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# Peak diversity of Cretaceous galatheoids (Crustacea, Decapoda) from northern Spain

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ABSTRACT

Galatheoids, squat lobsters, have recently received much systematic attention. We describe, discuss, and illustrate ten species of galatheoids found in the mid-Cretaceous (Albian/Cenomanian) Aldoirar patch reef in northern Spain. All are found in the abandoned Koskobilo quarry. The new taxa include two new genera, *Hispanigalathea* gen. nov. and *Nykteripteryx* gen. nov., and four new species: *Hispanigalathea pseudolaevis* sp. nov., *H. tuberosa* sp. nov., *Nykteripteryx rostrata* sp. nov., and *Eomunidopsis aldoirarensis* sp. nov. We redescribe *E. navarrensis*, *E. orobensis*, *Paragalathea ruizi*, *P. straeleni*, and *P. multisquamata*. Finally, an indeterminate galatheoid is also recognized. To date, this is by far the richest galatheoid fauna known in terms of the number of species and genera from the Cretaceous, both on the locality and formation level. This diversity is probably related to the reef facies in which the galatheoids were discovered.

## 1. Introduction

Suprageneric classification of Recent and fossil galatheoids has recently received attention by neontologists (Ahyong et al., 2010; Schnabel et al., 2011). From the fossil record, approximately 100 species have been described formally, whereas over 900 species of galatheoids excluding Chirostylidae are known from the Recent (De Grave et al., 2009) (the Chirostylidae were recently classified in their own superfamily, the Chirostyloidea (see Schnabel et al., 2011)). This suggests that many more species might be present in the fossil record, which is exemplified by Robins (2008) for the Upper Jurassic of Europe. The goal of this paper is to describe and discuss ten species of galatheoids referred to five genera from the mid-Cretaceous (Albian/Cenomanian) Aldoirar patch reef in northern Spain.

## 2. Geologic setting and previous research

The specimens described herein originate from three localities in northern Spain (Fig. 1). Approximately 2 km southwest of Alsasua are the Koskobilo (42° 52′ 56″ N / 2° 11′ 59″ W) and the Olazagutía (42° 53′ 03″ N / 2° 12′ 17″ W) quarries, of which the former is abandoned and the latter is still in use. Both are located in the fossil Aldoirar patch reef as part of the Albian/Cenomanian Albeniz Unit of the Eguino Formation (López-Horgue et al., 1996). The third locality is the contemporaneous Monte Orobe quarry in the Orobe patch reef (42° 55′00″ N / 2° 12′28″ W), 4 km north of Koskobilo (see López-Horgue et al., 1996), from which we used some comparative material. All localities are characterized by reef limestones containing mainly corals, algae, orbitolinid foraminifera, echinoid spines, sponges, brachiopods, bivalves, and decapod crustaceans.

Non-galatheoid decapod crustaceans have been reported previously from the Aldoirar patch reef by Fraaije et al. (2009, 2012) and Klompmaker et al. (2011a–c, 2012, in press). The Monte Orobe quarry has yielded many decapods including six galatheoids (Van Straelen, 1940, 1944; Ruiz de Gaona, 1943; Vía Boada, 1981, 1982; Gómez-Alba, 1989; López-Horgue et al., 1996; Fraaije et al., 2008; Artal et al., in press).

## 3. Systematic palaeontology

For this paper, the recent galatheoid classifications of Ahyong et al. (2010) and Schweitzer et al. (2010) are largely used. The terminology that is used for the carapace regions and grooves is given in Fig. 2. Symbols used for the synonymy lists are based on Matthews (1973, p. 718): v, specimens described in this article were physically studied; *, with the publication of this article the species

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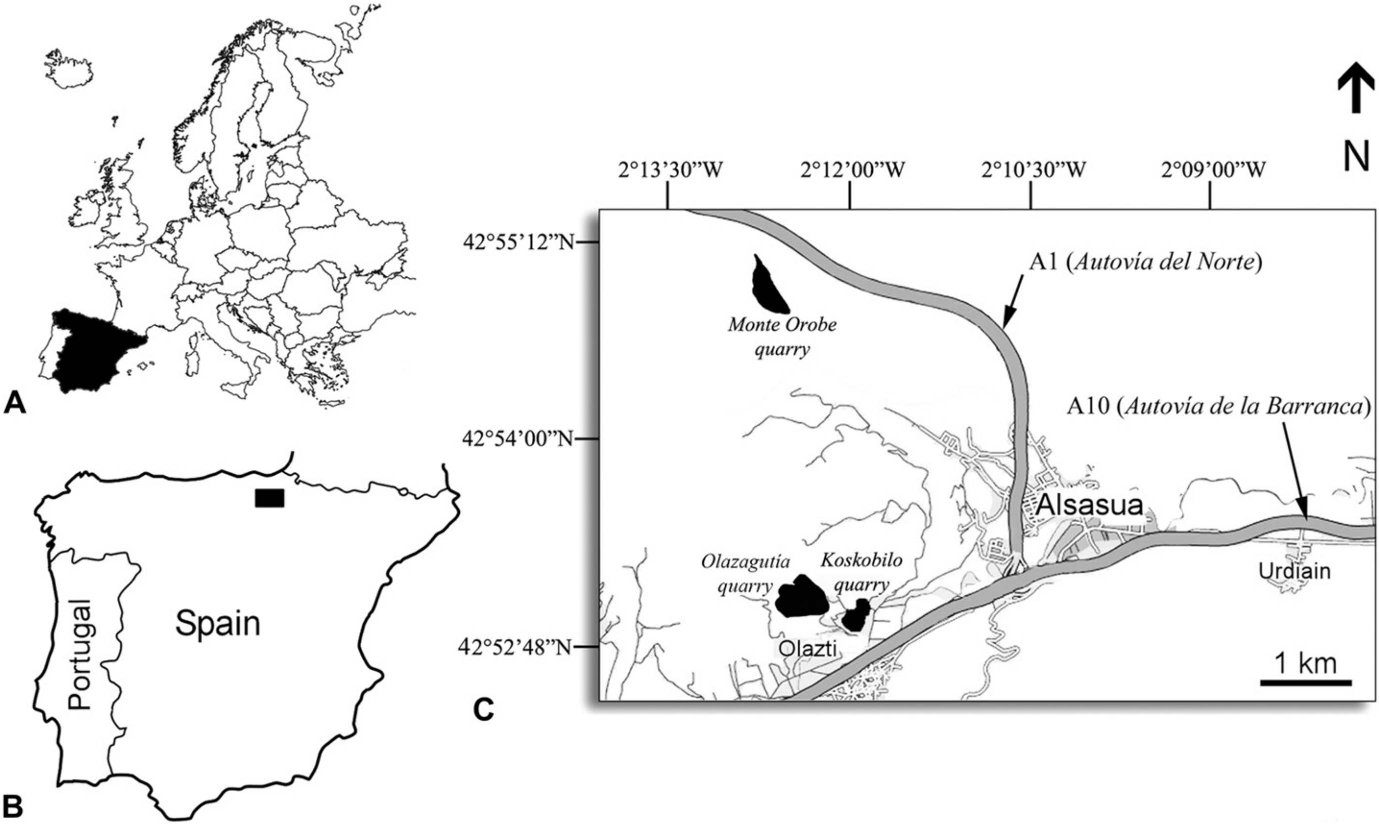

**Fig. 1.** A geographic overview of the location of the study area. A, location of Spain in Europe. B, location of the study area in northern Spain. C, location of the Koskobilo, Olazagutía, and Monte Orobe quarries in which the Albian/Cenomanian Albeniz Unit of the Eguino Formation is exposed and from which the decapods originate. Modified after Fraaije et al. (2008, fig. 1) and Klompmaker et al. (2011c, fig. 1).

is regarded as valid under the terms of article 11 of the ICZN; v*, we have seen the type of the species.

*Institutional abbreviations*. To denote the repositories of material described and illustrated, the following abbreviations are used: MAB, Oertijdmuseum De Groene Poort, Boxtel, The Netherlands, and MGSB, Museo Geológico del Seminario de Barcelona, Barcelona, Spain.

Order Decapoda Latreille, 1802
Suborder Pleocyemata Burkenroad, 1963
Infraorder Anomura MacLeay, 1838
Superfamily Galatheoidea Samouelle, 1819

*Included families*. Galatheidae Samouelle, 1819; Munididae Ahyong et al., 2010; Munidopsidae Ortmann, 1898; and Porcellanidae Haworth, 1825.

Family Galatheidae Samouelle, 1819

*Included fossil (F) and Recent (R) genera*. *Acanthogalathea* Müller and Collins, 1991 (F); *Alainius* Baba, 1991 (R); *Allogalathea* Baba, 1969 (R); *Allomunida* Baba, 1988 (R); *Coralliogalathea* Baba and Javed, 1974 (R); *Eomunidopsis* Vía Boada, 1981 (F); *Fennerogalathea* Baba, 1988 (R); *Galathea* Fabricius, 1793 (type) (R, F); *Hispanigalathea* herein (F); *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); *Mesogalathea* Houša, 1963 (F); *Nanogalathea* Tirmizi and Javed, 1980 (R); *Palaeomunida* Lőrenthey, 1901 (F); *Paragalathea* Patrulius, 1959 (F); *Phylladiorhynchus* Baba, 1969 (R); and *Spathagalathea* De Angeli and Garassino, 2002 (F).

Genus *Eomunidopsis* Vía Boada, 1981

*Type species*. *Eomunidopsis orobensis* (Ruiz de Gaona, 1943)

*Included species*. *Eomunidopsis aldoirarensis* new species herein; *E. eutecta* (Moericke, 1889); *E. kinokunica* Karasawa, Ohara, Kato, 2008; *E. limonitica* (Stenzel, 1945); *E. meerssensis* Collins, Fraaye, Jagt, 1995; *E. neojurensis* Patrulius, 1959 (=*Galathea antiqua* Moericke, 1889); *E. navarrensis* (Van Straelen, 1940); *E. orobensis* (Ruiz de Gaona, 1943); *E. portlandica* Fraaye and Collins, 1996; and *E. zitteli* (Moericke, 1889).

*Remarks*. Some confusion has arisen over which species is the type species of this genus. For example, Vía Boada (1982), Bishop (1985), and Karasawa et al. (2008) mentioned *E. navarrensis* as the type species. Vía Boada (1981, p. 249), however, stated that "*E. orobensis* est choisie comme espèce-type" in erecting *Eomunidopsis*, which is why we consider *E. orobensis* to be the type species of the genus.

The Jurassic species *E. neojurensis* and *E. portlandica* appear somewhat different from the other species in that their overall ornamentation is more tubercular. Additionally, *E. zitteli* has a differently styled keel on the rostrum compared to other species of *Eomunidopsis*. We suggest that a revision of the genus may be necessary, but this is not within the scope of this paper. A revision will be carried out by one of us (CMR) in the future.

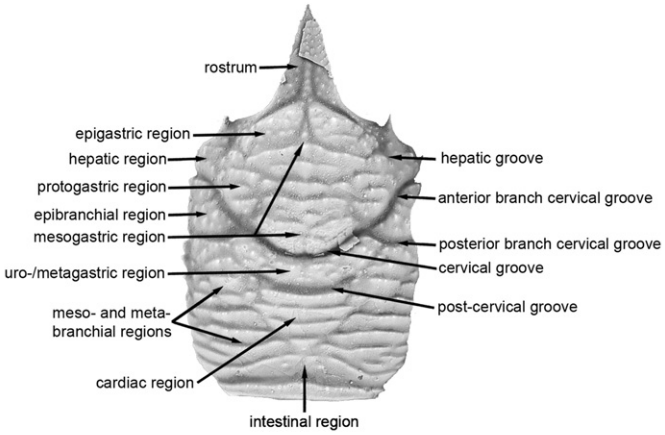

**Fig. 2.** The terminology for galatheoid carapace regions and grooves used in this study.

### *Eomunidopsis aldoirarensis* sp. nov.

Fig. 3

*Derivation of name*. After the fossilized Aldoirar patch reef in which the specimens were found.

*Types*. The holotype (MGSB 77716, Fig. 3C) is deposited in Museo Geológico del Seminario de Barcelona, Spain; paratypes (MAB k2529, 2530, 2534, 2974, 2975) are housed in the collections of the Oertijdmuseum De Groene Poort, Boxtel, The Netherlands.

*Other material examined*. Four specimens (MAB k2532, 2536, 2617, and 3059) from the abandoned Koskobilo quarry.

*Type locality*. Koskobilo quarry, northern Spain.

*Stratigraphic horizon*. The Albian/Cenomanian Aldoirar patch reef within the Albeniz Unit of the Eguino Formation (see López-Horgue et al., 1996).

*Diagnosis*. Carapace, excluding rostrum, 14–30% longer than wide, weakly convex longitudinally. Long, triangular rostrum with three spines at tip. Lateral margins approximately parallel, covered with anterolaterally directed spines on anterior half (rostrum not included). Posterior margin slightly concave. Protogastric and mesogastric regions confluent, the latter with relatively wide anterior process. Cardiac region subtriangular to rectangular transversely, best defined anteriorly. Carapace covered with transverse ridges, which show a more tubercular character anterior to cardiac region, may seem without ridges on epibranchial, epigastric, and hepatic regions.

*Description*. Carapace, excluding rostrum, 14–30% longer than wide (Table 1), moderately convex transversely, weakly so longitudinally. Long, triangular rostrum with three spines at tip, numerous tiny spines present on lateral borders; median ridge delimited by longitudinal grooves, fades out half-way along rostrum. Orbits seem shallow. Supraorbital margin with one forward directed spine. Lateral margins nearly parallel, rounded at posterior edges, covered with anterolaterally directed spines on anterior half (rostrum not included). Posterior margin slightly concave. Epigastric regions elongated transversely, divided axially by tip of mesogastric region. Protogastric and mesogastric regions confluent. Small hepatic region separated from protogastric region by weak posterolaterally oriented hepatic groove. Epibranchial region bounded between anterior and posterior branch of cervical groove on lateral part of carapace. Wider than long uro-/metagastric region well delimited anteriorly and posteriorly. Cardiac region subtriangular to rectangular transversely, best defined anteriorly. Meso- and metabranchial regions confluent. Intestinal region not observed. Strong cervical groove broadly concave forward, with two branches on lateral part of carapace; anterior one anterolaterally directed at first, then curves more laterally near lateral margin; posterior branch nearly straight. Moderately strong, straight post-cervical groove. Moderately strong, convex-forward groove just anterior to posterior margin. Carapace covered with transverse ridges, which show a more tubercular character anterior to cardiac region, may seem without ridges on epibranchial, epigastric, and hepatic regions. Rostrum covered with granules. Mesogastric region may show some scabrous ornamentation on posteriormost part. Venter, abdomen, appendages, and cuticle absent.

