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Mesogalathea ardua sp. nov., a new species of squat lobster (Decapoda, Galatheidae) from the Upper Jurassic olistolith at Velika Strmica (Dolenjska, Slovenia)

Nova vrsta raka *Mesogalathea ardua* sp. nov. (Decapoda, Galatheidae) iz zgornjejurskega olistolita pri Veliki Strmici (Dolenjska, Slovenija)

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Ključne besede: Anomura, Galatheoidea, kimmeridgij-tithonij, Slovenija, nova vrsta

Abstract

A new species of squat lobster, *Mesogalathea ardua* sp. nov., is described on the basis of newly collected dorsal carapaces from an Upper Jurassic reefal limestone olistolith at Velika Strmica. The fossiliferous olistolith is situated within Upper Cretaceous flysch-type deposits, but originally formed within the central parastromatoporoid zone of a Jurassic reef complex. *Mesogalathea ardua* sp. nov. represents the first formal description of a Jurassic squat lobster from Slovenia and extends the known palaeobiogeographical distribution of galatheoid anomurans.

Izvleček

Predstavljena je nova zgornjejurska vrsta raka skakača *Mesogalathea ardua* sp. nov., opisana na podlagi na novo zbranih primerkov iz grebenskega olistolita pri Veliki Strmici. S fosili bogat olistolit se nahaja znotraj zgornjekrednih flišnih plasti, njegov izvor pa je v parastromatoporoidni coni centralnega dela jurskega koralnega grebena. Novo opisana vrsta *Mesogalathea ardua* sp. nov. je prvi opis jurskega raka skakača iz Slovenije in širi do sedaj znano paleobiogeografsko razširjenost galatheoidnih rakov.

Introduction

The Upper Jurassic of Europe was a hotspot in galatheoid speciation (Bracken-Grissom et al., 2013; Klompmaker et al., 2013; Fraaije, 2014; Robins et al., 2012, 2013, 2015, 2016; Robins & Klompmaker, 2019). These so-called squat lobsters inhabited primarily shallow areas of the tropical Tethys Ocean. Many of the fossil galatheoids are found within limestone blocks interpreted as parts of former coralgal reefs. The largest number of Late Jurassic galatheoid species (and greatest number of specimens) come from a series of olistoliths in the vicinity of Ernstbrunn (Austria), as well as from numerous other olistoliths labelled "Štramberk Limestones" across the border of the modern-day Czech Republic and Poland (for further details, see Robins et al., 2013, 2016). Several galatheoid-producing localities within modern-day Romania are in place (Feldmann et al., 2006; Schweitzer et al., 2017); however, several others within the Carpathians represent olistoliths as well (Schweitzer et al., 2018). All of these originate from reefal environments. This redeposition of Jurassic material within Cretaceous deposits adds additional levels of complexity as far as their depositional and palaeoenvironmental history is concerned. The better-known Jurassic Solnhofen-type limestones, in contrast, are not reefal in nature. Galatheoids are incredibly rare there, with only a single species recorded to date from the area (Feldmann et al., 2016). In non-Solnhofen carbonate rocks in southern Germany, only a single munidopsid species, *Gastrosacus wetzleri* von Meyer, 1851, is present. This species is known mainly from sponge-microbial reefs and associated limestones (Robins et al., 2015).

The present study discusses a new record of Late Jurassic squat lobsters from Slovenia, describing a new species of *Mesogalathea* Houša, 1963, on the basis of newly collected material. These specimens extend the palaeobiogeographical distribution of Late Jurassic galatheoids.

Geological setting

The locality of Velika Strmica, some 10 km northwest of Novo mesto, belongs structurally to the Dinarides, i.e. the folded and thrusted former northeastern margin of the Adria tectonic microplate (Placer, 1999, 2008; Vrabec & Fodor, 2006). According to Kastelic et al. (2008), the main phase

