

**Triassic clam shrimps (“Conchostraca”; Branchiopoda: Diplostraca) from
Mallorca: Taxonomic description and interregional comparisons**

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Abstract

We describe four upper Lower Triassic to lower Middle Triassic clam shrimp-bearing intervals from Mallorca, which include the clam shrimp species *Hornestheria* sp. aff. *Hornestheria sollingensis* and several other forms of carapace valve morphology: *Hornestheria*? Morphotype 1, *Hornestheria*? Morphotype 2, and other undetermined carapace valves. All of this material was obtained from red-bed units cropping out in the Serra de Tramuntana mountains of Mallorca (western Mediterranean). Except for a few morphologically similar carapace valves of Middle Triassic age from China, *Hornestheria* is known only from the type locality of its type species, *Hornestheria sollingensis* Kozur et

Lepper, in the Solling Formation (Middle Buntsandstein Subgroup) in the German part of the Central European Basin. According to its original definition, the larval carapace valve of *Hornestheria* Kozur et Lepper is characterized by a radial sculpture, but this characteristic apparently is only variably developed. Due to both a limited number of previously known occurrences of *Hornestheria* and its poorly known carapace valve morphology, open nomenclature is applied to the taxonomy herein. The studied specimens were freshly collected from outcrop sections composed of greyish-green to greyish-red laminated claystones and siltstones that accumulated in a fluvial facies. The clam shrimp specimens are accompanied by remains of insects and fishes, invertebrate and tetrapod ichnofossils, and micro-/macroplant remains, all of which either have been described by previous workers or are currently part of a separate study.

Key words: Crustacea, Spinicaudata, *Hornestheria*, Pangaea, Balearic Islands, western Mediterranean

Introduction

The traditional term ‘conchostracans’ designates a group of small-sized branchiopod crustaceans, which are known from Devonian to recent times (e.g., Tasch 1969; Hegna & Astrop 2020). They have a chitinous, bivalved carapace, composed of two symmetric valves laterally enclosing their crustacean body. However, it is difficult to link their fossil forms to the zoological classification scheme of their recent relatives (i.e., clam shrimps and waterfleas) due to the often poorly preserved morphological characteristics of fossil carapace valves. Therefore, fossil ‘Conchostraca’ are treated as a paraphyletic taxonomic group corresponding to a composite of the extant monophyletic suborders Spinicaudata,

Laevicaudata, Cyclestherida, and Cladocera (e.g., Rogers & Hegna 2020). In both fossil and recent taxonomic systematics, these four suborders comprise the order Diplostraca within the class Branchiopoda. Occurrences of modern clam shrimps in continental deposits are known from all continents other than Antarctica (Frank 1988). Fossil clam shrimps are mostly found in continental bodies of water, but can also be found in both brackish and shallow marine deposits (e.g., Webb 1979; Liu & He 2000; Scholze *et al.* 2020).

Both modern and fossil clam shrimps are (palaeo-)geographically widely distributed from the Devonian to the present, because of the very high dispersal potential of their minute, drought and/or frost resistant, wind-transportable dormant eggs. Their eggs can also be attached to other animals or survive passage through the digestive system of predators, thus adding to their geographic dispersal mechanisms (e.g., Vanschoenwinkel *et al.* 2008). As noticed by previous workers (e.g., Schneider *et al.* 2020), clam shrimp habitats changed during the late Palaeozoic from perennial lakes to seasonal and temporary lakes, ponds, and puddles, coincident with a nearly global palaeoclimate aridification that began at that time. Like other pioneering organisms, many clam shrimp species (including all modern species of spinicaudatans and laevicaudatans) became adapted to thrive in ephemeral freshwater pools, as well as in water bodies with elevated salinities because of evaporation, where their carapace valves often accumulated in mass occurrences that are useful for biostratigraphy.