*Remarks*. Intraspecific variation can be observed in the shape of the cardiac region. Some specimens seem more subtriangular and some subrectangular (compare Fig. 3B, F with A, D, and C). Ontogenetic variation could not be found.

*Eomunidopsis aldoirarensis* has only been found in the Koskobilo quarry so far. Evidence suggests that it is endemic to the Aldoirar patch reef.

*Eomunidopsis aldoirarensis* differs from *E. eutecta* from the Late Jurassic (Tithonian) Stramberk Limestones of Poland in that the latter widens toward the posterior carapace, whereas the lateral margins of *E. aldoirarensis* are parallel. Additionally, the transverse ridges on the gastric region are less continuous in character in *E. aldoirarensis*, and the base of the rostrum bears some granules, whereas it is covered with scale-like ornamentation in *E. eutecta*. *Eomunidopsis aldoirarensis* differs from *E. kinokunica* from the Lower Cretaceous (Barremian) of Japan in that the former bears more irregular/tubercular ridges in the anterior half of the carapace (rostrum excluded). Karasawa et al. (2008) reported the lateral margins of *E. kinokunica* to be smooth and without spines; in *E. aldoirarensis* they contain spines on the anterior part. They also reported that the carapace is moderately convex longitudinally in *E. kinokunica*, but it is only slightly convex in *E. aldoirarensis*. Furthermore, the anterior border of the cardiac region is less defined in *E. kinokunica*. Lastly, the posterior margin and the groove anterior to it in *E. kinokunica* appear nearly straight, but both are slightly concave in *E. aldoirarensis*. *Eomunidopsis aldoirarensis* is different from *E. limonitica* from the mid-Cretaceous (Albian/Cenomanian) of the United States (Texas) in that the latter has well-defined mesogastric and cardiac regions, which is less so in *E. aldoirarensis* in which the mesogastric and protogastric regions are confluent and the cardiac region is weakly defined laterally. Hence, the ridges in the gastric region are less wide in *E. limonitica*. These ridges are more irregular/tubercular ridges in the anterior half of the carapace (rostrum excluded) in *E. aldoirarensis*. Moreover, the anterior process of the mesogastric region is longer in *E. limonitica*. Additionally, the hepatic groove of *E. limonitica* is longer. Lastly, the anterior branch of the cervical groove appears straight in *E. limonitica*, but somewhat curved to a more lateral course in its lateralmost part in *E. aldoirarensis*. Collins et al. (1995) mentioned that the upper orbital margin of *E. meerssensis* from the Upper Cretaceous (Maastrichtian) of the Netherlands possessed 4–5 uneven spinules, in *E. aldoirarensis* there is only one. Transverse ridges are present on the epibranchial and protogastric regions in *E. meerssensis*, but they are more irregular/tubercular in *E. orobensis*. *Eomunidopsis aldoirarensis* differs from *E. navarrensis* from the mid-Cretaceous (Albian/Cenomanian) of Spain in that the former exhibits a broader, more pronounced anterior process of the mesogastric region. Additionally, the ornamentation is distinctly


A
B
C
D
E
F
G
H
I
J

**Table 1**
Measurement of specimens of nine galatheoid species. Measurements from the undetermined galatheoid could not be given due to the incompleteness of the specimen. Specimens are from Koskobilo, unless indicated otherwise.

| | Maximum length incl. rostrum (mm) | Maximum length excl. rostrum (mm) | Maximum width (mm) | Length from base rostrum to cervical groove (mm) | Length (incl. rostrum)/ Width | Length (excl. rostrum)/ Width | Length from base rostrum to cervical groove/ Maximum length excl. rostrum |
|---|---|---|---|---|---|---|---|
| *Eomunidopsis aldoirarensis* sp. nov., MAB k2534, paratype | | | 6.8 | 4.5 | | | |
| *E. aldoirarensis* sp. nov., MAB k2529, paratype | 8.0 | 5.7 | 5.0 | 3.0 | 1.61 | 1.14 | 0.52 |
| *E. aldoirarensis* sp. nov., MGSB 77716, holotype | 8.2 | 6.0 | 4.9 | 3.1 | 1.69 | 1.24 | 0.51 |
| *E. aldoirarensis* sp. nov., MAB k2530, paratype | 8.0 | 5.9 | 4.7 | 3.2 | 1.72 | 1.27 | 0.54 |
| *E. aldoirarensis* sp. nov., MAB k2974, paratype | | | 4.2 | 2.7 | | | |
| *E. aldoirarensis* sp. nov., MAB k2975, paratype | | 3.4 | 2.7 | 1.8 | | 1.25 | 0.53 |
| *E. navarrensis*, MAB k2924 | | | 10.6 | | | | |
| *E. navarrensis*, MAB k2925 | | | | 5.9 | | | |
| *E. navarrensis*, MAB k2926 | 9.2 | 6.9 | 5.6 | 3.7 | 1.63 | 1.22 | 0.54 |
| *E. navarrensis*, MAB k2618 | | 12.5 | 11.3 | 6.2 | | 1.11 | 0.50 |
| *E. navarrensis*, MAB k2535 | 8.4 | 6.2 | 5.7 | 3.2 | 1.48 | 1.10 | 0.51 |
| *E. navarrensis*, MAB k2927 | 5.1 | 3.9 | 3.3 | 2.1 | 1.57 | 1.21 | 0.52 |
| *E. navarrensis*, MAB k2928 | | 1.5 | 1.4 | 0.8 | | 1.05 | 0.56 |
| *E. orobensis*, MAB k2929 | | | 8.0 | | | | |
| *E. orobensis*, MAB k2930 | | 12.8 | 10.1 | 6.7 | | 1.26 | 0.52 |
| *E. orobensis*, MAB k2817 | | 7.5 | 6.1 | 3.9 | | 1.23 | 0.52 |
| *E. orobensis*, MAB k2931 | | | 9.6 | 6.0 | | | |
| *E. orobensis*, MAB k2932 | 9.4 | 7.1 | 5.5 | 3.6 | 1.70 | 1.29 | 0.51 |
| *E. orobensis*, MAB k2933 | | 4.5 | 3.6 | 2.4 | | 1.25 | 0.53 |
| *Paragalathea multisquamata*, MAB k2977 | | | 2.3 | 1.5 | | | |
| *P. multisquamata*, MAB k3179 | | 5.0 | 4.6 | 2.7 | | 1.11 | 0.53 |
| *P. multisquamata*, MAB k2579 | | | 5.9 | 3.9 | | | |
| *P. multisquamata*, MGSB 28118, holotype, Monte Orobe | | 7.6 | 6.6 | 4.3 | | 1.16 | 0.56 |
| *P. ruizi*, MAB k2598 | 7.1 | 5.5 | 5.2 | 3.1 | 1.36 | 1.05 | 0.56 |
| *P. ruizi*, MAB k2971 | | 5.8 | 5.0 | 3.4 | | 1.16 | 0.57 |
| *P. ruizi*, MAB k2833 | | 4.2 | 3.7 | 2.4 | | 1.14 | 0.58 |
| *P. ruizi*, MAB k2972 | 4.8 | 3.5 | 3.1 | 2.0 | 1.55 | 1.14 | 0.57 |
| *P. ruizi*, MAB k2973 | | 2.2 | 1.9 | 1.3 | | 1.13 | 0.58 |
| *P. straeleni*, MAB k2978 | | | 11.0 | | | | |
| *P. straeleni*, MAB k3171 | | 19.2 | 17.1 | 10.8 | | 1.13 | 0.56 |
| *P. straeleni*, MAB k3173 | | 6.9 | 6.1 | 3.9 | | 1.13 | 0.57 |
| *P. straeleni*, MGSB 11519/2, “neotype”, Monte Orobe | 20.8 | 17.6 | 15.1 | 9.7 | 1.38 | 1.17 | 0.55 |
| *Hispanigalathea pseudolaevis* gen. et sp. nov., MAB k2976, paratype | | 3.3 | 2.8 | 1.6 | | 1.15 | 0.50 |
| *H. pseudolaevis* gen. et sp. nov., MAB k2847, paratype | 4.8 | 3.9 | 3.2 | 1.9 | 1.47 | 1.21 | 0.49 |
| *H. pseudolaevis* gen. et sp. nov., MGSB 77717, holotype | 4.6 | 3.6 | 3.1 | 1.8 | 1.49 | 1.18 | 0.49 |
| *H. pseudolaevis* gen. et sp. nov., MAB k3073, paratype | | 4.0 | 3.3 | 1.8 | | 1.20 | 0.46 |
| *H. pseudolaevis* gen. et sp. nov., MAB k3016, paratype | 3.0 | 2.4 | 2.0 | 1.2 | | 1.16 | 0.50 |
| *H. tuberosa* gen. et sp. nov., MGSB 77718, holotype | | 5.9 | 4.6 | 3.1 | | 1.28 | 0.53 |
| *Nykteripteryx rostrata* gen. et sp. nov., MGSB 77719, holotype | 3.2 | 2.4 | 2.6 | 1.3 | 1.27 | 0.95 | 0.54 |
| *N. rostrata* gen. et sp. nov., MAB k2979, paratype | | | 2.6 | 1.4 | | | |
| *N. rostrata* gen. et sp. nov., MAB k3187, paratype | | | 2.9 | | | | |
| *N. rostrata* gen. et sp. nov., MAB k2980, paratype | | 2.0 | 2.4 | 1.2 | | 0.85 | 0.58 |

**Fig. 3.** Specimens of *Eomunidopsis aldoirarensis* sp. nov. from Koskobilo. A–F, dorsal carapaces. A, MAB k2534, paratype. B, MAB k2529, paratype. C, MGSB 77716, holotype. D, MAB k2530, paratype with a bopyrid swelling. E, MAB k2974, paratype. F, MAB k2975, paratype. G–J, lateral carapaces. G, MAB k2529, paratype. H, MGSB 77716, holotype. I, MAB k2530, paratype with a bopyrid swelling. J, MAB k2975, paratype. All scale bars represent 1 mm.

different: *E. aldoirarensis* possesses more irregular/tubercular transverse ridges anterior to the cardiac region in comparison to *E. navarrensis*. *Eomunidopsis aldoirarensis* differs substantially from *E. neojurensis*, first described from the Late Jurassic (Tithonian) Stramberk Limestones of Poland, because the former does not exhibit a well-defined mesogastric region, which the latter does. The cervical groove of *E. neojurensis* intersects the anterolateral margin more anteriorly than in the case of *E. aldoirarensis*. The ornamentation of the carapace is vastly different: *E. neojurensis* bears tubercles on the carapace except for the cardiac region and posterior to it where transverse ridges seem to prevail, whereas *E. aldoirarensis* exhibits transverse ridges mostly. Furthermore, the uro-/metagastric region is much shorter longitudinally than that of *E. aldoirarensis*. *Eomunidopsis neojurensis* does not show spines on the lateral margin, as seen in *E. aldoirarensis*. Lastly, the cardiac region of *E. neojurensis* is wider. The mesogastric region of *Eomunidopsis aldoirarensis* is less defined in the posterior part than in *E. orobensis* from the mid-Cretaceous (Albian/Cenomanian) of Spain. The rostrum of *E. aldoirarensis* is different in that it bears two lateral spines near the tip, which is not the case in *E. orobensis*. The cardiac region is delimited anteriorly by a somewhat concave-forward post-cervical groove in *E. orobensis*, whereas it is delimited anteriorly by a straight post-cervical groove in *E. aldoirarensis*. The posterior margin of *E. orobensis* is straight; it is slightly concave in *E. aldoirarensis*. Other differences are the wider anterior process of the mesogastric region in *E. aldoirarensis*, the straighter posterior branch of the cervical groove on the lateral part of the carapace, and a lower number and less prominent spines on the lateral margins. *Eomunidopsis aldoirarensis* differs from *E. portlandica* from Late Jurassic rocks in England in that the latter bears tubercles on the carapace except on the cardiac region and posterior to it where transverse ridges seem to prevail, whereas *E. aldoirarensis* bears transverse ridges on the majority of the carapace. The sole specimen of *E. portlandica* does not show the spines on the lateral margin, as seen in *E. aldoirarensis*. Lastly, *E. aldoirarensis* exhibits a broader, more pronounced anterior process of the mesogastric region. *Eomunidopsis aldoirarensis* differs from *E. zitteli* from the Late Jurassic (Tithonian) Stramberk Limestones of Poland in several aspects: the entire mesogastric region is only defined at the anteriormost part in *E. aldoirarensis*, whereas the entire mesogastric region of *E. zitteli* is defined by grooves; the rostrum of *E. aldoirarensis* does not have a keel along the entire axis, whereas *E. zitteli* does; and *E. aldoirarensis* bears a relatively small cardiac region.

*Eomunidopsis navarrensis* (Van Straelen, 1940)
Fig. 4

* 1940 *Galathea navarrensis* Van Straelen, pp. 2, 3, pls. 1.3, 1.4.
1950 *Galathea navarrensis* Van Straelen: Bataller, p. 421, 1 fig.
1981 *Eomunidopsis navarrensis* (Van Straelen): Vía Boada, p. 250, fig. 4.
v 1982 *Eomunidopsis navarrensis* (Van Straelen): Vía Boada, pp. 119–122, fig. 4, pls. 2.3–2.7.
1989 *Eomunidopsis navarrensis* (Van Straelen): Gómez-Alba, p. 26, pl. 1.5.