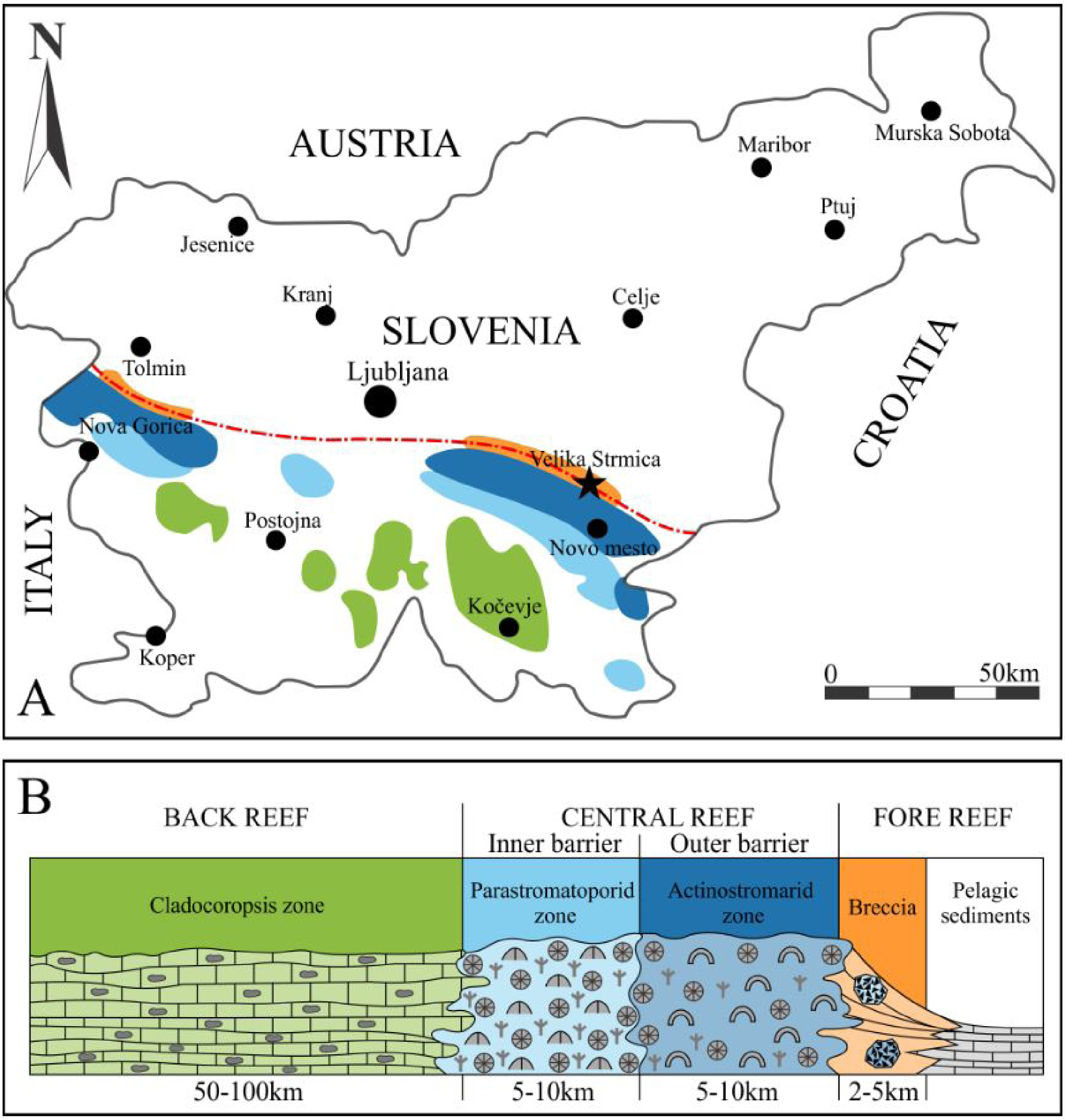

Fig. 1. Position of the locality. A - Simplified geographical map showing the locality of Velika Strmica (star) and present-day position of the Upper Jurassic barrier reef complex in Slovenia. B - Palaeoenvironmental differentiation of the Jurassic barrier reef complex (adapted after Turnšek, 1997).

of the NE- to SW-directed folding and thrusting took place during the Eocene. The northeastern part of the Dinarides was further dissected after the Miocene by the SE-NE trending, post-Miocene strike-slip faults of the Mid-Hungarian tectonic zone. These faults, together with the W-E striking Periadiatic tectonic zone to the north and the NW-SE trending strike-slip faults of the Idrija tectonic zone to the east, form the so-called Sava compressive wedge (Placer, 1999).

