 269890: reef limestone of the Štramberk Limestone of locality 3 at level 6 of the Kotouč quarry, Czech

Republic (Google Earth coordinates: 49.583°N, 18.116°E), Late Jurassic (late early Tithonian) (Vašíček and Skupien, 2016; Vašíček et al., 2018).

Description.—Reference is made to Robins et al. (2013, p. 241). In addition, rostrum with broad base, triangular, with moderately strong keel along entire axis, lateral margins of rostrum containing spines, rostral surface with granules.

Materials.—UF 269890.

Measurements.—L = ~3.0 mm, W = 3.2 mm.

Remarks.—The new specimen represents the second occurrence and the third specimen of this species in addition to the holotype and paratype from the Tithonian of Ernstbrunn, Austria. The Czech specimen is slightly smaller than the holotype and shows additional features not seen in the type specimens, such as a complete rostrum.

Discussion

As of July 2021, 199 galatheoid species have been recorded from the fossil record, mostly originating from Europe. We add five species, thereby expanding their diversity by 2.5%. The Early Cretaceous (Barremian) Mexican galatheoid fauna was initially thought to consist of three known species (Vega et al., 2019), but the fauna is more endemic and consists of at least two new species as described herein. Consequently, the North American fossil record of galatheoids now consists of 17 species. As for most fossil galatheoids, most taxa discussed herein were found among reef-associated limestones. Although coral reefs are suggested to have played a key role in the high diversity and radiation of galatheoids in those environments during the Late Jurassic (e.g., Robins and Klompmaker, 2019), the

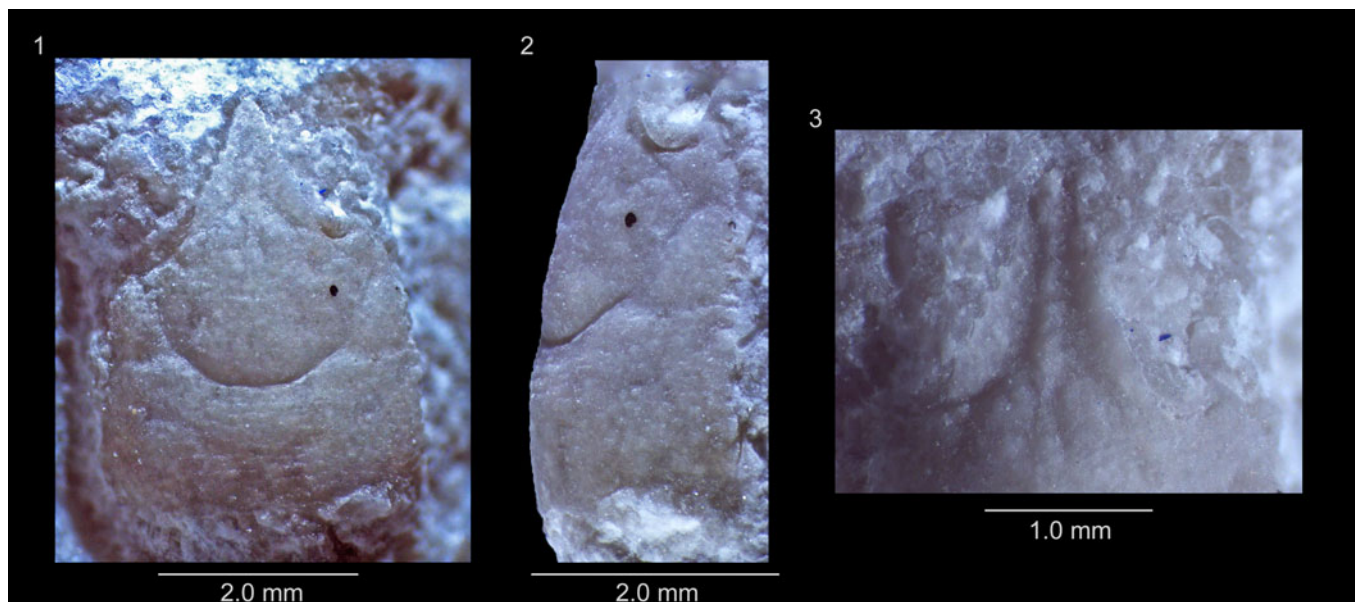


Figure 14. *Vetoplautus latimarginus* Robins et al., 2013, from the Upper Jurassic (Tithonian) Štramberk Limestone of the Czech Republic, UF 269890, carapace: (1) dorsal view; (2) right lateral view; (3) rostral view.