*Material*. Twenty-four specimens (MAB k2533, 2535, 2580, 2616, 2618, 2621, 2652, 2798, 2799, 2803, 2805, 2807, 2924–2928, 3064, 3066, 3067, 3070, and 3074–3076) from the abandoned Koskobilo

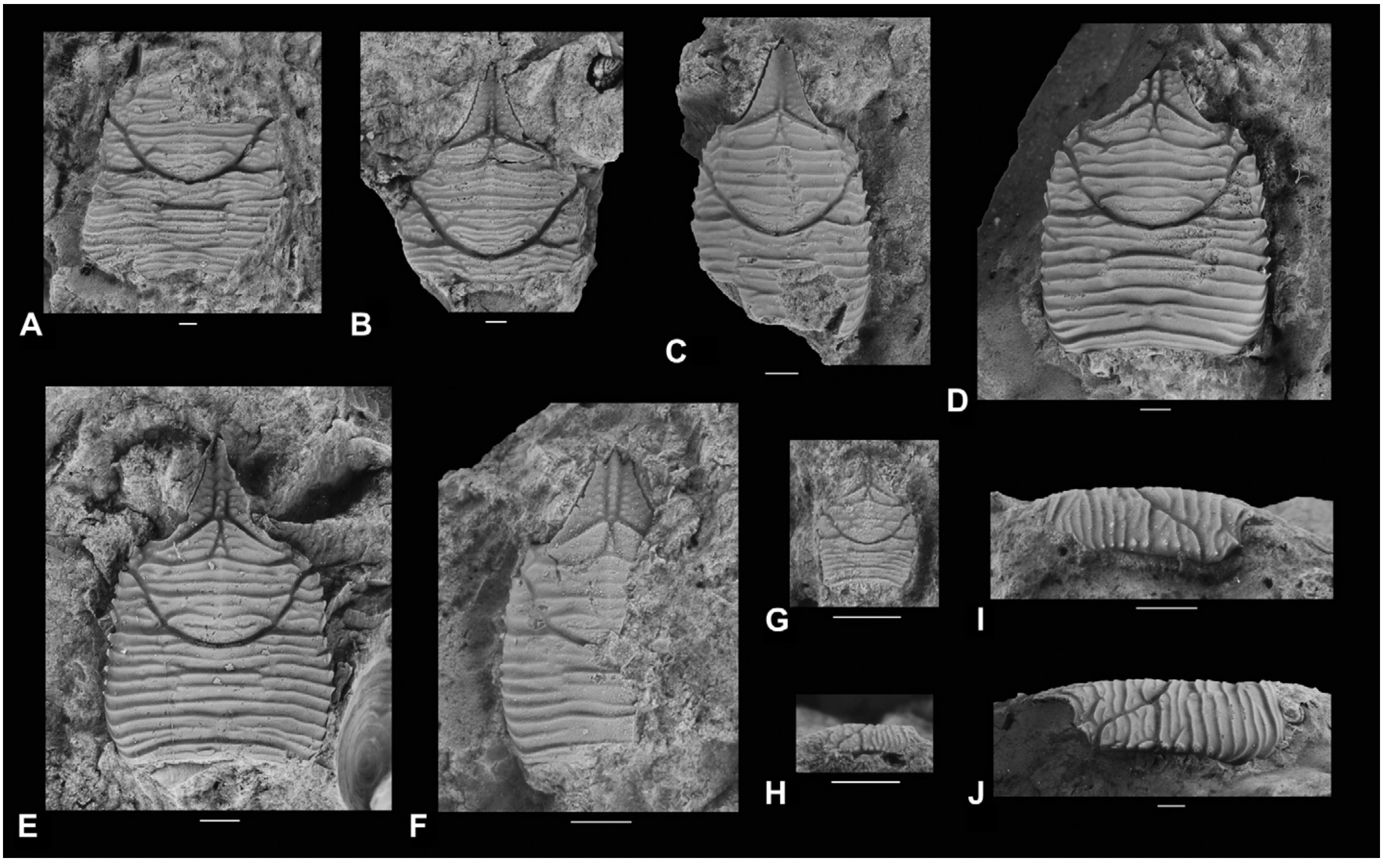

**Fig. 4.** Specimens of *Eomunidopsis navarrensis* (Van Straelen, 1940) from Koskobilo. A–G, dorsal carapaces. A, MAB k2924 with a bopyrid swelling. B, MAB k2925. C, MAB k2926. D, MAB k2618. E, MAB k2535. F, MAB k2927. G, MAB k2928. H–J, lateral carapaces. H, MAB k2928. I, MAB k2805. J, MAB k2618. All scale bars represent 1 mm.

quarry southwest of Alsasua (northern Spain). The neotype from the contemporaneous strata of Monte Orobe (MGSB 28122) was also studied.

*Stratigraphic horizon*. The species was collected from the abandoned Koskobilo quarry in the Albian/Cenomanian Aldoirar patch reef. It is also found in the Monte Orobe quarry in the Albian/Cenomanian Orobe patch reef.

*Diagnosis*. Carapace, excluding rostrum, 5–22% wider than long, narrowing toward the anterior, maximum width near posterior of carapace, weakly convex longitudinally. Anterior two-thirds of lateral margin with anterolaterally directed spines. Posterior margin slightly concave. Long triangular rostrum with pointed tip and two adjacent spines. Mesogastric and protogastric regions confluent. Cardiac region rectangular transversely. Dorsal carapace covered with many regular, transverse ridges.

*Emended description*. Carapace, [excluding] rostrum, [5–22%] longer than wide (Table 1), with the lateral sides converging slightly forward [in larger specimens]; dorsal surface covered with broad, transverse, overlapping, very sharp ridges (striations), [moderately convex transversely, weakly so longitudinally]. The ends of each lateral ridge possess a spine, very well preserved on large specimens. These spines are aligned on the lateral edges, almost straight from the carapace. Three [or four] of these spines correspond to the ridges that are connected to the [epibranchial region], five or six correspond to the anterior and middle lobes of the branchial region. The ridges on the postbranchial lobes do not end in a lateral spine and curl and shrink sharply downward to the posterior edge, rounded to the carapace. The posterior edge of the carapace is perfectly defined by a broad post-cardiac groove that fades toward the edges. The rostrum is triangular trifid, very broad at its base. The central spine, very long compared to the lateral spines, is [occasionally] an extension of the median ridge, which runs from the front from the anterior border of the gastric region. On either side of this ridge, the surface of the rostrum is covered with tubercles, flat, rounded, scaly toward the edges, which are very finely serrated. The orbits are small, due to the great development of the base of the rostrum and slightly arched, without a supraorbital rim. The outer orbital angle is clearly separated from the hepatic region and bears a rarely preserved a spine. Gastric and [epibranchial] regions are well delimited by the cervical groove, which is very deep throughout its course including in its two distal branches, of which the anteriormost one clearly separates the anterior orbital [hepatic] region from the hepatic [epibranchial] region. [Transversely elongated] epigastric lobes stand out sharply in front, above the basal level of the rostrum and reaching the base of the median rostral ridge. Between these two lobes is the [narrow tip of the] mesogastric lobe. [Mesogastric region and protogastric regions confluent. Hepatic region small, lateral to epigastric regions, with some spines on lateral margin.] The [uro-metagastric] and cardiac regions are delimited laterally by the discontinuity [and offset] of transverse ridges. [Cardiac region separated from uro-/metagastric region by distinct, straight groove. Ventral surface, abdomen, and appendages absent. Cuticle mostly absent in specimens from Koskobilo.] (Translated and modified after Van Straelen, 1940, pp. 2, 3; emendations are in brackets.)

*Remarks*. Intraspecific variation can be observed in the extent of the axial ridge on the rostrum (compare Fig. 4B, C, and F), by the extent of broadening toward the posterior carapace (compare Fig. 4C and E), in the posterior branch of the cervical groove on the lateral carapace being approximately straight (Fig. 4E, F) to slightly concave forward (Fig. 4B, C), and the strength of the ornamentation on the rostrum (compare Fig. 4E and B with C). Variation exists in the length (excluding rostrum)/width ratio (Table 1).

In terms of ontogenetic variation, the number of transverse ridges increases with the carapace size. Hence, larger specimens may appear to have more irregular ornamentation (compare Fig. 4A and B with the rest). The smallest specimen (Fig. 4G) appears to have the lowest number of ridges covering the gastric region. These slightly different ornamentation types, especially comparing the larger ones to the smaller ones, are judged to be insufficient for erecting a new species, because no small specimens have been found that bear ornamentation as seen in Fig. 4A, B. The same is true for the small specimens.

*Eomunidopsis navarrensis* has only been found in the Eguino Formation in Spain. Evidence thus far suggests that it is endemic to the Orobe and Aldoirar patch reefs.

For differences from *Eomunidopsis aldoirarensis* see above. *Eomunidopsis navarrensis* is close to *E. eutecta*, but differs in that *E. eutecta* widens more toward the posterior carapace compared to *E. navarrensis*. Additionally, the epigastric regions of *E. navarrensis* are less ornamented than in *E. eutecta*. *Eomunidopsis navarrensis* differs from *E. kinokunica* in that the former often narrows anteriorly, whereas the latter does not show this. Additionally, the maximum width is near mid-length in *E. kinokunica* (excluding the rostrum), but is posterior to it in *E. navarrensis*. Karasawa et al. (2008) reported the lateral margins of *E. kinokunica* to be smooth and without spines; in *E. navarrensis* they possess spines on the anterior part. Karasawa et al. (2008) also reported that the carapace is moderately convex longitudinally in *E. kinokunica*, but is only slightly convex in *E. navarrensis*. Lastly, the anterior border of the cardiac region is less defined in *E. kinokunica*. *Eomunidopsis navarrensis* is different from *E. limonitica* in that the latter has well-defined mesogastric and cardiac regions which are less so in *E. navarrensis* in which the mesogastric and protogastric regions are confluent and the cardiac region is weakly defined laterally. Hence, the ridges in the gastric region are less wide in *E. limonitica.* Additionally, the anterior process of the mesogastric region is longer in *E. limonitica*, and the hepatic groove of *E. limonitica* is longer. Lastly, the anterior branch of the cervical groove appears straight in *E. limonitica*, but is curved to a more lateral course in its lateralmost part in *E. navarrensis*. *Eomunidopsis navarrensis* has its widest point usually posterior to mid-length (rostrum excluded), whereas it is located at approximately mid-length in *E. meerssensis*. Collins et al. (1995) mentioned that the upper orbital margin of *E. meerssensis* possesses 4–5 uneven spinules, which are absent in *E. navarrensis*. *Eomunidopsis navarrensis* differs substantially from *E. neojurensis* because the former does not exhibit a well-defined mesogastric region, which the latter does. The cervical groove of *E. neojurensis* intersects the anterolateral margin more anteriorly than is the case on *E. navarrensis*. The ornamentation of the carapace is vastly different: *E. neojurensis* bears tubercles on the carapace except on the cardiac region and posterior to it where transverse ridges seem to prevail, whereas *E. navarrensis* bears transverse ridges only. Furthermore, the uro-/metagastric region is much shorter longitudinally than that of *E. navarrensis*. *Eomunidopsis neojurensis* does not show the spines on the lateral margin, as seen in *E. navarrensis*. Lastly, the cardiac region of *E. neojurensis* is wider. *Eomunidopsis navarrensis* bears a narrower groove just posterior to the posterior margin than in *E. orobensis*. Moreover, *E. orobensis* is more rectangular, the transverse ridges are more irregular/more tubercular in the anterior half of the carapace excluding the rostrum, and the mesogastric region is better defined than in *E. navarrensis*. The rostrum of *E. orobensis* is different in that it does not bear two lateral spines near the tip, which is the case in *E. navarrensis*. The cardiac region is triangular and is delimited anteriorly by a somewhat concave-forward post-cervical groove in

*E. orobensis*, whereas the cardiac region is transversely rectangular and is delimited anteriorly by a straight post-cervical groove in *E. navarrensis*. Lastly, the posterior margin of *E. orobensis* is straight; it is slightly concave in *E. navarrensis*. *Eomunidopsis navarrensis* differs from *E. portlandica* in that the latter bears tubercles on the carapace except on the cardiac region and posterior to it where transverse ridges seem to prevail, whereas *E. navarrensis* bears transversely ridges only. The sole specimen of *E. portlandica* does not show the spines on the lateral margin, as seen in *E. navarrensis*. *Eomunidopsis navarrensis* differs from *E. zitteli* in several aspects: the entire mesogastric region is only defined at the anterior- and posteriormost part in *E. navarrensis*, whereas the entire mesogastric region of *E. zitteli* is defined by grooves; the rostrum of *E. navarrensis* does not have a keel along the entire axis, whereas *E. zitteli* does; and *E. navarrensis* bears a relatively small cardiac region.

*Eomunidopsis orobensis* (Ruiz de Gaona, 1943)
Fig. 5

* 1943 *Galathea orobensis* Ruiz de Gaona, pp. 426, 427, pl. 28.2.
1950 *Galathea orobensis* Ruiz de Gaona: Bataller, p. 422, 1 fig.
1981 *Eomunidopsis orobensis* (Ruiz de Gaona): Vía Boada, p. 250, fig. 5.
v 1982 *Eomunidopsis orobensis* (Ruiz de Gaona), pp. 122–124, fig. 5, pls. 2.8, 2.9.

*Material*. Nine specimens (MAB k2539, 2614, 2817, 2929–2933, and 3069) from the abandoned Koskobilo quarry. Additionally, the neotype from the contemporaneous strata of Monte Orobe (MGSB 28120) was studied.

*Stratigraphic horizon*. The species was collected from the abandoned Koskobilo quarry in the Albian/Cenomanian Aldoirar patch reef. It is also known from the Monte Orobe quarry in the Albian/Cenomanian Orobe patch reef.

*Diagnosis*. Carapace, excluding rostrum, 20–30% longer than wide, moderately convex longitudinally. Long, triangular rostrum with one spine at tip. Lateral margins approximately parallel, covered with anterolaterally directed spines on anterior two-thirds (rostrum not included). Posterior margin nearly straight. Mesogastric region pyriform, delimited at anterior process and on posterior part, less so in middle part. Cardiac region subtriangular, best defined anteriorly by concave-forward post-cervical groove. Groove anterior to posterior margin broadens toward axis. Carapace covered with transverse ridges, more tubercular anterior to cardiac region.

*Description*. Carapace, excluding rostrum, 20–30% longer than wide (Table 1), moderately convex transversely, weakly so longitudinally. Long, triangular rostrum with one spine at tip, triangular in cross section, numerous tiny spines cover lateral borders; median ridge delimited by longitudinal grooves, may not reach the tip of rostrum. Orbits seem shallow. Supraorbital margin biconcave, with one forwardly directed spine in between concavities. Lateral margins approximately parallel, rounded at posterior and anterior edges, covered with anterolaterally directed spines on anterior two-thirds (rostrum not included). Posterior margin nearly straight. Epigastric regions elongated transversely, divided axially by narrow tip of mesogastric region, which is pyriform and also delimited posteriorly, but not in middle part. Protogastric and small hepatic regions divided by longitudinally oriented hepatic groove. Epibranchial region bounded between anterior and posterior branch of cervical groove on lateral part of carapace when viewed in dorsal aspect. Wider than long uro-/metagastric region well delimited anteriorly and posteriorly, less so laterally by weak anterolaterally directed groove extending from post-cervical groove. Cardiac region subtriangular, best defined anteriorly. Meso- and metabranchial regions confluent. Intestinal region not observed. Strong cervical groove broadly concave forward, with two branches on lateral part of carapace; anterior one anterolaterally directed at first, then curves more laterally near lateral margin; posterior branch concave forward. Strong post-cervical groove concave forward. Strong groove just anterior to posterior margin, broadens substantially toward the axis. Carapace covered with transverse ridges, more tubercular anterior to cardiac region. Rostrum covered with granules. Mesogastric region may show some scabrous ornamentation on posteriormost part. Cuticle, where present in specimens from Koskobilo, covered with granules. Specimens from Monte Orobe typically have the cuticle preserved. Venter, abdomen, appendages, and majority of cuticle absent.