The stratigraphical succession at Velika Strmica is incomplete due to the strongly faulted structure of the area. The lower part of the succession comprises Triassic, Jurassic and Lower Cretaceous carbonates (Pleničar & Premru, 1977; Trotošek, 2002; Buser, 2009), deposited on or at the margin of the Adriatic carbonate platform, which covered large parts of the continental crust of the Adria microplate during the Mesozoic (Buser, 1989; Vlahović et al., 2005). Platform carbonates are discordantly overlain by upper Santonian to mid-Campanian grey and red marly limestone with chert and subordinate intercalations of calcarenite and calcrudite (Trotošek, 2002), or by Campanian-Maastrichtian flysch-type deposits, comprising basal carbonate breccia or calcarenite and marlstone (Pleničar & Premru, 1977; Trotošek, 2002). West of the village of Velika Strmica, the marlstone from the flysch series comprises also a series of Upper Jurassic (Kimmeridgian/Tithonian) carbonate blocks of reefal limestone (Fig. 1). The fossils studied originate from one of these olistoliths, from which a diverse decapod crustacean fauna has been recovered (Gašparič & Gale, 2018). The Late Jurassic age of the olistolith has previously been determined on the basis of occurrences of the corals *Dermoseris* sp. and *Dermosmilia etalloni* Koby, 1884 (Trotošek, 2002).

Material and methods

The present study is based on 15 specimens of galatheoid preserved in a coral limestone matrix. They were mostly found by mechanically breaking down a rock sample, except in rare cases where specimens were visible on weathered surfaces. Because specimens are heavily recrystallised, there is only poor separation between the rock and the thin cuticle. Cuticle is partially preserved in some specimens, although occasionally damaged in weathered or prepared specimens. However, presence or absence of cuticle seemingly has no significant impact on carapace ornamentation in galatheoids (Robins et al., 2016). Material described and illustrated are part of the collections of the Natural History Museum Ljubljana (Slovenia).

Decapod specimens were prepared and studied under a stereomicroscope Leica EZ 4D. Photographs were taken with a digital camera Nikon D750. Some specimens were whitened with ammonium chloride sublimate prior to photography in order to enhance details of cuticle ornamentation.

Microfacies analysis was performed on nine thin sections, prepared from four samples. Thin sections are now held in the repository of one of us (L.G.; thin sections with number 1231). Microfacies types are characterised according to the classifications of Dunham (1962) and Embry & Klovan (1971). Quantity grain analysis for grainstone was done on three images at magnifications of ×12.5 and ×25 with JMicroVision v2.7 computer software (Nicolas Roduit, 2002-2008). Over 200 points per image were counted. Completely micritized grains were counted as peloids, in contrast to intraclasts, which still preserve original texture. Rounded (abraded) fragments of bounding organisms were also treated as intraclasts. Whenever the origin of a peloid could be recognised, e.g., due to incomplete micritization, such a grain was added to non-micritized grains of the same type.

Description of olistolith

The isolated limestone block, measuring approximately 2 m in diameter, consists of grainstone in its lower part, followed by sponge floatstone. Macroscopically, the latter facies contains a rich fauna with sponges, decapod crustaceans, corals and brachiopods. Within the grainstone, clasts represent 70 % of the bulk rock. They range in size from 0.08 to 1.32 mm, with most grains around 0.25 mm in diameter. The sediment is moderately well sorted. Grains are subangular to subrounded, mostly with point contacts. Intraclasts account for 28 % of the area. Most are strongly micritized. Unclear particles can be detected, and some represent abraded fragments of encrusting algae. Boring and predating abrasion is seen in some of the latter. Sparitic fragments, abraded and micritized to various degrees, are the next common grain type (21.5 %). Peloids account for 14.5 %, and echinoderms for 5 %. Other components (foraminifera, bryozoans, brachiopods) are very rare. Bryozoan colonies were fragmented and later abraded. Zooecia are filled with micrite. Most of the benthic foraminifera are fragmentary, whereas planktonic forms are much better preserved, with numerous short spines apparent at the surface. Among the former, *Protopeneroplis striata* Weynschenk, 1950 and *Ammobaculites* sp. were identified. Other forms present belong to lagenids, miliolids and planktonic taxa. Intergranular space is filled with drusy-mosaic calcite cement.

In the sponge floatstone, clasts larger than 2 mm represent 20-40 % of the area. Sorting is very poor. Most of these are tabular sponges; corals and brachiopods are subordinate. Sponges and corals are commonly encrusted by *Lithocodium/Pseudolithocodium*-like crusts (see comments in Schlagintweit et al., 2010), sessile foraminifera, serpulids, red algae and sponges. Serpulids are also found within internal canals of sponges. Microborings are also very common on the outer surface of sponges and corals. Brachiopod shells are preserved with closed valves. The matrix consists of bioclastic wackestone and packstone. Clasts are strongly fragmented and sparitic fragments predominate. Complete bivalve and gastropod shells are rarely preserved. Original shells seem to have been dissolved during diagenesis and moulds were first lined with bladed rim cement, followed by clear drusy-mosaic calcite cement. Other grains include foraminifera, echinoderm ossicles (including echinoid spines), fragmented bryozoans and ostracods. Among foraminifera, *Protopeneroplis striata*, *Earlandia tintinniformis* (Mišik, 1971), indeterminate miliolids and nodosariids of the meandrospiroid form, and *Astacolus* sp. were identified.