relative preservation potential of galatheoids in reef environments versus other habitats has been insufficiently studied. However, squat lobsters are not exquisitely preserved in these environments generally because appendages and ventral surface are nearly always disarticulated from dorsal appendages. Moreover, many extant galatheoids are found in the Indo-West-Pacific Coral Triangle region (Schnabel et al., 2011) and various galatheoids live in symbiosis with corals (Baeza, 2011). Therefore, although a preservational signal cannot be fully excluded, a biological explanation for their high diversity in reef-associated settings is plausible.

Another aspect of preservation relates to anatomical details on the carapace. Whereas the fossil record of galatheoids relies heavily on internal molds and carapace specimens with cuticle preserved, external molds are often not collected. A substantial part of extant galatheoids show spines on multiple carapace regions, which are used to diagnose taxa (Baba et al., 2009; Macpherson and Robainas-Barcia, 2015; Rodríguez-Flores et al., 2018; Schnabel and Ah Yong, 2019). The discovery of *Protomunida eurekantha* n. sp. from the Danian of Denmark, principally by making casts of external molds, led to the discovery of distinct spines on the posterior margin by one of us (S.L.J.) in many specimens (Fig. 12). Small spines in the already small galatheoid carapaces often break, making them harder to observe on internal molds and specimens with cuticle. Whereas the Faxe decapod fauna has been very well studied systematically (von Fischer-Benzon, 1866; Segerberg, 1900; Jakobsen and Collins, 1997; Jakobsen et al., 2020), this relative common galatheoid species remained undescribed till now. Therefore, more frequent collecting and studying of external molds for galatheoids and other decapods could aid in the discovery of more cryptic species.

Acknowledgments

We thank E. MacPherson (Centro de Estudios Avanzados de Blanes, Spain) for sharing insights on morphological details of modern galatheoids; A. Busulini (Società Veneziana di Scienze Naturali, Museo di Storia Naturale) helped to get permission to reuse images in Beschin et al. (2016) and kindly provided Figure 4; M. Nose (Bayerische Staatssammlung für Paläontologie und Geologie, Germany) provided access to specimens and museum numbers; A. Nützel (Bayerische Staatssammlung für Paläontologie und Geologie, Germany) provided access to photography equipment for the same specimens in 2014. We are grateful to the two anonymous reviewers and the editors for providing comments that improved this paper. The specimen of *Vetoplautus latimarginus* was collected in 2013 by the authors during a field trip as part of the 5th Symposium on Mesozoic and Cenozoic Decapod Crustaceans, so we thank the organizing committee; R. Portell (Florida Museum of Natural History) arranged a loan of the specimen, photographed using equipment of the University of California Museum of Paleontology. L. Appleton (University of Texas at Austin) arranged the loan of the holotype of *Galathea? cretacea* and a specimen previously assigned to this species. We thank M. Florence (Smithsonian National Museum of Natural History) for access to the holotype of *Eomunidopsis cobhani* after the

9th International Crustacean Congress in 2018 and J. Milàn (Geomuseum Faxe) for providing museum numbers. S.B. Andersen collected part of the *Protomunida* specimens from Faxe and P. Bennicke collected all *Protomunida* specimens from Hesnæs Beach. A.R. Bashforth (Natural History Museum of Denmark) provided information on the lectotype specimen museum numbers. C. Olsen (GEUS) is thanked for preparing the nannofossil sample from the Hesnæs Beach chalk.

Data availability statement

Data available (Appendix 1) from the Zenodo Digital Repository: <https://doi.org/10.5281/zenodo.6380818>.

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