*Remarks*. Not much intraspecific variation can be observed: some transverse ridges may appear more or less interrupted and the mesogastric region may be slightly better defined in some specimens (compare Fig. 5C with the rest). Ontogenetic variation might manifest itself in the number of tubercles on the ridges on the anterior carapace: there are more in the larger specimen (compare Fig. 5A with the rest), but the density seems to remain stable.

*Eomunidopsis orobensis* has only been found in the Eguino Formation in Spain. Evidence thus far suggests that it is endemic to the Orobe and Aldoirar patch reefs.

For differences with *Eomunidopsis aldoirarensis* see above. *Eomunidopsis orobensis* differs from *E. eutecta* in that *E. eutecta* widens toward the posterior carapace, whereas *E. orobensis* exhibits parallel lateral margins. Additionally, the transverse ridges on the gastric region are less continuous in character in *E. orobensis*, and the base of the rostrum bears some granules, whereas it is covered with scale-like ornamentation in *E. eutecta*. *Eomunidopsis orobensis* differs from *E. kinokunica* in that the former exhibits a better defined cardiac region anteriorly, a better defined mesogastric region posteriorly, and its longitudinal axis appears less convex. Lastly, Karasawa et al. (2008) reported the lateral margins of *E. kinokunica* to be smooth and without spines; in *E. orobensis* they contain spines on the anterior two-thirds. The groove just anterior to the posterior margin appears wider axially in *E. orobensis*. *Eomunidopsis orobensis* bears a less well-defined mesogastric region in the middle part, a less well-defined cardiac region laterally, and a longer hepatic groove than *E. limonitica*. The ridges in the protogastric regions are anterolaterally oriented in *E. limonitica*, and not transversely as in *E. orobensis*. Lastly, the anterior branch of the cervical groove appears straight in *E. limonitica*, but curved to a more lateral course in its lateralmost part in *E. orobensis*. Collins et al. (1995) mentioned that the upper orbital margin of *E. meerssensis* possessed 4–5 uneven spinules; in *E. orobensis* one large spine is present on this margin. Transverse ridges are present on the epibranchial and protogastric regions of *E. meerssensis*, but they are more irregular/tubercular in *E. orobensis*. *Eomunidopsis orobensis* differs substantially from *E. neojurensis* because the former exhibits a less well-defined mesogastric region. The cervical groove of *E. neojurensis* intersects the anterolateral margin more anteriorly than in the case of *E. orobensis*. The ornamentation of the carapace is vastly different: *E. neojurensis* bears tubercles on the carapace except on the cardiac region and posterior to it where transverse ridges seem to prevail, whereas *E. orobensis* bears transverse ridges on the majority of the regions. Furthermore, the uro-/metagastric region is much shorter longitudinally than that of *E. orobensis*. *Eomunidopsis neojurensis* does not show the spines on the lateral margin, as seen in *E. orobensis*. Lastly, the cardiac region of *E. neojurensis* is wider. *Eomunidopsis orobensis* differs from

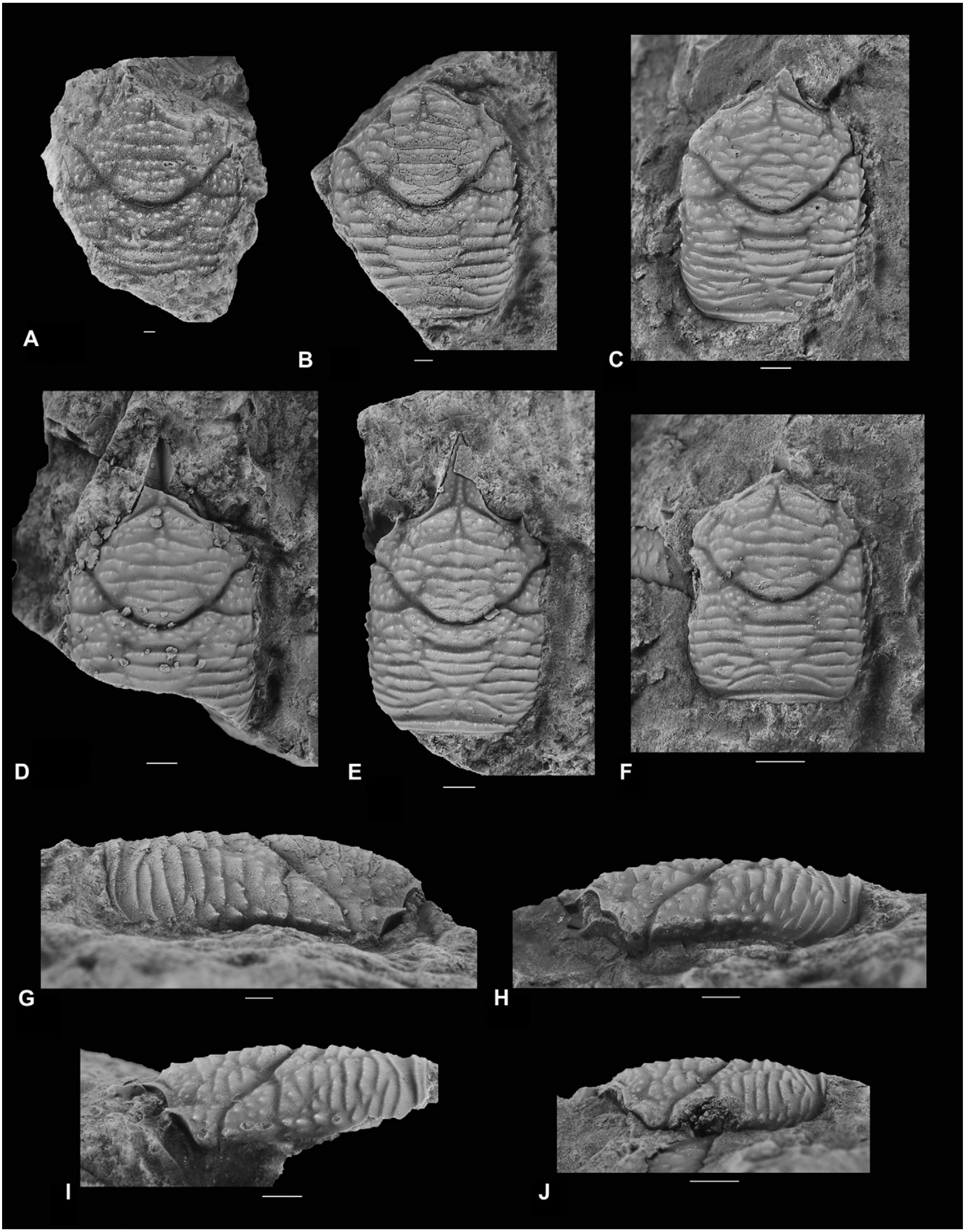

**Fig. 5.** Specimens of *Eomunidopsis orobensis* (Ruiz de Gaona, 1943) from Koskobilo. A–F, dorsal carapaces. A, MAB k2929. B, MAB k2930. C, MAB k2817. D, MAB k2931. E, MAB k2932. F, MAB k2933. G–J, lateral carapaces. G, MAB k2930. H, MAB k2817. I, MAB k2932. J, MAB k2933. All scale bars represent 1 mm.

*E. portlandica* in that the latter bears tubercles on the carapace except on the cardiac region and posterior to it where transverse ridges seem to prevail, whereas *E. orobensis* bears transverse ridges on the majority of the dorsal carapace. The sole specimen of *E. portlandica* does not show the spines on the lateral margin, as seen in *E. orobensis*.

For differences from *Eomunidopsis navarrensis* see above. *Eomunidopsis orobensis* differs from *E. zitteli* in several aspects: the mesogastric region is less defined in the middle part of *E. orobensis*, the rostrum of *E. orobensis* is narrower, and *E. aldoirarensis* exhibits a relatively small cardiac region.

Genus *Paragalathea* Patrulius, 1959

*Type species*. *Paragalathea verrucosa* (Moericke, 1889)

*Included species*. *Paragalathea africana* Garassino, De Angeli, Pasini, 2008; *P. miyakoensis* Takeda and Fujiyama, 1983; *P. multisquamata* Vía Boada, 1981; *P. neocomiensis* (Van Straelen, 1936); *P. ornatissima* Patrulius, 1966; *P. ruizi* (Van Straelen, 1940); *P. straeleni* (Ruiz de Gaona, 1943); *P. substriata* (Blaschke, 1911); *P. ubaghsi* (Pelseneer, 1886); and *P. verrucosa* (Moericke, 1889).

*Remarks*. The members of this genus have a heterogeneous nature in that the rostra and ornamentation differ vastly (compare for example *Paragalathea verrucosa*, *P. multisquamata*, *P. ubaghsi*, and *P. africana*). Species that do resemble each other closely are *Paragalathea ruizi* and *P. straeleni*. A revision of the genus is necessary, but this is not within the scope of this paper. A revision will be carried out by one of us (CMR) in the future.

*Paragalathea multisquamata* Vía Boada, 1981
Fig. 6

v* 1981 *Paragalathea multisquamata* Vía Boada, p. 250, fig. 3.
v 1982 *Paragalathea multisquamata* Vía Boada: Vía Boada, pp. 117, 118, fig. 3, pls. 2.1, 2.2.

*Material*. Three specimens (MAB k2579, 2977, and 3179) from the abandoned Koskobilo quarry. The holotype from the contemporaneous strata of Monte Orobe (MGSB 28118) was also studied.

*Stratigraphic horizon*. The species was collected from the Koskobilo quarry in the Albian/Cenomanian Aldoirar patch reef. The species is also present in the Monte Orobe quarry in the Albian/Cenomanian Orobe patch reef.

*Diagnosis*. Small carapace, excluding rostrum, 11–16% longer than wide. Rostrum broad at base, rounded to triangular in outline, margins bearing forwardly directed spines that diminish in size posteriorly; tiny spines cover lateral borders; has a median groove that diminishes toward tip. Epigastric regions raised and relatively narrow. Pronounced cervical groove broadly concave forward, with two branches on lateral part carapace. Carapace, except rostrum, covered with rounded tubercles, seemingly more elongated transversely around cardiac region, largest tubercle on axis of mesogastric region.

*Description*. Small carapace, excluding rostrum, 11–16% longer than wide (Table 1), moderately to strongly convex transversely, weakly to strongly convex longitudinally, widest point in posterior third of carapace. Rostrum broad at base, rounded to triangular in outline, margins covered with forwardly directed spines diminish in size posteriorly; tiny spines cover lateral borders; median groove that diminishes toward tip. Orbits not well exposed, but seem small and forwardly directed. Supraorbital margin concave forward, smooth, with a forwardly directed outer orbital spine. Lateral margins diverge toward posterior of carapace, rounded at posterior edges, covered with laterally directed spines. Posterior margin slightly concave. Epigastric regions raised and relatively narrow, not well delimited from protogastric regions, divided axially by narrow tip of mesogastric region and the groove arising from it. Mesogastric region triangular with concave lateral margins, well delimited posteriorly and anteriorly, may be less so in middle portion. Hepatic region small, delimited laterally by lateral margin and by part of groove forming anterior border of epigastric and protogastric regions, and posteriorly by anterior branch of cervical groove. Epibranchial region subtriangular, bounded between anterior and posterior branch of cervical groove on lateral part of carapace. Uro-/metagastric region much wider than long, well delimited anteriorly, less so posteriorly, and not delimited laterally. Cardiac region weakly defined, may appear wider than long. Meso- and metabranchial regions confluent. Intestinal region not observed. Pronounced cervical groove broadly concave forward, with two branches on lateral part carapace; anterior one anterolaterally directed; transverse posterior branch may be weaker. Weak postcervical groove parallels cervical groove and only expressed axially. Pronounced, convex-forward groove just anterior to posterior margin. Carapace, except rostrum, covered with rounded tubercles, seemingly more elongated transversely around cardiac region, largest tubercle on axis mesogastric region. Venter, abdomen, and appendages and absent. Cuticle absent in specimens from Koskobilo, present in specimens from Monte Orobe.

*Remarks*. Intraspecific variation cannot be detected because of the paucity of specimens. Ontogenetic variation can, however, be found. The smallest specimen from Koskobilo (Fig. 6A, D) is much more convex longitudinally than the larger specimen (Fig. 6C, F). Moreover, the posterolateral grooves defining the mesogastric region may be better visible in the smallest specimen. Lastly, granules on the rostrum of the larger specimens are better visible.

Vía Boada (1981) erected the species, Vía Boada (1982) illustrated the holotype (his pl. 2.2) and the paratype (his pl. 2.1). The paratype was not found in the collection of the Museo Geológico del Seminario de Barcelona in Spain. This paratype appears to be different from the holotype in that the mesogastric region exhibits transverse ornament, which the holotype does not. Moreover, the anterior branch of the cervical groove on the lateral part of the dorsal carapace curves laterally in the paratype, which is not seen in the holotype nor in the two specimens from Koskobilo. Thus, the paratype seems atypical for the species. It resembles *Eomunidopsis orobensis* more because this species shows this curve; it also exhibits a relatively well-defined mesogastric region, and it bears transverse ridges on this region.

*Paragalathea multisquamata* has only been found in the Eguino Formation in Spain. Evidence thus far suggests it is endemic to the Orobe and Aldoirar patch reefs.