Abbreviations

Abbreviations of dorsal carapace characters of Galatheoidea used in the illustrations are as follows: L – length, excluding rostrum; R – rostrum length; LR – total length, including rostrum; GH – gastric region length, from base of rostrum to cervical groove; MW – maximum width of specimen; RW – maximum rostrum width; TW – width at anterior margin; ro – rostrum; os – orbital sinus; as – anterolateral spine; cg – cervical groove; gr – undifferentiated gastric region; br – undifferentiated branchial region.

RGA/SMNH - Slovenian Museum of Natural History, Ljubljana, Slovenia (R. Gašparič Collection).

Systematic palaeontology

Order Decapoda Latreille, 1802

Infraorder Anomura MacLeay, 1838

Superfamily Galatheoidea Samouelle, 1819

Family Paragalatheidae Robins, Feldmann, Schweitzer & Bonde, 2016

Genus *Mesogalathea* Houša, 1963

Type species: *Galathea striata* Remeš, 1895, by original designation.

Diagnosis: Carapace subrectangular to suboval; strongly convex, maximum width roughly equal to length; ornamented exclusively with transverse ridges. Rostrum very broad, without keel, ending in broadly tridentate tip. Cervical groove weakly to moderately defined; regions usually undefined (after Robins et al., 2016).

Remarks: This genus is known exclusively from the Upper Jurassic, with records from Austria, the Czech Republic, Poland, Romania and Slovenia, of the following species: *Mesogalathea striata* Remeš, 1895, *M. macra* Robins, Feldmann, Schweitzer & Bonde, 2016, *M. pyxis* Robins, Feldmann, Schweitzer & Bonde, 2016 and *M. retusa* Robins, Feldmann, Schweitzer & Bonde, 2016.

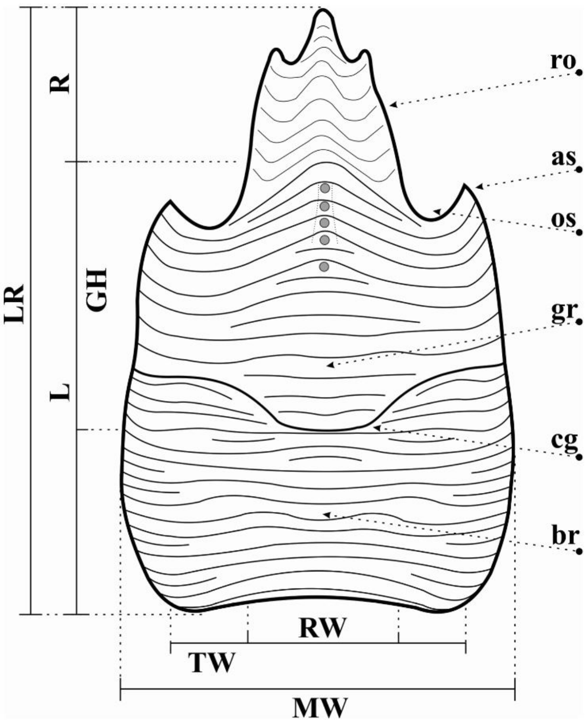

Fig. 2. Schematic reconstruction of the dorsal carapace of *Mesogalathea ardua* sp. nov., with descriptive terminology and carapace measurements used in the text (for terminology see "Abbreviations").

Mesogalathea ardua sp. nov.

(Figs. 3-5)

Etymology: from the Latin "*ardus*" meaning steep, in reference to the locality name Velika Strmica, which translates as "steep hill".

Diagnosis: Carapace L/MW 1.3; L/TW 1.4 (average). Lateral margins straight; arching inwards anteriorly and posteriorly; maximum width posterior of cervical groove. Rostrum large, spatulate; covering approximately half total width of anterior of dorsal carapace and representing more than one-third of carapace length (L). Lateral edges of rostrum converging anteriorly; distinctly tridentate, with three pointed tips; central tip extending furthest. Carapace and rostrum ornamented with continuous transverse ridges that extend to lateral margins. Defined cervical groove extending across carapace, broadly concave and straightening at centre; turning sharply anteriorly at lateral margins.

Holotype: RGA/SMNH 1783 (Figs. 3A-B, 4A).