Here, we study the clam shrimps from the lower Middle Triassic continental units of Mallorca. The deposits of the study area are known for their occurrences of insects (Calafat & Sáez 1987; Calafat 1988; Zessin 2008a, 2008b; Aristov & Zessin 2009; Juárez-Ruiz & Wachtler 2015) and tetrapod trace fossils (Juárez-Ruiz & Wachtler 2015). Additionally, records of clam shrimps (“*Euestheria* sp.”), shark egg capsules (“*Palaeoxyris* sp.”), a fish of unknown affinities, and arthropod trace fossils also have been mentioned by Calafat & Sáez (1987), Calafat (1988), and Zessin (2008b). Additionally, occurrences of conifers and other

micro- and macroplant remains have been reported in detail by previous workers (e.g.,
Álvarez-Ramis *et al.* 1995; Grauvogel-Stamm & Álvarez Ramis 1996; Diez *et al.* 2010;
Juárez-Ruiz & Wachtler 2015). All of these records open a window into a local biota that
succeeded the aftermath of the end-Permian (e.g., Joachimski *et al.* 2012; Shen & Bowring
2014; Biswas *et al.* 2020) to the Early Triassic (e.g., Galfetti *et al.* 2007; Stanley 2009;
Hochuli *et al.* 2016; Zhang *et al.* 2019) mass extinction event, which is known to be the most
profound biotic crisis in the history of multicellular life on Earth (e.g., Benton 1995, 2018;
Stanley 2016; Delfino *et al.* 2020). From the upper Lower Triassic to the lower Middle
Triassic, fossil clam shrimps are known from only a few of localities apart from the ones
studied herein, such as France (e.g., Gall & Grauvogel-Stamm 2005), Germany (e.g., Kozur *et al.*
1993; Mahler & Sell 2015), Poland (e.g., Żyła *et al.* 2013), Tunisia (Soussi *et al.* 2017),
and Argentina (e.g., Tassi *et al.* 2015). Comparing these occurrences with our new data from
Mallorca contributes to a better understanding of the Early–Middle Triassic post-crisis fauna
within a wider palaeogeographic realm than has been previously possible. Additionally, it is
hoped that our present study will motivate future working groups to improve the general
knowledge on transitional Lower Triassic–Middle Triassic clam shrimp biostratigraphy
through additional future studies, as clam shrimps have great potential for both fine-scale
biozonation and regional to interregional biostratigraphic correlations (e.g., Kozur & Weems
2010; Scholze *et al.* 2016; Schneider *et al.* 2020).

Geologic setting

The study area is located in the Serra de Tramuntana, a mountainous area in the northwest of
the island of Mallorca (western Mediterranean). The studied sections, comprising a Lower(?)–
Middle Triassic interval of predominantly siliciclastic red-beds (*‘Buntsandstein facies’*), crop
out along the coastal cliffs between Cala d’Estellencs and Punta de son Serralta (Fig. 1A).

Gómez-Gras (1993) recognised four (herein called A–D) main lithostratigraphic units in these outcrops: (A) a basal sandstone unit representing braided rivers, (B) a lower sandstone and siltstone unit corresponding to meandering rivers, (C) a middle sandstone unit of meandering or braided river deposits, and (D) an upper siltstone and sandstone unit (Fig. 1B) deposited in tidal flats transitional to the overlying shallow marine deposits of the so-called ‘*Muschelkalk* facies’ (e.g., Matamales-Andreu *et al.* 2020). The lithostratigraphic units A–D have not been formally described so far. Diez *et al.* (2010) provided age attributions based on their review of palynomorphs found in some beds of the units B, C, and D, attributing the lowest two to the Aegean Substage (lower Anisian Stage, lower Middle Triassic), and the upper one to an indeterminate substage within the Anisian.