Major differences between *Paragalathea multisquamata* and *P. africana* from the Upper Cretaceous (Cenomanian/Turonian) of Morocco are the rostrum and the ornamantation. The rounded rostrum of *P. multisquamata* bears smaller spines at the margins, which appear to be absent in the preserved part of the rostrum of *P. africana* and the ornamentation is tubercular instead of elongated granules as in *P. africana*. This tubercular character of *P. multisquamata* is also a major difference from *P. miyakoensis* from the Lower Cretaceous (Aptian) of Japan because the holotype of the latter bears a weak transverse ornamentation. *Paragalathea multisquamata* resembles *P. neocomiensis* from the Lower Cretaceous (Hauterivian) of France, but differs in that the former appears to exhibit a weaker delimited cardiac region, larger tubercles on the mesogastric and

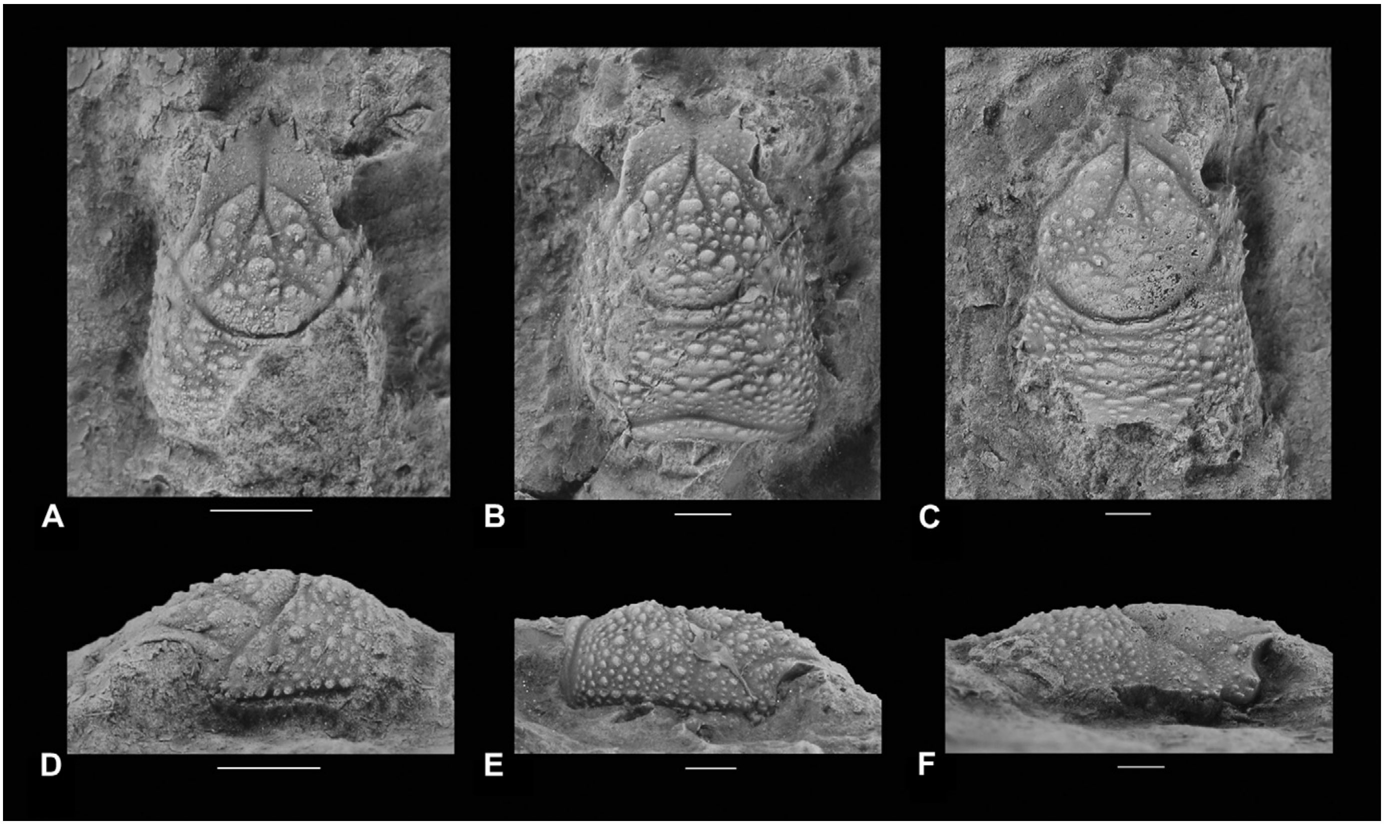

**Fig. 6.** Specimens of *Paragalathea multisquamata* Vía Boada, 1981 from Koskobilo. A–C, dorsal carapaces. A, MAB k2977. B, MAB k3179. C, MAB k2579. D–F, lateral carapaces. D, MAB k2977. E, MAB k3179. F, MAB k2579. All scale bars represent 1 mm.

cardiac regions, and possibly a narrower epigastric region. *Paragalathea multisquamata* bears larger tubercles on the mesogastric and cardiac regions in comparison to *P. ornatissima* from Late Jurassic (Tithonian) sediments in Romania. Additionally, the epigastric regions of *P. multisquamata* are better defined. *Paragalathea ruizi* from the mid-Cretaceous (Albian/Cenomanian) of Spain exhibits a triangular rostrum, whereas *P. multisquamata* bears a subrounded rostrum bearing spines on the margins. Moreover, *P. ruizi* exhibits a weak transverse ornamentation, whereas *P. multisquamata* bears tubercles across the dorsal carapace. *Paragalathea straeleni* from the mid-Cretaceous (Albian/Cenomanian) of Spain exhibits a subtriangular rostrum with three spines on the tip, whereas *P. multisquamata* bears a subrounded rostrum bearing spines on the margins. Additionally, *P. straeleni* exhibits a weak transverse ornamentation on the posterior carapace and tubercles on the anterior carapace, whereas *P. multisquamata* bears larger tubercles across the carapace. *Paragalathea multisquamata* bears larger tubercles on the entire dorsal carapace, whereas *P. substriata* from the Upper Jurassic (Tithonian) of the Czech Republic bears a transverse ornamentation. *Paragalathea multisquamata* differs from *P. ubaghsi* from the Upper Cretaceous (Maastrichtian) of the Netherlands in that the former does not exhibit spines on lateral margins unlike *P. ubaghsi*. Additionally, the cervical groove of *P. multisquamata* is less sinuous. The larger tubercles of *P. multisquamata* distinguish it from *P. verrucosa*, first described from the Late Jurassic (Tithonian) Stramberk Limestones of Poland. Lastly, the tip of the mesogastric region and the epigastric region are better defined in *P. multisquamata*. Surprisingly, *Paragalathea multisquamata* resembles *Eomunidopis neojurensis*, but differs from the latter by the larger tubercles on the mesogastric region, and more spinose anterolateral margin.

*Paragalathea ruizi* Van Straelen, 1940
Fig. 7

* 1940 *Galathea ruizi* Van Straelen, pp. 1, 2, pls. 1.1, 1.2.
1950 *Galathea ruizi* Van Straelen: Bataller, p. 423, 1 fig.
1952 *Galathea ruizi* Van Straelen: Vía Boada, p. 73, 1 fig.
1981 *Paragalathea ruizi* (Van Straelen): Vía Boada, p. 250, fig. 1.
v 1982 *Paragalathea ruizi* (Van Straelen): Vía Boada, pp. 110–113, fig. 1, pls. 1.1, 1.2.
1989 *Paragalathea ruizi* (Van Straelen): Gómez-Alba, p. 26, pl. 1.6.

*Material*. Ten specimens (including MAB k2528, 2598, 2823, 2824, 2841, 2845, 2971–2973, and 3077) from the abandoned Koskobilo quarry. One specimen (MAB k3014) showing the only abdominal fragment known from a galatheoid from the Aldoirar patch reef is from the Olazagutía quarry, a few hundreds of meters west of the Koskobilo quarry. The neotype from the contemporaneous strata of Monte Orobe (MGSB 9021) was also studied.

*Stratigraphic horizon*. The species was collected from the Koskobilo and Olazagutía quarries in the Albian/Cenomanian Aldoirar patch reef. The species is also present in the Monte Orobe quarry in the Albian/Cenomanian Orobe patch reef.

*Diagnosis*. Small carapace, excluding rostrum, 5–16% longer than wide. Long, triangular rostrum with three spines, without tiny spines on lateral borders and without clear median ridge. Lateral margins approximately parallel, slightly convex, sharp, without spines. Cervical groove strong and broadly concave forward on middle part of carapace, then fades abruptly. Carapace covered with

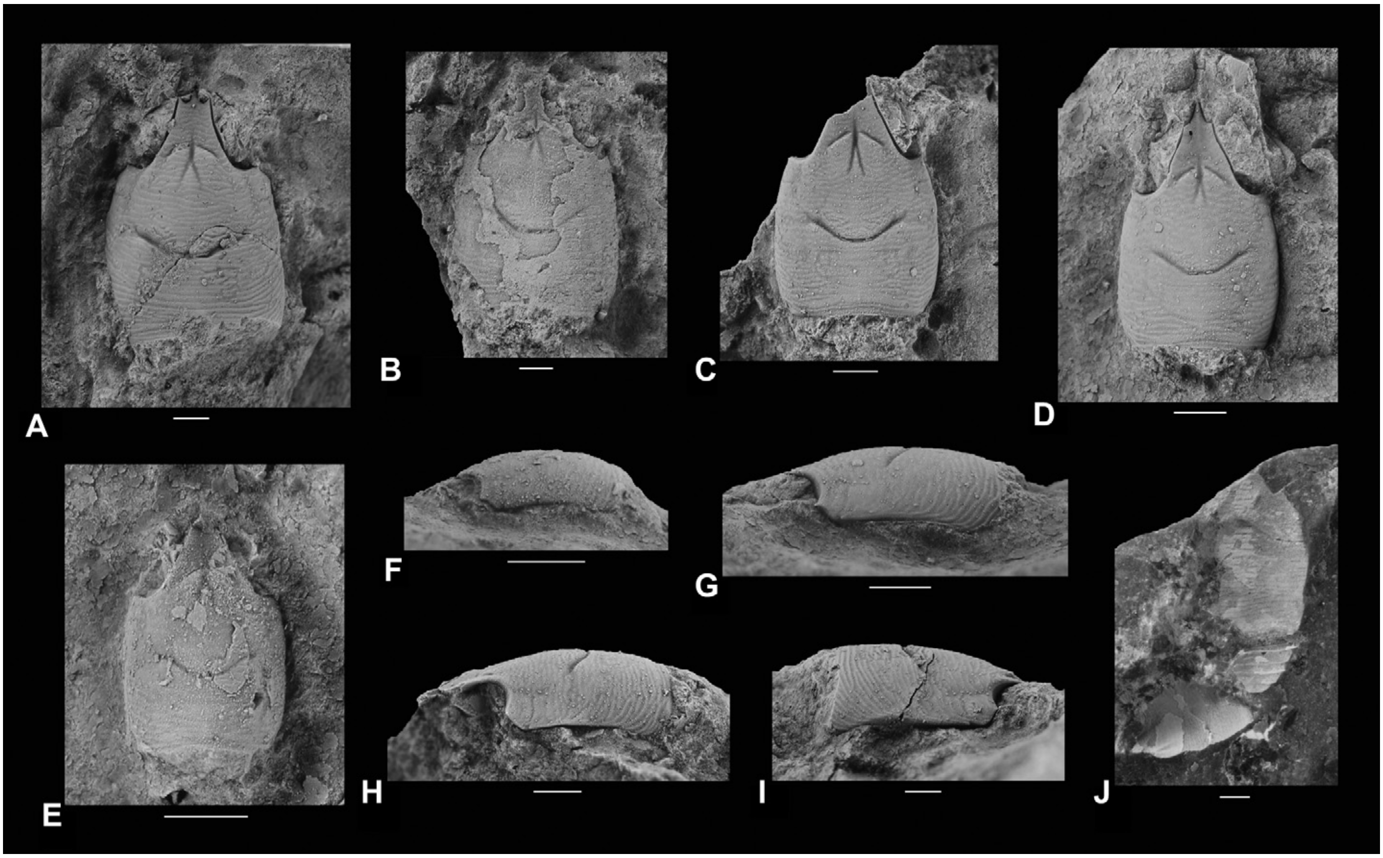

**Fig. 7.** Specimens of *Paragalathea ruizi* Van Straelen, 1940 from Koskobilo (A–I) and Olazagutía (J). A–E, dorsal carapaces. A, MAB k2598. B, MAB k2971. C, MAB k2833. D, MAB k2972. E, MAB k2973. F–I, Lateral carapaces. F, MAB k2973. G, MAB k2972. H, MAB k2833. I, MAB k2598. J, Internal view of the right half of the cuticle (MAB k3014). Part of abdomen, presumably from the same specimen, below it. Another internal view of a cuticle can be seen at the lower left corner. All scale bars represent 1 mm.

weak transverse ridges, which appear somewhat more irregular, wavy on the anterior part of carapace.

*Description*. Small carapace, excluding rostrum, 5–16% longer than wide (Table 1), moderately–strongly convex transversely, weakly so longitudinally. Long, triangular rostrum with three spines, without tiny spines on lateral borders and without clear median ridge. Orbits seem shallow and forwardly directed. Supraorbital margin concave forward, smooth, with one forwardly directed spine at outer orbital angle. Lateral margins approximately parallel, slightly convex, sharp, without spines with exception of small, blunt, forwardly directed spine just posterior to weak transverse groove defining posterior boundary of hepatic region. Posterior margin approximately straight. Epigastric regions defined anteriorly, divided axially by tip of mesogastric region. Protogastric and mesogastric regions entirely confluent. Small hepatic region separated from protogastric region by weak anteriorly oriented hepatic groove, and from epibranchial region by faint transverse groove. Epibranchial region not clearly differentiated from mesobranchial region. Uro-/metagastric region wider than long, well delimited anteriorly, very weak to not delimited posteriorly, not delimited laterally. Cardiac region occasionally weakly defined, wider than long, defined anteriorly by straight post-cervical groove, laterally and posteriorly by subcircular groove. Meso- and metabranchial regions confluent. Intestinal region not observed. Cervical groove strong and broadly concave forward on middle part of carapace, then fades abruptly, axial part located 56–58% of length carapace excluding rostrum. Weak groove just anterior to posterior margin convex forward. Carapace covered with weak transverse ridges, which appear more irregular and wavy on the anterior part of carapace; ridges occasionally also present on rostrum; curve forward on posterior part of carapace in lateral view. Similar ornament can be observed when cuticle is present (Fig. 7B). Mesogastric region may show some scabrous ornamentation on posteriormost part. A unique part of the abdomen appears preserved in a single specimen from the Olazagutía quarry in northern Spain. Space between each individual ridge of the abdominal transverse ornamentation appears larger in comparison to ornamentation on carapace. Venter, appendages, majority of abdomen, and majority of cuticle are absent in specimens from Koskobilo. Cuticle typically present in specimens from Monte Orobe.

*Remarks*. Intraspecific variation within the species can be found in the degree of expression of the transverse ridges, the cardiac region, the grooves on the anterolateral part of the carapace, and the length and width of the anterior process of the mesogastric region. The only ontogenetic difference found between the smallest specimen (Fig. 7E, F) compared to the other specimens is that this specimen is somewhat more convex longitudinally.

*Paragalathea ruizi* has only been found in the Eguino Formation in Spain. Evidence thus far suggests it is endemic to the Orobe and Aldoirar patch reefs.

*Paragalathea ruizi* differs from *P. africana* in that the latter bears a longer, rounder cervical groove. Moreover, *P. ruizi* exhibits clearer transverse ridges, instead of elongated granules as in *P. africana*.