Paratypes: RGA/SMNH 2173 (Fig. 4D), RGA/SMNH 1786 (Fig. 4C), RGA/SMNH 2215 (Fig. 5A), RGA/SMNH 2115 (Fig. 4B), RGA/SMNH 2117 (Fig. 5B) and RGA/SMNH 2094.

Type locality: Velika Strmica, Slovenia.

Type age: Late Jurassic, Kimmeridgian/Tithonian.

Distribution: Only known from the type locality.

Measurements: details in Table 1.

Description: Carapace subrectangular to suboval in shape; narrows slightly at extreme anterior and posterior, maximum width (MW) in posterior third. Carapace strongly convex transversely; moderately convex longitudinally; longer than wide, L/MW relatively constantly at 1.3, L/TW ranging between 1.3 and 1.5. Rostrum very large, spatulate; covering approximately half anterior width of frontal margin of dorsal carapace; representing more than one-third of carapace length (L); rostrum comprising larger portion of total carapace length in smaller than in larger specimens. Rostrum with lateral edges higher at midpoint; smooth lateral margins; moderately deflected; bearing no keel. Lateral edges of rostrum subparallel, converging in anterior-most third; rostrum ending in distinct tridentate tip; all three tips pointed, central tip of trident extending more than double the length of lateral

Table 1. Dimensions (in millimetres) of *Mesogalathea ardua* sp. nov.

Spec. No.	L	LR	R	MW	RW	TW	GH	L/MW	L/TW	RW/TW
RGA 1783	8.4	10.9	2.5	6.4	2.8	5.5	4.5	1.3	1.5	0.5
RGA 2173	5.0	6.6	1.6	4.0	2.0	3.9	3.0	1.3	1.3	0.5
RGA 1786	4.1	5.6	1.5	3.1	1.4	2.7	2.2	1.3	1.5	0.5
RGA 2215	—	—	—	8.8	3.6	6.8	5.8	—	—	0.5
RGA 2115	—	—	2.6	—	3.0	5.6	—	—	—	0.5
RGA 2117	—	—	2.9	—	3.5	5.4	—	—	—	0.6
RGA 2094	9.3	—	—	7.2	4.1	7.1	5.4	1.3	1.3	0.6