Clam shrimps studied in the present work were all collected *in situ* from four different stratigraphic horizons, all of them consisting of greenish or reddish grey, finely laminated claystones/siltstones, possibly representing small, dysoxic pools formed on fluvial floodplains near meandering channels or in abandoned channels of the braided rivers during low-water intervals. The four sites have been named (in ascending stratigraphic order) “Punta Roja” (middle part of Unit B; Fig. 1C), “Pedra Alta” (upper part of Unit B; Fig. 1D), “Punta Negra 1” (base of Unit C; Fig. 1E) and “Punta Negra 2” (top of Unit C; Fig. 1F). Figure 1B shows a synthetic stratigraphic log that indicates the location of the four sites.

Material and methods

Systematic, bed-by-bed collection of freshly exposed claystone and siltstone slabs from the studied outcrop sections was carried out during a field campaign in 2019 (which was authorized through an excavation permit granted by the Consell de Mallorca under the ref. 305-19, code 0313JUL2019ARQ.305-19.estellencs). About 47 slabs were obtained, each

121 containing between one and 20 clam shrimp carapace valves, resulting in a total collection of
122 112 individual carapace valves. The best preserved individuals (25 in total) were selected for
123 both microscope drawing and photography of their carapace valves, using a LEICA MZ12
124 stereo-microscope with a WILD drawing mirror tube, and a BRESSER MikroCamII digital
125 camera. Multiple photographs were taken of each of these clam shrimp carapace valves at
126 different focus distances, which were later vertically stacked automatically using the software
127 ADOBE Photoshop CS4. To make the microscope line drawings by hand with the drawing
128 mirror tube, a cold light source equipped with a flexible rubber light guide was used for
129 variable illumination of the specimens. The vector graphic software COREL DRAW 20 was
130 used for digitizing the microscope line drawings.

131 The microscope drawings were used for precisely measuring a set of carapace valve
132 parameters (e.g., total valve height [H], valve length [L], dorsal margin length [l], larval valve
133 height [h], total number of growth lines), according to the procedure and terminology
134 proposed by Scholze & Schneider (2015). In order to make a taxonomic determination of the
135 clam shrimp material, carapace valve parameters such as the total size values (valve length
136 and height) and their ratio values (total valve height/total valve length, dorsal margin
137 length/total valve length), as well as the positions of points of maximum curvature at the outer
138 margins of the carapace valve, were used for comparison with literature data, which primary
139 includes Triassic clam shrimps (e.g., Reible 1962; Gall 1971; Chang *et al.* 1976; Kozur &
140 Seidel 1983a; Kozur & Weems 2010).

141 During the stereomicroscopic investigation, it was observed that some microstructures
142 (i.e., remnants of ornamentation on the carapace valves) were partially preserved on a few
143 individuals. Initial attempts to photograph these ornamentation patterns under higher
144 magnifications, utilizing a KEYENCE VHX 6000 digital microscope failed due to ineffective
145 illumination through the inner lens of this digital microscope. Therefore, selected individuals

were permanently coated with gold films, and then photographed using a PHILIPS XL30 Environmental Scanning Electron Microscope (ESEM) with an acceleration voltage of 10 kV and up to 600x magnification. The resulting descriptions on observed microstructures could serve as additional criteria in clam shrimp taxonomy, as generally discussed in previous studies on other clam shrimp occurrences (e.g., Orlova 1978; Li 2017).

All specimens figured herein are permanently stored at Museu de Mallorca in the city of Palma (Mallorca, Balearic Islands, Spain).

Results

The studied clam shrimp carapaces are preserved as a dark greyish to slightly patchy yellowish brown-coloured substance with irregular thicknesses, which represent either remnants of organic materials and/or a derivate of the primary (chitinous) shell substance. An overview of their occurrences in their respective fossiliferous sites, along with a summary of the coordinates, lithostratigraphy, and the taxonomy of the recorded clam shrimp occurrences, is given in Table 1.

For the following morphologic description of the clam shrimp carapace valves, the terminology proposed by Scholze & Schneider (2015) is used. The systematic hierarchy (see below Subchapter ‘Systematic palaeontology’) follows Kozur & Weems (2010), Hegna & Astrop (2020), and Hegna & Olesen (2020), except for taxonomically indeterminate individuals (see Subchapter ‘Indeterminate clam shrimps’).