*Paragalathea ruizi* bears less pronounced grooves anterolaterally and exhibits a less transversely oriented cervical groove axially compared to *P. miyakoensis*. *Paragalathea ruizi* bears less pronounced grooves anterolaterally and exhibits a weak transverse ornamentation instead of tubercles on the dorsal carapace as in *P. neocomiensis*. The rostrum of *Paragalathea ruizi* is less wide at the base in comparison to *P. ornatissima*. Moreover, *P. ruizi* exhibits a weak transverse ornamentation instead of tubercles on the dorsal carapace. The principal differences between *P. ruizi* and *P. straeleni* are the larger maximum size of *P. straeleni* and the more tubercular character on the anterior carapace instead of a weak transverse ornamentation as in *P. ruizi*. Judging from the illustration in Blaschke (1911, pl. 4.10) and a cast of the type species, the cervical groove of *P. substriata* extends onto the anterolateral corner, which is not the case *in P. ruizi* in which the cervical groove becomes obsolete before reaching one of the margins. *Paragalathea ruizi* differs vastly from *P. ubaghsi* in that the former bears less pronounced grooves anterolaterally and does not exhibit spines on lateral margins unlike *P. ubaghsi*. An important differences between *P. ruizi* and *P. verrucosa* is the more pronounced cervical groove anterolaterally in *P. verrucosa*. For differences with respect to *P. multisquamata*, see above.

### *Paragalathea straeleni* Ruiz de Gaona, 1943
Fig. 8

v* 1943 *Galatheites straeleni* Ruiz de Gaona, p. 128, fig. 1.
1944 *Galathea alsasuensis* Van Straelen, pp. 2–4, fig. 1.
1950 *Galatheites straeleni* Ruiz de Gaona: Bataller, p. 421, 1 fig.
1981 *Paragalathea straeleni* (Ruiz de Gaona): Vía Boada, p. 250, fig. 2.
v 1982 *Paragalathea straeleni* (Ruiz de Gaona): Vía Boada, pp. 114–117, fig. 2, pls. 1.3–1.6.

*Material*. Three specimens (MAB k2978, 3171, and 3173) from the abandoned Koskobilo quarry southwest of Alsasua (northern Spain) were studied as well as the holotype (MGSB 11519.1) and a “neotype” (MGSB 11519.2) from the contemporaneous strata of Monte Orobe (MGSB 28118).

*Stratigraphic horizon*. The specimens were collected from the Koskobilo quarry in the Albian/Cenomanian Aldoirar patch reef. The species is also known from the Monte Orobe quarry in the Albian/Cenomanian Orobe patch reef.

*Diagnosis*. Carapace, excluding rostrum, 13–17% longer than wide, large maximum size with lengths including rostrum over 20 mm. Rostrum broad at base, tapers somewhat to the anterior, with one central spine and two adjacent spines near the tip. Pronounced cervical groove concave forward, may appear approximately straight on axial part, diminishes quickly in strength lateral to mesogastric region, with two weak branches on lateral part of carapace, one forwardly directed and one laterally directed and being most pronounced. Carapace covered with rounded tubercles anterior to cardiac region and on anterior part of branchial region, transverse ridges on posterior part.

*Description*. Carapace, excluding rostrum, 13–17% longer than wide (Table 1), moderately to strongly convex transversely, weakly to moderately longitudinally, widest point in posterior third of carapace, large maximum size with lengths including rostrum over

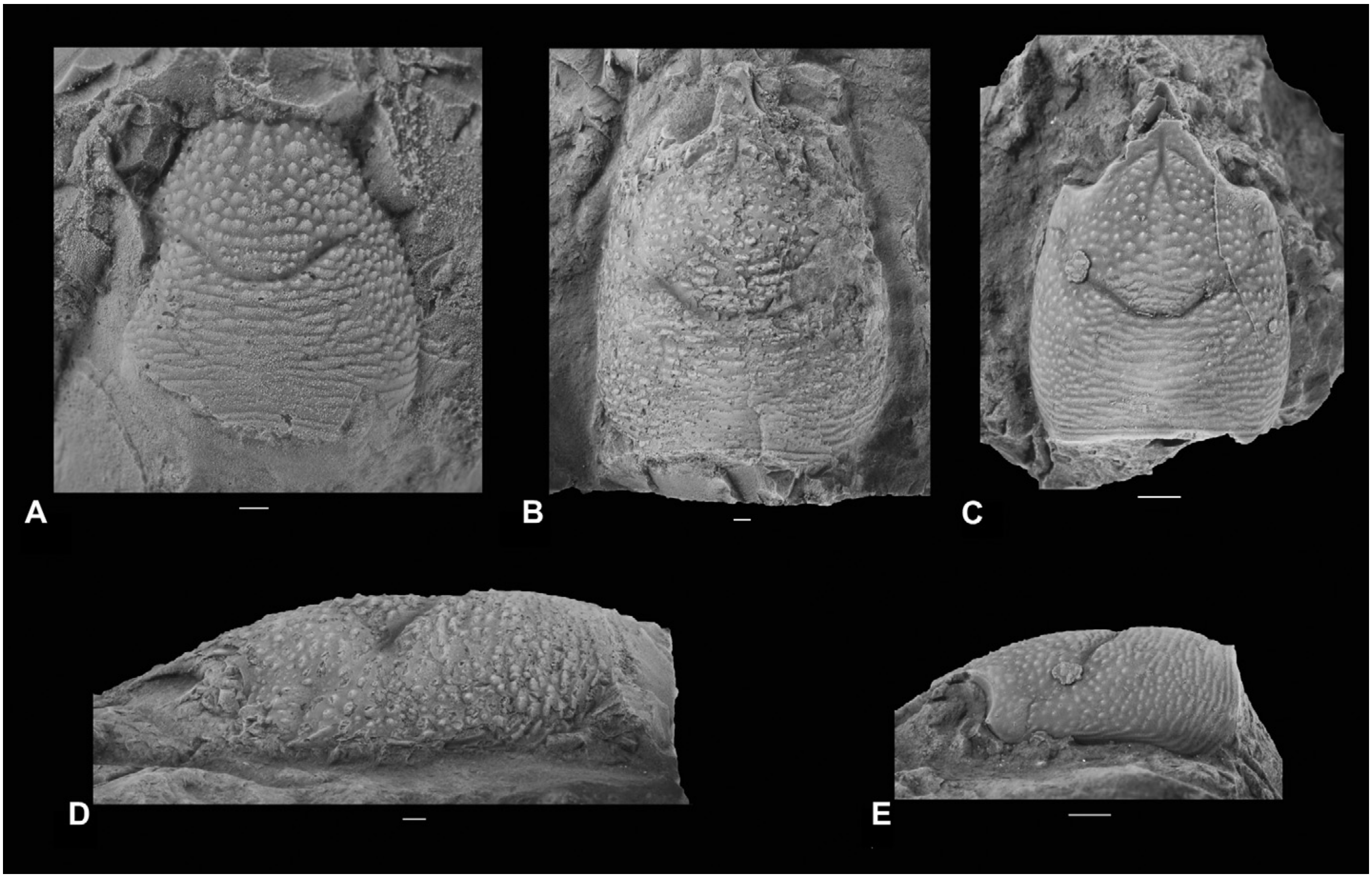

**Fig. 8.** Specimens of *Paragalathea straeleni* Ruiz de Gaona, 1943 from Koskobilo. A–C, dorsal carapaces. A, MAB k2978, cast from an external mold. B, MAB k3171. C, MAB k3173. D, E, lateral carapaces. D, MAB k3171. E, MAB k3173. All scale bars represent 1 mm.

20 mm. Rostrum broad at base, tapers somewhat to the anterior, with one central spine and two adjacent spines near the tip, somewhat concave transversely. Orbits shallow, forwardly directed. Supraorbital margin concave forward, smooth. Lateral margins diverge posteriorly, rounded at posterior edges. Posterior margin weakly concave to straight. Epigastric regions raised, not delimited from protogastric regions, divided axially by narrow tip of mesogastric region and groove arising from it. Mesogastric region well delimited posteriorly and anteriorly, not delimited in middle portion. Hepatic region small, delimited laterally by lateral margin and by hepatic groove, and posteriorly by anterior branch of cervical groove. Epibranchial region bounded between anterior and posterior branch of cervical groove on lateral part of carapace. Uro-/metagastric region much wider than long, well delimited anteriorly, less so posteriorly, and not delimited laterally. Cardiac region weakly defined, subtriangular with apex directed posteriorly, may appear wider than long. Meso- and metabranchial regions confluent. Intestinal region not observed. Pronounced cervical groove concave forward, may appear approximately straight on axial part, diminishes quickly in strength lateral to mesogastric region, with two weak branches on lateral part of carapace, one forwardly directed and one laterally directed, the latter most pronounced. Weak post-cervical groove, may appear absent. Weak groove just anterior to posterior margin. Carapace covered with rounded tubercles on carapace anterior to cardiac region and on anterior part of branchial region, transverse ridges on posterior part. Rostrum appears to exhibit granules. Venter, abdomen, and appendages absent. Cuticle largely absent in specimens from Koskobilo; present in specimens from Monte Orobe.

*Remarks*. Based on the illustrations in Vía Boada (1982, pls. 1.3–1.6) and the three specimens from Koskobilo, no obvious intraspecific variation can be found. The position of maximum width might be somewhat more anteriorly located in the small specimen. The small specimen also exhibits scabrous ornamentation on the posterior part of the mesogastric region, which appears less obvious in larger specimens.

*Paragalathea straeleni* has only been found in the Eguino Formation in Spain. Evidence thus far suggests it is endemic to the Orobe and Aldoirar patch reefs.

*Paragalathea straeleni* differs from *P. africana* in that the latter bears a longer, rounder cervical groove. Moreover, it exhibits tubercles and weak transverse ridges instead of elongated granules across the entire carapace as in *P. africana*. *Paragalathea straeleni* bears less pronounced grooves anterolaterally and exhibits a less transversely oriented cervical groove axially compared to *P. miyakoensis*. *Paragalathea straeleni* resembles *P. neocomiensis*, but the rostrum of *P. neocomiensis* appears somewhat broader at the base, exhibits a more tubercular character posterior to the cardiac region, and more pronounced branches of the cervical groove on the lateral part of the carapace. The rostrum of *Paragalathea straeleni* is less wide at the base in comparison to *P. ornatissima*. Moreover, *P. straeleni* appears to exhibit more transverse ornamentation on the posterior carapace instead of tubercles as in *P. ornatissima*. The cervical groove of *P. substriata* extends to the anterolateral corner, which is not the case in *P. straeleni*, in which the cervical groove becomes obsolete before reaching one of the margins. *Paragalathea straeleni* differs from *P. ubaghsi* in that the former bears less pronounced grooves anterolaterally and does not exhibit spines on lateral margins, which is the case in *P. ubaghsi*.

Important differences between *P. straeleni* and *P. verrucosa* are the rostrum, which appears broader at the base in *P. verrucosa*; the epigastric region and tip of the mesogastric region are more pronounced *in P. straeleni*. The differences between the morphologically close species *P. straeleni* and *P. ruizi* are described above. For differences between *P. multisquamata* and *P. straeleni* see above.

Vía Boada (1982, p. 128) mentioned the existence of a neotype in the explanation along with the plates, but he also illustrated the holotype designated by Ruiz de Gaona (1943), which is still present in the Museo Geológico del Seminario de Barcelona. In the article itself, he did not mention the neotype, but comments about that particular specimen: “specimen serves to complement the description” (p. 114). The erection of a neotype is inconsistent with ICZN article 75.1. Hence, the neotype designation is invalid, despite the fact that the specimen is useful in describing the species.

Genus *Hispanigalathea* gen. nov.

*Type species*. *Hispanigalathea pseudolaevis* sp. nov.

*Derivation of name*. After the country in which the type species was found, the former Roman province of Hispania (Spain).

*Diagnosis*. Carapace, excluding rostrum, 15–28% longer than wide, moderately to strongly convex transversely, weakly so longitudinally. Rostrum broad at base, subtriangular with rounded tip, margins and tip bearing small spines. Orbits small, forwardly directed. Supraorbital margin contains spine at outer orbital corner. Lateral margins parallel. Epigastric regions raised. Mesogastric region well delimited posteriorly by cervical groove and anteriorly at the tip, not delimited in middle portion. Cardiac region weakly defined, approximately as long as wide. Pronounced cervical groove concave forward, with anterior and posterior branch. Carapace covered with granules or tubercles that appear transversely elongated in posterior part carapace.

*Remarks*. This genus is placed within the Galatheidae (sensu Ahyong et al., 2010) on account of its well-developed, flattened, subtriangular rostrum that is broad at the base (definition Ahyong et al., 2010). The Munidopsidae and the Munididae do not exhibit this form of rostrum: the former exhibit a “well developed, subtriangular or spiniform” rostrum, the latter exhibits a “slender, dorsally ridged, usually spiniform” rostrum (Ahyong et al., 2010, pp. 63 and 59, respectively). Also, the rostrum of genera within the Munidopsidae is generally less wide at the base (*Faxegalathea* and *Calteagalathea* also have a rostrum with a broad base), and their rostrum is often keeled. Moreover, most genera within the Munidopsidae exhibit a circular groove pattern enclosing most of the gastric region (*Leiogalathea, Shinkaia*, and *Munitheities* being the exceptions). The Porcellanidae also have a similarly broad rostrum at the base, but the Porcellanidae clearly have a more rounded-shaped carapace and a smaller l/w ratio (see examples in De Angeli and Garassino, 2002). Another characteristic of the Galatheidea is their transverse ornamentation or striae. *Hispanigalathea* bears weak ornamentation unlike other fossil galatheid genera, which show strong transverse ridges. Some Recent genera show weak transverse ridges on the posterior part of the carapace (the type species of *Fennerogalathea* and *Macrothea*). Another Recent genus, *Lauriea*, shows only short transverse ridges. The new genus seems to lack transverse ornamentation, but many granules on the posterior part of the dorsal carapace appear transversely elongated. However, when the specimens are viewed laterally, the transverse ornamentation is clearly visible in the type species. Thus, is it suggested here that the new genus is best accommodated within the Galatheidae.