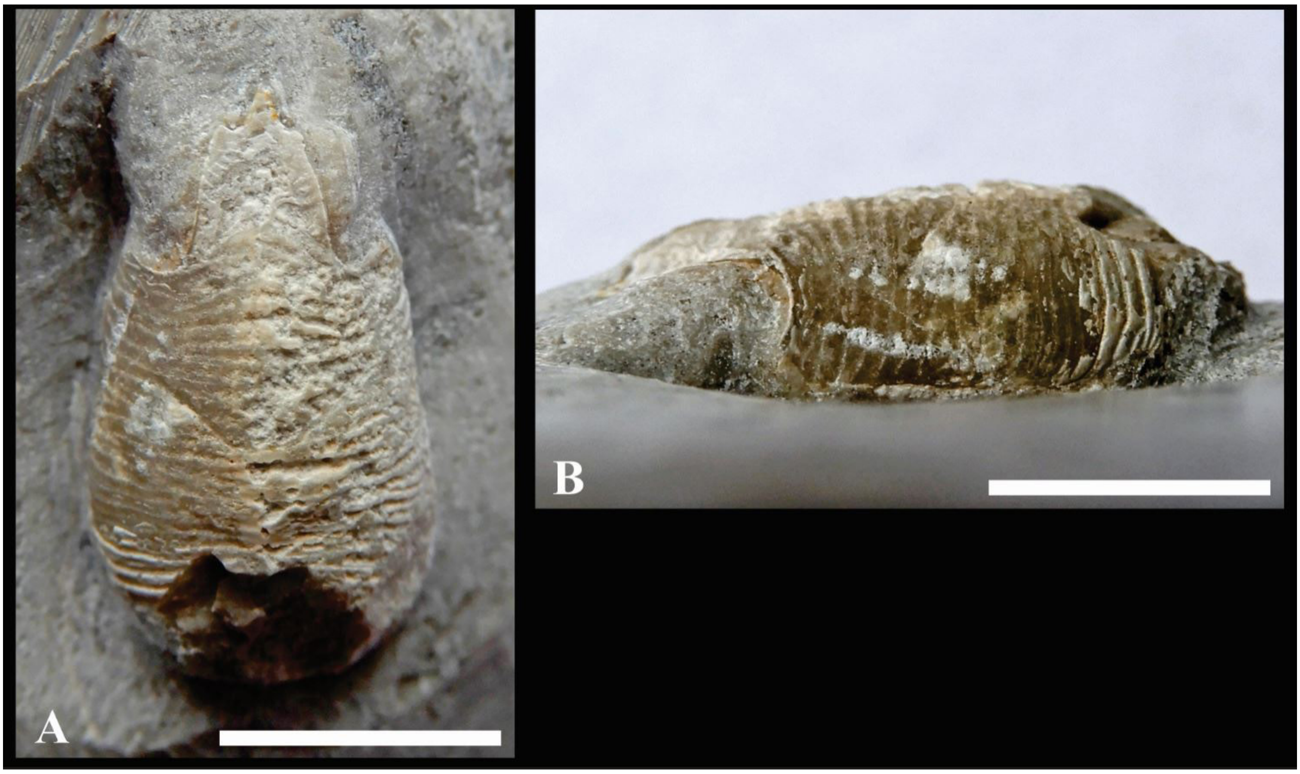

Fig. 3. *Mesogalathea ardua* sp. nov. A - RGA/SMNH 1783 (holotype), dorsal carapace; B - RGA/SMNH 1783 (holotype), lateral view of carapace. Scale bars equal 5 mm.