Table 1. Summary of the (?)upper Lower Triassic–lower Middle Triassic clam shrimp occurrences from the present study.

Name of the fossil site	Coordinates	Lithostratigraphy	Identified clam shrimp taxa
Punta Negra 2	39°39'41"N, 02°28'33"E	Uppermost part of Unit C	<i>Hornestheria</i> sp. aff. <i>Hornestheria sollingensis</i>
Punta Negra 1	39°39'42"N, 02°28'31"E	Lowermost part of Unit C	Indeterminate
Pedra Alta	39°39'41"N, 02°28'28"E	Upper part of Unit B	<i>Hornestheria</i> ? Morphotype 1; <i>Hornestheria</i> ? Morphotype 2
Punta Roja	39°39'54"N, 02°28'39"E	Middle part of Unit B	Indeterminate

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170

171 *Systematic palaeontology*

172 Class **Branchiopoda** Lamarck, 1801

173 Subclass **Phyllopoda** Preuss, 1951

174 Order **Diplostraca** Gerstaecker, 1866

175 Superfamily **Lioestheriacea** Raymond, 1946 emended Holub et Kozur, 1981

176 Family **Xiangxiellidae** Shen in Chang *et al.*, 1976

177

178 **Remarks.** Xiangxiellidae was defined as a subfamily in Chang *et al.* (1976) and attributed
179 therein to the family Vertexiidae Kobayashi, 1954. Carapace valves of Vertexiidae have
180 concavely recurved growth lines along the upper posterior margin below the dorsal margin,

and sometimes a spine-like sculpture on its larval carapace valve (Kobayashi 1954, Astrop & Hegna 2015). These two characteristics are absent in Xiangxiellinae, which excludes this taxon from the family Vertexiidae sensu stricto. Instead, Xiangxiellidae became elevated to family rank by Kozur & Weems (2010), which is followed herein.

Genus ***Hornestheria*** Kozur et Lepper in Kozur et Weems, 2010

Type species. *Hornestheria sollingensis* Kozur et Lepper (in Kozur & Weems, 2010); from the Frohrieper Berg Quarry (East of the town of Lauenförde, Lower Saxony, Germany), Solling Formation (Middle Buntsandstein Subgroup, Buntsandstein Group), uppermost Spathian (uppermost Olenekian, uppermost Lower Triassic) (Kozur & Weems 2010: p. 395). *Hornestheria sollingensis* was used in stratigraphic charts (e.g., Bachmann & Kozur 2004) before the taxonomic characteristics for its genus and species levels were formally published by Kozur & Weems (2010: appendix 1).

Remarks. A diagnosis of this genus was proposed by H.W. Kozur and J. Lepper (in Kozur & Weems 2010), but metric values for total carapace valve length and height were not provided. Besides a low convexity of the carapace valves and their almost straight dorsal margin, other characteristics of *Hornestheria* included the location of points of maximum curvature of the anterior margin in the horizontal midline of the carapace valve and of the posterior margin below the horizontal midline (Kozur & Weems 2010). The larval carapace valve (= umbonal area of the valve free of growth lines) bore a rather enigmatic radial element, which was either “often quite distinct” (Kozur & Weems 2010: p. 395) or unrecognizable, depending on the respective preservation state of individual carapace valves.

Based on the description of *Hornestheria* in Kozur & Weems (2010), the radial element on the larval carapace valves of *Hornestheria* most closely resembles that of *Lioestheria* Depéret et Mazeran, 1912, which has both nodular and radial sculptures on its larval carapace valves (e.g., Kozur *et al.* 1981). In contrast, however, the size of the larval carapace valve in adult individuals of *Lioestheria* is greater than 1/3 of the total carapace valve length (Holub & Kozur 1981), and this is much larger relatively than the size of the larval valve seen in the carapace of the genus *Hornestheria*. This difference provides a clear distinction between *Hornestheria* and *Lioestheria* sensu Holub & Kozur (1981).