*Hispanigalathea* differs from all other genera within the Galatheidae except *Fennerogalathea*, *Lauriea*, *Macrothea*, and *Paragalathea* in that it does not exhibit pronounced transverse ridges across the carapace. *Fennerogalathea* and *Lauriea* exhibit a weaker/absent cervical groove in comparison to *Hispanigalathea*. *Macrothea* broadens toward the posterior carapace, whereas the lateral margins are parallel in *Hispanigalathea*, and *Macrothea* exhibits a row of spines on the epigastric regions, which is absent in *Hispanigalathea*. The type species of *Paragalathea* exhibits a more tubercular character and has grooves on the lateral carapace less defined than *Hispanigalathea*. Furthermore, *Hispanigalathea* also does not bear a groove delimiting the posterior border of the epigastric region, which is present in *Acanthogalathea, Allogalathea*, *Allomunida*, *Eomunidopsis*, *Galathea, Janetogalathea*, *Lessinigalathea, Luisogalathea, Macrothea*, *Nanogalathea*, and *Palaeomunida*. The rostrum appears somewhat different from other genera. It is narrower at the base and more spinose at the margins in *Acanthogalathea, Janetogalathea, Lessinigalathea,* and *Palaeomunida*; narrower and with a sharper tip in *Alainius, Allomunida, Eomunidopsis, Fennerogalathea*, *Luisogalathea*, and *Phylladiorhynchus*; and more spinose in *Coralliogalathea, Galathea, Lauriea*, and *Macrothea*. The rostrum of *Spathagalathea* is subcircular instead of subtriangular; the rostrum of *Allogalathea* is longer and sharper at the tip; *Nanogalathea* exhibits a sharper tip of the rostrum; *Mesogalathea* exhibits a wider midpoint of the rostrum and has an undefined cardiac region, whereas *Hispanigalathea* has a defined cardiac region.

*Hispanigalathea pseudolaevis* sp. nov.
Fig. 9

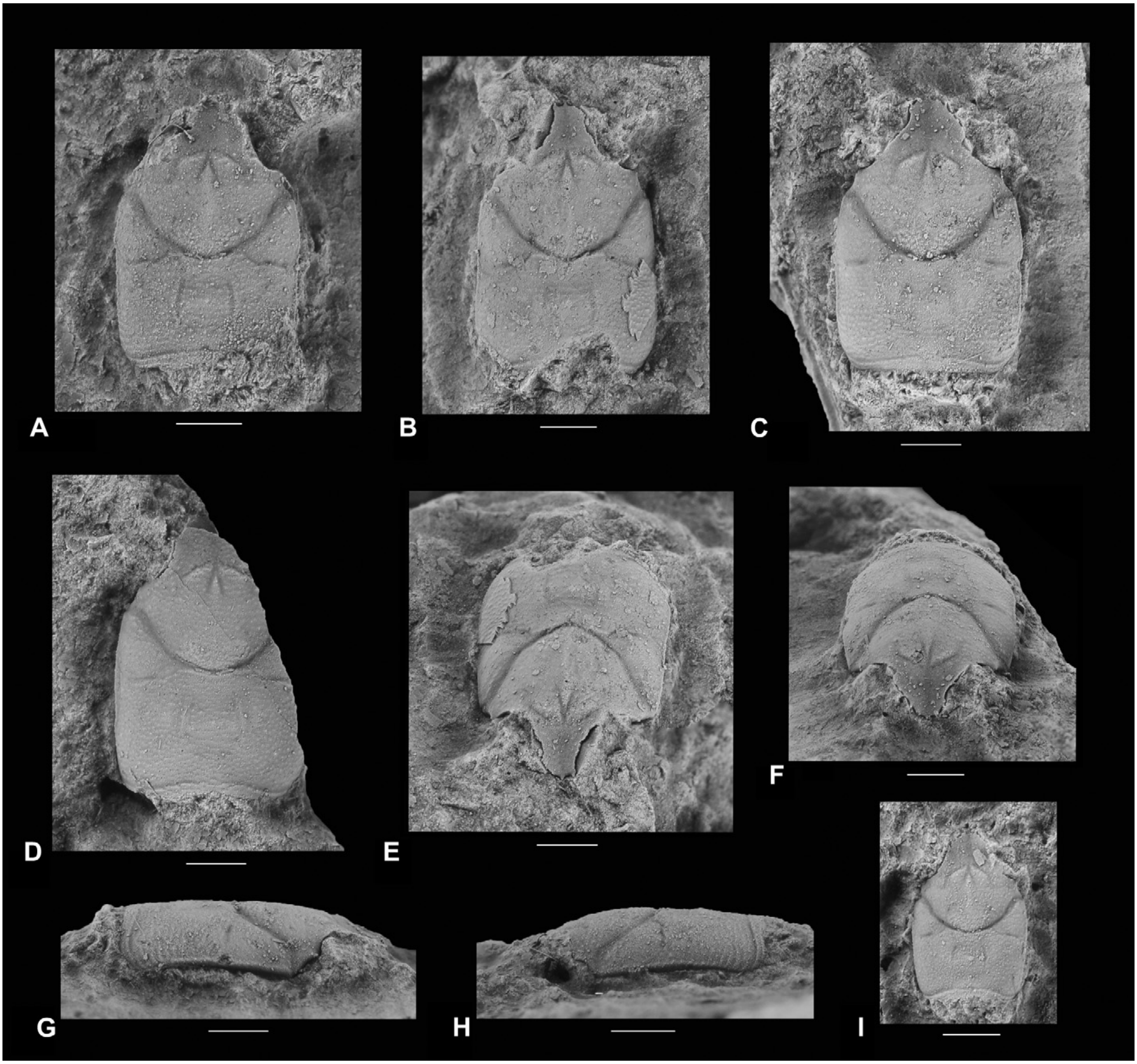

**Fig. 9.** Specimens of *Hispanigalathea pseudolaevis* gen. et sp. nov. from Koskobilo. A–D, I, dorsal carapaces. A, MAB k2976, paratype. B, MAB k2847, paratype. C, MGSB 77717, holotype. D, MAB k3073, paratype. I, MAB k3016, paratype. E, F, rostral views. E, MAB k2847, paratype. F, MGSB 77717, holotype. G, H, lateral carapaces. G, MGSB 77717, holotype. H, MAB k2976, paratype. All scale bars represent 1 mm.

*Derivation of name*. After the dorsal surface that may appear smooth (L., *laevis*), but is in fact covered with small granules (*pseudo*-).

*Types*. The holotype (MGSB 77717; Fig. 9C, F, G) is deposited in the Museo Geológico del Seminario de Barcelona, Spain and the paratypes (MAB k2847, 2976, 3016, and 3073) are housed in the collections of the Oertijdmuseum De Groene Poort, Boxtel, The Netherlands.

*Additional material*. MAB k3180 and 3188.

*Type locality*. The species was collected from the Koskobilo quarry, northern Spain.

*Stratigraphic horizon*. The Albian/Cenomanian Aldoirar patch reef within the Albeniz Unit of the Eguino Formation (see López-Horgue et al., 1996).

*Diagnosis*. Carapace, excluding rostrum, 15–21% longer than wide, moderately to strongly convex transversely, weakly so longitudinally. Rostrum broad at base, subtriangular, tapers toward to the broadly rounded tip, margins and tip covered with small spines. Lateral margins parallel, rounded at posterior edges, without spines. Epigastric regions somewhat raised. Large epibranchial region. Weak to moderately strong groove just anterior to posterior margin. Carapace, including rostrum, covered with small granules, may appear somewhat transversely elongated on posterior part carapace.

*Description*. Carapace, excluding rostrum, 15–21% longer than wide (Table 1), moderately to strongly convex transversely, weakly so longitudinally. Rostrum broad at base, subtriangular, tapers toward the broadly rounded tip, margins and tip covered with small spines. Orbits small, forwardly directed. Supraorbital margin concave in anterolateral direction, smooth, contains spine at outer orbital corner. Anterolateral margin small, nearly straight, between lateral margin and supraorbital margin. Lateral margins parallel, rounded at posterior edges, without spines. Posterior margin nearly straight. Epigastric regions somewhat raised, divided axially by narrow tip of mesogastric region. Mesogastric region well delimited posteriorly by cervical groove and anteriorly at the tip, not delimited in middle portion. Hepatic region not delimited from protogastric region. Large epibranchial region bounded between anterior and posterior branch of cervical groove on lateral part carapace. Uro-/metagastric region appears somewhat wider than long, well delimited anteriorly, weakly posteriorly, and not delimited laterally. Cardiac region weakly defined, approximately as long as wide, subquadrate. Meso- and metabranchial regions confluent. Intestinal region not observed. Pronounced cervical groove concave forward, anterior branch curves transversely in lateralmost part, posterior branch weaker, more transversely directed. Weak post-cervical groove marks anterior border of cardiac region. Weak to moderately strong groove just anterior to posterior margin, slightly convex forward, weakest on axis. Carapace including rostrum covered with small granules, may appear somewhat elongated transversely on posterior part of carapace. Posterior part of mesogastric region exhibits scabrous ornamentation. Venter, abdomen, and appendages absent. Part of cuticle absent in one specimen, showing a similar ornamentation as internal molds.

*Remarks*. Intraspecific variation can be observed in the width of the anterior process of the mesogastric region (compare Fig. 9A with C), the strength of definition of the cardiac region (compare Fig. 9A with D), in the shape of the cervical groove being more V-shaped axially in Fig. 9B and more rounded in other specimens. Ontogenetic variation is not apparent as the smallest specimen (Fig. 9I) is similar in dimensions, ornamentation, and the relative size of the regions. However, the lateral margins may be slightly more convex on the small specimen. *Hispanigalathea pseudolaevis* has only been found in the Koskobilo quarry so far. Evidence thus far suggests it is endemic to the Aldoirar patch reef.

Numerous differences with *Hispanigalathea tuberosa* (see below) are observed, but since this species has the same outline, and the same groove pattern, they are judged here to belong to the same genus. The differences are: epigastric region of *H. pseudolaevis* is less inflated, the groove just anterior to the posterior margin is less pronounced in *H. pseudolaevis*, specimens of *H. pseudolaevis* have a smaller length (excluding rostrum)/width ratio and a smaller "length from base of the rostrum to the cervical groove"/length (excluding rostrum) ratio, the lateral margin of *H. pseudolaevis* do not contain spines as is the case in *H. tuberosa*, *H. pseudolaevis* exhibits a larger epibranchial region, and *H. pseudolaevis* bears a less coarse ornamentation on the dorsal carapace.

*Hispanigalathea tuberosa* sp. nov.
Fig. 10

*Derivation of name*. *Tuberose* (L.), full of lumps or protuberances, after the tuberculate nature of the species compared to the type species.

*Holotype*. The holotype (MGSB 77718; Fig. 10C, F, G) is deposited in the Museo Geológico del Seminario de Barcelona, Spain.

*Type locality*. The species was collected from the Koskobilo quarry, northern Spain.

*Stratigraphic horizon*. The Albian/Cenomanian Aldoirar patch reef within the Albeniz Unit of the Eguino Formation (see López-Horgue et al., 1996).

*Diagnosis*. Carapace, excluding rostrum, 28% longer than wide, moderately to strongly convex transversely, weakly so longitudinally. Rostrum broad at base. Lateral margins parallel, with spines increasing in size toward posterior carapace. Epigastric regions strongly raised. Moderately strong groove just anterior to posterior margin. Carapace including rostrum covered with tubercles, may appear somewhat elongated transversely on posterior part carapace.

*Description*. Carapace, excluding rostrum, 28% longer than wide (Table 1), moderately to strongly convex transversely, weakly so longitudinally. Rostrum broad at base, not well preserved. Orbits not visible. Supraorbital margin anterolaterally oriented, contains spine at outer orbital margin. Anterolateral margin small, nearly straight, between lateral margin and supraorbital margin. Lateral margins parallel, rounded at posterior edges, with spines increasing in size posteriorly. Posterior margin nearly straight. Epigastric regions strongly raised, divided axially by narrow tip of mesogastric region. Mesogastric region well delimited posteriorly by cervical groove and anteriorly at the tip, not delimited in middle portion. Hepatic region not delimited from protogastric region. Epibranchial region situated between anterior and posterior branch of cervical groove on lateral part carapace. Uro-/metagastric region appears somewhat wider than long, well delimited anteriorly, weakly posteriorly, and not delimited laterally. Cardiac region weakly defined, approximately as long as wide, subquadrate/subrounded. Meso- and metabranchial regions confluent. Intestinal region not observed. Pronounced cervical groove concave forward, posterior branch

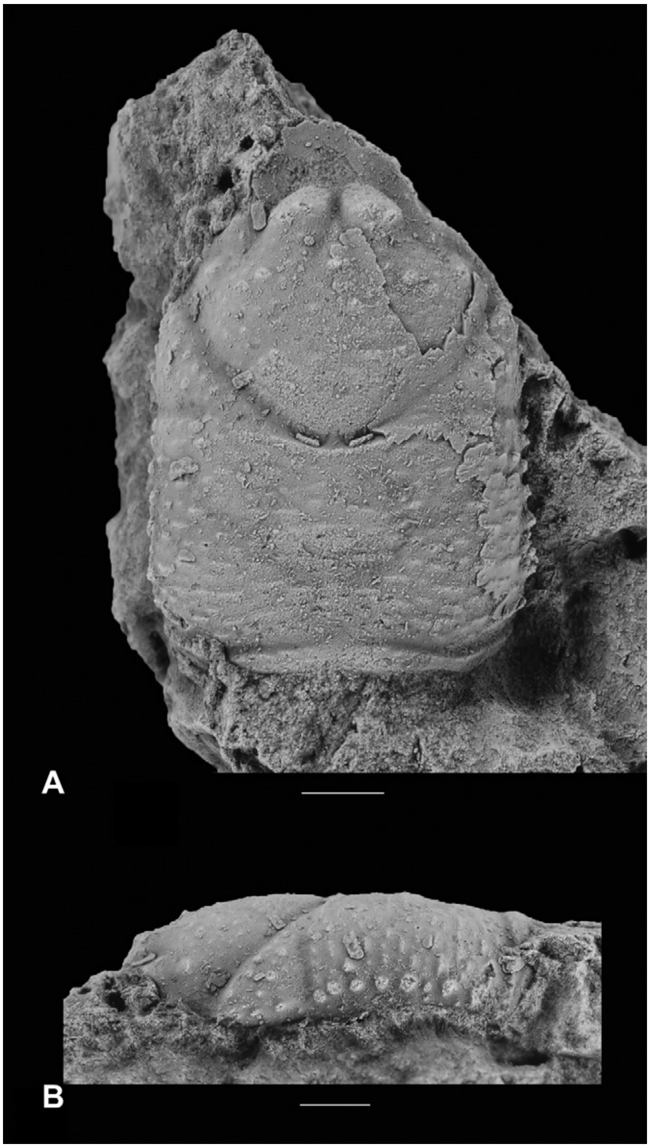

**Fig. 10.** The sole specimen of *Hispanigalathea tuberosa* gen. et sp. nov. from Koskobilo. A, dorsal carapace, MGSB 77718, holotype. B, lateral carapace. Scale bars represent 1 mm.

weaker, more transversely directed. Weak post-cervical groove marks anterior border of cardiac region. Moderately strong groove just anterior to posterior margin, slightly convex forward, weakest on axis. Carapace including rostrum covered with tubercles, may appear somewhat elongated transversely on posterior part of carapace. Venter, abdomen, and appendages absent. Part of cuticle present shows similar ornamentation to internal molds.