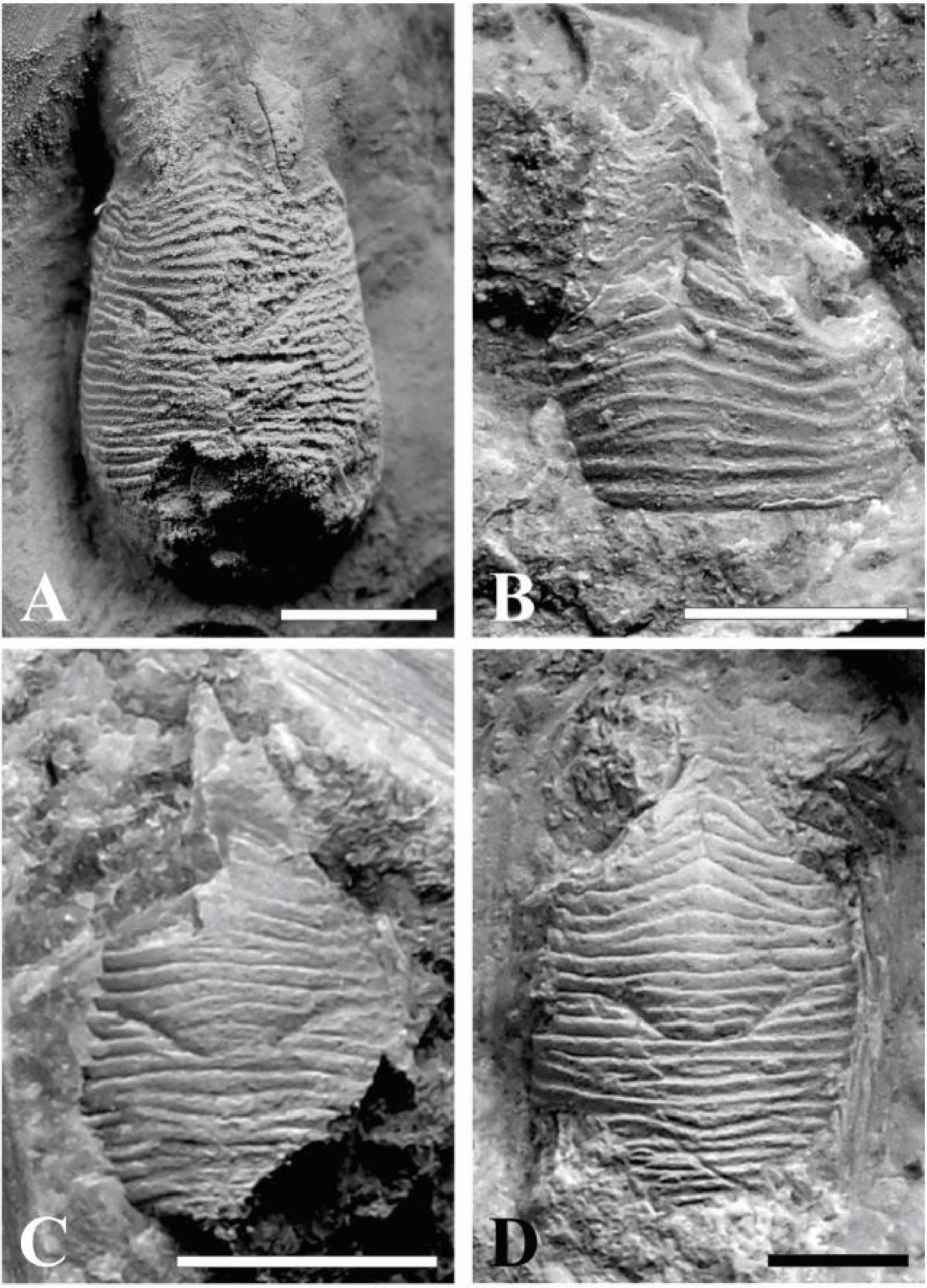

Fig. 4. *Mesogalathea ardua* sp. nov. A - RGA/SMNH 1783 (holotype), dorsal carapace; B - RGA/SMNH 2115 (paratype), partial dorsal carapace; C - RGA/SMNH 1786 (paratype), dorsal carapace; D - RGA/SMNH 2173 (paratype), dorsal carapace. Scale bars equal 3 mm (A, B) and 2 mm (C, D).