*Remarks*. Differences from *Hispanigalathea pseudolaevis* have been discussed above. *Hispanigalathea pseudolaevis* has only been found in Koskobilo quarry so far. Evidence thus far suggests it is endemic to the Aldoirar patch reef.

Family Munidopsidae Ortmann, 1898

*Included fossil (F) and Recent (R) genera*. *Galacantha* A. Milne-Edwards, 1880 (R), *Leiogalathea* Baba, 1969 (R), *Munidopsis* Whiteaves, 1874 (R, F), *Shinkaia* Baba and Williams, 1998 (R, F), *Brazilomunida* Martins-Neto, 2001 (F), *Calteagalathea* De Angeli and Garassino, 2006 (F), *Faxegalathea* Jakobsen and Collins, 1997 (F), *Gastrosacus* von Meyer, 1851 (F), *Munitheities* Lőrenthey in Lőrenthey and Beurlen, 1929 (F), and *Palaeomunidopsis* Van Straelen, 1925 (F).

Genus *Nykteripteryx* gen. nov.

*Type species*. *Nykteripteryx rostrata* sp. nov.

*Derivation of name*. A contraction of *nykteris* (Gr., bat) and *pteryx* (Gr., wing), with reference to the bat-like rostrum of the genus.

*Diagnosis*. Carapace length, excluding rostrum, wider than long, longer than wide including rostrum, widest at mid length (rostrum not included). Rostrum broad at base, subtriangular in general outline, with axial ridge on anterior part of rostrum and forming tip of rostrum and two anterolaterally oriented smaller ridges adjacent to axial ridge, most visible in anterior part and protruding at margins of rostrum. Lateral margins with distinct, unarmed rim, weakly concave, not rounded at posterior edges. Large epigastric regions strongly raised, elongated longitudinally. Strong cervical groove concave forward on axial part, sinuous, with strong, approximately transversely oriented posterior branch, anterior branch anterolaterally directed and weakly connected to central part of cervical groove. Anterior carapace ornamented with tubercles, posterior with transverse striae.

*Remarks*. The genus fits best within the Munidopsidae because it bears a well-developed, subtriangular rostrum and lacks supraocular spines (Munidopsidae definition Ahyong et al., 2010). Somewhat atypical for the Munidopsidae is that the rostrum of *Nykteripteryx* bears two smaller, distally diverging ridges lateral to the median ridge on the rostrum. Additionally, the length (excluding rostrum)/width ratio is less than 1, which is rare in munidopsids. The sole exception found is "*Gastrosacus* sp. nov. 4" (Robins, 2008, fig. 12). However, *Nykteripteryx* shows a circular groove pattern in the gastric region which is seen in most munidopsid genera except in *Leiogalathea*, *Shinkaia*, and *Munitheities*. Also, as with most genera within the Munidopsidae, a median ridge or keel is present on the rostrum, with the exceptions of *Leiogalathea*, *Shinkaia*, and *Faxegalathea*. Additionally, the sinuous cervical groove (posterior branch) is reminiscent of the type genus of the Munidopsidae, *Munidopsis*. Therefore, we tentatively place *Nykteripteryx* within the Munidopsidae. The Porcellanidae have also been considered because the specimen is wider than long (rostrum not included for length) and the small size of many porcellanids is comparable to *Nykteripteryx*. However, fossil genera within the Porcellanidae typically have "carapace regions usually weakly defined" (Schweitzer and Feldmann, 2010, p. 243), which is not the case for *Nykteripteryx* (see below, Fig. 11), at least for the anterior part. According to McLaughlin et al. (2007, table 1) porcellanids are characterized by a weakly delimited cervical groove, which is not the case in *Nykteripteryx*. The carapace of porcellanids is ovate (Schweitzer and Feldmann, 2010, p. 243), which is true for all fossil representatives. This cannot, however, be said for *Nykteripteryx*, where the posterolateral margin exhibits a clear angle with the posterior margin; the posterolateral angle is not rounded as is the case in porcellanids. Another characteristic of almost all fossil porcellanid genera is that the rostrum exhibits an axial groove, with the exception of *Juranella* Schweitzer and Feldmann, 2010, in which no clear groove could be seen. Some Recent species of *Porcellana* Lamarck, 1801, also exhibit this groove. Instead, the rostrum of *Nykteripteryx* exhibits three ridges, one on the axis, which is not

**Fig. 11.** Specimens of *Nykteripteryx rostrata* gen. et sp. nov. from Koskobilo. A–C, F, dorsal carapaces. A, MGSB 77719, holotype. B, MAB k2979, paratype. C, MAB k3187, paratype. F, MAB k2980, paratype. D, rostral view, MGSB 77719, holotype. E, reconstruction based on MGSB 77719, holotype. G, lateral carapace, MGSB 77719, holotype. All scale bars represent 1 mm.

seen in any fossil porcellanid. Thus, placement within the Porcellanidae is judged to be unlikely.

*Nykteripteryx rostrata* sp. nov.
Fig. 11

*Derivation of name*. Referring to *rostrum* (L.).

*Types*. The holotype (MGSB 77719; Fig. 11A) is deposited in the Museo Geológico del Seminario de Barcelona, Spain and the paratypes (MAB k2979, 2980, and 3187) are housed in the collections of Oertijdmuseum De Groene Poort, Boxtel, The Netherlands.

*Type locality*. The species was collected from the Koskobilo quarry, northern Spain.

*Stratigraphic horizon*. The Albian/Cenomanian Aldoirar patch reef within the Albeniz Unit of the Eguino Formation (see López-Horgue et al., 1996).

*Diagnosis*. As for the genus.

*Description*. Carapace length, excluding rostrum, 85–95% of width, 27% longer than wide including rostrum (Table 1), widest at mid length (rostrum not included), moderately convex transversely, weakly so longitudinally. Rostrum broad at base, slightly downturned, subtriangular in general outline, with axial ridge on anterior part of rostrum and forming tip of rostrum and two anterolaterally oriented smaller ridges adjacent to axial ridge, best developed in anterior part and protruding at margins of rostrum. Orbits not visible. Supraorbital margin short, concave forward, with anterolaterally directed outer orbital spine. Lateral margins with distinct, unarmed rim, weakly convex, not rounded at posterior edges. Posterior margin slightly concave. Large epigastric regions strongly raised, elongated longitudinally, divided axially anterior part of mesogastric region and groove arising from it. Mesogastric region well delimited generally, less so at posterolateral corners, pyriform. Protogastric region well delimited anteriorly, less so posteriorly, between epigastric and epibranchial regions. Hepatic region appears absent. Epibranchial region bounded between anterior and posterior branch of cervical groove on lateral part carapace. Uro-/metagastric region very narrow, broad, well defined anteriorly, weakly defined posteriorly, and not delimited laterally. Cardiac region weakly defined, appears wider than long. Meso- and metabranchial regions confluent. Intestinal region not observed. Strong cervical groove concave forward on axial part, sinuous with strong, transversely oriented posterior branch, anterior branch weakly connected to central part of cervical groove, anterolaterally directed. Shallow, broad, post-cervical groove marks anterior border of cardiac region. Moderately strong groove just anterior to posterior margin, slightly convex forward. Carapace including rostrum covered with some tubercles on epi-, meso-, and protogastric regions, and with transverse striae on posterior part. Venter, abdomen, appendages, and cuticle absent.

*Remarks*. Ontogenetic variation cannot be discussed because all three specimens are of similar size. Intraspecific variation was not found based on the three partly preserved specimens. *Nykteripteryx rostrata* has only been found in the Koskobilo quarry so far. Evidence thus far suggests it is endemic to the Aldoirar patch reef.

Indeterminable galatheoid family, genus, and species
Fig. 12

*Material*. One incomplete specimen from the Koskobilo quarry, northern Spain (MGSB 77722).

*Stratigraphic horizon*. The Albian/Cenomanian Aldoirar patch reef within the Albeniz Unit of the Eguino Formation (see López-Horgue et al., 1996).

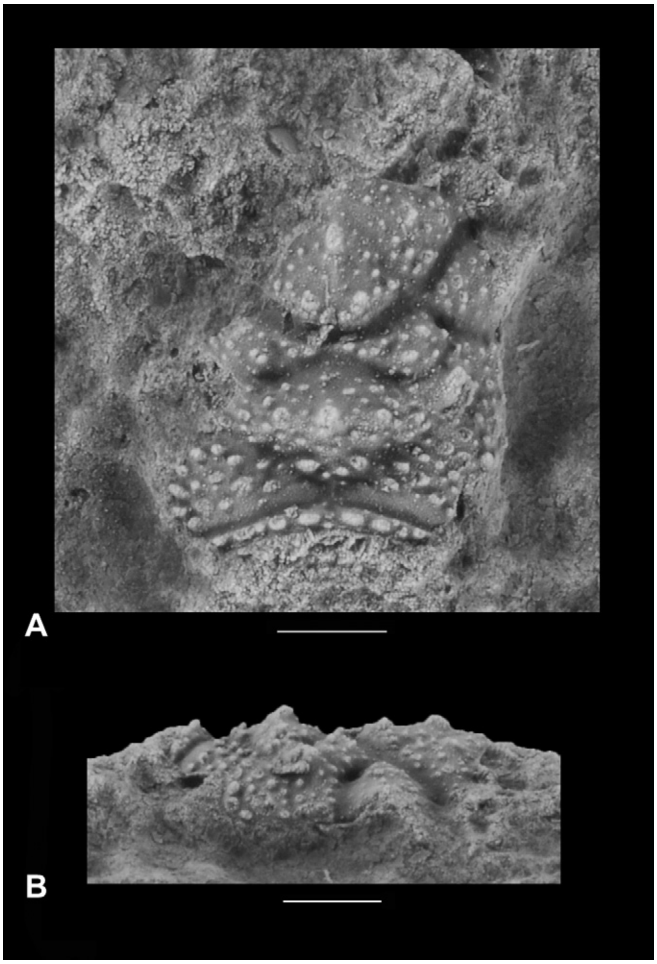

**Fig. 12.** The sole specimen of the inderminate galatheoid from Koskobilo, MGSB 77722. A, dorsal carapace. B, lateral carapace. Scale bars represent 1 mm.

*Description*. Carapace appears longer than wide, moderately convex transversely, straight longitudinally. Frontal region not preserved. Posterior margin weakly concave. Mesogastric region well defined posteriorly by cervical groove, moderately so laterally, with strong tubercle just posterior to point where mesogastric region narrows. Protogastric region partially preserved. Epibranchial region well defined laterally by groove arising from anterolateral corner of cardiac region and posterior branch of cervical groove. Uro-/metagastric region well defined, consisting of a right and left lobe, weakly connected axially. Cardiac region hexagonal, well defined anteriorly by posteriorly directed, wide V-shaped, strong groove; posteriorly by anteriorly directed, wide V-shaped groove; undefined laterally; with strong tubercles in central part. Meso- and metabranchial regions not differentiated, with tubercles at height of cardiac region. Intestinal region not identifiable. Cervical groove pronounced, with posterior and anterior branch on lateral part of carapace. Branchiocardiac groove appears absent. Moderate to weak groove just anterior to posterior margin. Carapace covered with granules, which seem to become larger toward to posterior part. Venter, abdomen, appendages, and cuticle not preserved.

*Remarks*. The specimen is thought to be closest to species within the Galatheoidea on account of the arrangement of the preserved grooves and regions. Many galatheoids also exhibit a posterior and anterior branch of the cervical groove on the lateral part of the dorsal carapace, and some also have a granular character on the dorsal carapace (e.g., Munidopsidae sensu Ahyong et al., 2010). The shape of the cardiac region, especially the anterior part, seems different from the cardiac region of munidopsids that are usually subtriangular or subrectangular. The Gastrodoroidea (see Klompmaker et al., 2011a) have also been considered. The cervical groove, the posterior margin, the granular character (except for some larger tubercles in the specimen under study), and groove arising from the anterolateral corner of the cardiac region seem to match gastrodoroids closely. However, the cardiac region is distinctly different in that it is spade-shaped to subtriangular in gastrodoroids, whereas the region is hexagonal in this specimen. Moreover, no branchiocardiac groove is observed in the specimen under study, which all gastrodoroids exhibit. In conclusion, given the similarities to munidopsids, placement within the Galatheoidea seems most likely at this point until more specimens are found. The specimen is distinctly different from all other galatheoids from Koskobilo quarry, at least at the species and generic level.

## 4. Discussion

The Koskobilo quarry in the Aldoirar patch reef has yielded as many as ten galatheoid species from five different genera. This is the first time this many different galatheoid species and genera have been found in one locality exposing Cretaceous strata. The richest locality previously known was the Monte Orobe quarry in the neighboring, contemporaneous Monte Orobe patch reef, yielding six species (*Eomunidopsis navarrensis*, *E. orobensis*, *Paragalathea ruizi*, *P. straeleni*, *P. multisquamata*, and *Annieporcellana dhondtae* Fraaije et al., 2008) arranged within three genera of galatheoids (Vía Boada, 1982; Fraaije et al., 2008). The Eguino Formation, in which the Koskobilo and Monte Orobe are located, now yields as many as eleven galatheoid species within six genera. The richest formations are the Eguino Formation (Vía Boada, 1982; Fraaije et al., 2008; herein) followed by the Cenomanian/Turonian Kem Kem Beds (no official formation known) exposed in the Moroccan Gara Sbaa locality yielding three species from three different genera (Garassino et al., 2008).

We speculate that the peak in diversity in Cretaceous galatheoids is at least in part related to the coral reefal facies. This is supported by the results from the work of Robins (2008), who reported as many as 25 galatheoids from the Upper Jurassic (Tithonian) coralgal reefal limestones of Ernstbrunn, Austria. Relatively diverse galatheoid faunas are found in reef facies from modern habitats as well. By extracting data from Abele (1976), nine species of galatheoids were found in a *Pocillopora damicornis* coral habitat off the coast of Panama. The sandy beach environments of the Pacific and Caribbean coasts of Panama were not a home to galatheoids. This was largely the case in mangrove habitats on both coasts of Panama as well, as collecting efforts on the Pacific side resulted in only two galatheoid species. The only environment in Panama that approached the number of galatheoids in coral facies were the rocky intertidal zones of the Pacific and Caribbean coasts, yielding twelve and six species, respectively. Collecting efforts in all environments were continued until the “accumulated-species curve became asymptotic” (Abele, 1976, p. 264), so that the number of species from the different habitats could be compared.

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