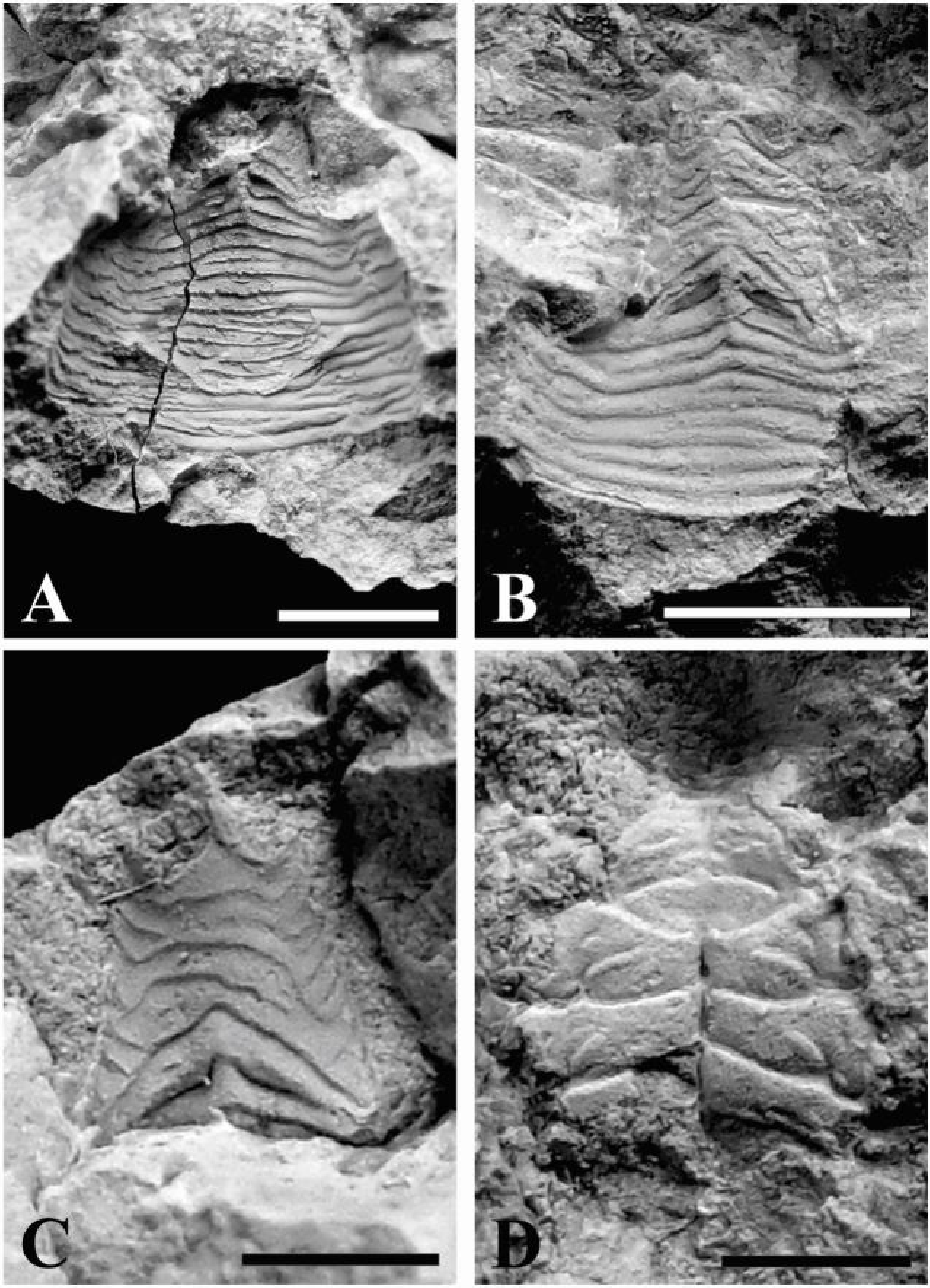

Fig. 5. *Mesogalathea ardua* sp. nov. A - RGA/SMNH 2215 (paratype), partial dorsal carapace; B - RGA/SMNH 2217 (paratype), partial dorsal carapace; C - RGA/SMNH 2101, rostrum; D - RGA/SMNH 1784a, sternal plastron. Scale bars equal 3 mm (A, B) and 2 mm (C, D).

tips. Rostrum adorned throughout by strong meandering, transverse ornamentation; ornamentation of rostrum mirroring trident rostrum shape. Orbits shallow and directed forwards, apparently continuing under rostrum. Supraorbital margin concave, unornamented, with one forwardly directed spine at anterolateral angle.

Lateral margin straight; smoothly arching inwards both anteriorly and posteriorly. Defined cervical groove extending across carapace, broadly concave and straightening at centre; running progressively anteriorly across carapace and turning sharply anteriorly immediately prior to lateral margins. Branchio-cardiac groove not present. Regions not defined; depressed subparallel converging tip of mesogastric region located posteriorly to rostrum, intersected by ornamentation, longitudinally depressed and adorned with circular depressions interspaced between transverse ridges. Carapace ornamented with long prominent, uninterrupted, transverse ridges; occasionally interspersed with smaller ridges. In anterior part of gastric region, ornamentation continuing smoothly onto rostrum, ridges centrally convex; posterior gastric ridges straightening and becoming concave, reflecting cervical groove. Anterior branchial regions ornamented with slight concave transverse ridges; straightening where approaching posterior part of branchial region. All ornamentation extending to lateral edges and turning sharply anteriorly at lateral margins.

Ventral surface (sternal plastron) (Fig. 5D) and preserved appendages disarticulated; hence it is not possible to assign them to *Mesogalathea ardua* sp. nov. with any confidence, but this is likely in view of size, abundance and relative proximity.

Discussion: Based on overall carapace shape, a long, broad and tridentate rostrum without a keel, ornamentation of exclusively transverse ridges; a defined cervical groove, but a lack of other defined grooves or regions, the new species can be confidently assigned to the genus *Mesogalathea*. *Mesogalathea ardua* sp. nov. resembles *Mesogalathea striata* in overall carapace shape and prominent transverse ornamentation, whereas the ridges in the new species are straighter and more regularly continuous across the carapace. Additionally, *Mesogalathea ardua* sp. nov. possesses a wider, more concave and more deeply incised cervical groove and a pointed tridentate ornamented rostrum, with a longer median tip and a well-developed tip of the mesogastric region. The new species has a more prominent transverse ornamentation, a rostrum with a distinctly longer tridentate tip, anterolateral spines and a deeper cervical groove than in *Mesogalathea macra* and *Mesogalathea retusa*. *Mesogalathea pyxis* has a more convex carapace, a more irregular transverse ornamentation and ornamented orbits that lack anterolateral spines, as in *Mesogalathea ardua* sp. nov.

Palaeoecology and palaeoenvironment

The fossil assemblage recovered from the olistolith studied hints at its provenance from the Upper Jurassic reef complex which stratigraphically underlies the Lower Cretaceous flysch-type deposits. The Late Jurassic reef complex of the External Dinarides is considered the largest preserved fossil reef in Slovenia. It was a barrier reef that extended along the northern margin of the Dinaric Carbonate Platform, which passes northwards into the deep-marine Slovenian Basin (Fig. 1A; Turnšek et al., 1981; Turnšek, 1997). Turnšek et al. (1981) subdivided the Upper Jurassic reef complex of the External Dinarides into fore-reef, central reef and back-reef, the last-named containing local patch reefs. Based on reefal communities, the central reef area was further subdivided into an outer "actinostromarid zone" and an inner "parastromatoporoid zone" (Fig. 1B). The relative abundance of *Protopeneroplis striata* in the olistolith studied, as well as the presence of planktonic foraminifera, is suggestive of original deposition on the upper slope. This view is supported by the occurrence of *Lithocodium/Pseudolithocodium*, also known from shallow- to deeper-water settings (see Schlagintweit et al., 2010). We conclude that the Upper Jurassic olistolith that has yielded the decapod crustaceans described here developed in the central parastromatoporoid zone of a Jurassic coral reef complex.

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