Prominent sculptures are also found on the larval carapace valves of the clam shrimp genus *Cornia* Lutkevich, 1937, which is widely distributed in the Lower Triassic (e.g., Kozur & Seidel 1983a; Kozur & Mock 1993; Tassi *et al.* 2013; Scholze *et al.* 2016). This genus is characterized by an umbonal spine with a circular base located on the larval carapace valve. The spine can be variably preserved (Kozur 1983), being either perpendicular or obliquely embedded in the sediment or being broken, due to variable deformation (e.g., sedimentary compaction) of the rock. According to the description for *Hornestheria* provided by Kozur & Weems (2010), the generally radial shape of its larval sculpture makes it consistently different from the circular shape of the base of the umbonal spine in *Cornia*.

A further characteristic of *Hornestheria* in the sense of H.W. Kozur and J. Lepper (in Kozur & Weems 2010) is the presence of certain types of microsculpture (ornamentation) located on the growth bands of the carapace valves. The ornamentation of the genus *Hornestheria* was originally described as a dense, fine reticulation, which became replaced by fine, short, radial lirae in the outer margins in adult individuals (Kozur & Weems 2010). However, it should be noted that the figures of *H. sollingensis* in Kozur & Weems (2010: fig. A2) show only indistinct reticulation.

In lateral view, the carapace valves of *Hornestheria* are morphologically similar to *Euestheria* Depéret et Mazeran, 1912 and *Magniestheria* Kozur, 1982. However, in contrast to *Hornestheria*, the carapace valves of *Euestheria* have a more strongly convex shape with its highest convexity in the umbonal area. The highest convexity in carapace valves of *Magniestheria* is located in its central area. Both *Euestheria* and *Magniestheria* differ in their ornamentation from *Hornestheria*. The ornamentation of *Euestheria* is either finely dotted to weakly reticulated (Kozur & Seidel 1983a) or very finely pitted, having pits of round to round-oval shapes with diameters of about 10 µm (Sell 2018), that appear generally to be more regular and smoother than the ornamentation seen in *Hornestheria*. The ornamentation of *Magniestheria* is indistinct, varying between coarse pits and very short, irregular, radial lirae (Kozur & Seidel 1983a); their expression is less intense than in *Hornestheria*.

Occurrence. Uppermost Spathian (uppermost Olenekian; upper Lower Triassic) and Anisian (lower Middle Triassic) in Germany (Kozur & Weems 2010), China (see discussions on “*Protomonocarina*” in Kozur & Weems 2010: p. 395), and Mallorca (the present study).

Hornestheria* sp. aff. *Hornestheria sollingensis Kozur et Lepper (in Kozur & Weems 2010) (Figures 2–7)

Material. DA21/03/02/58, DA21/03/02/68, DA21/03/02/72, DA21/03/02/75, DA21/03/02/77, DA21/03/02/78, DA21/03/02/80, DA21/03/02/81.

Description. Carapace valve medium-sized to large, elongated-oval to oval shape; dorsal margin straight, short to long; larval carapace valve very small; umbo located submedial and marginal to inframarginal; anterior and posterior margins sharply curved to very sharply curved; points of maximum curvature along the anterior and posterior margins located in the median-dorsal to median-ventral region, and along the ventral margin in the median to median-posterior region; ornaments fine, indistinct or irregularly reticulated.

Dimensions. Height (H) of the carapace valve between 1.6–3.9 mm; length (L) of the valve between 2.5–3.9 mm; $0.57 < H/L < 0.7$; dorsal margin length (l) between 1.8–2.3 mm; $0.51 < l/L < 0.70$; larval carapace valve height (h) between 0.1–0.5 mm; $0.04 < h/H < 0.19$; up to 20 growth lines; all measurements based on 8 valves.

Occurrence. Pedra Alta site; upper Unit B; lower Anisian (lower Middle Triassic), dated as Aegean by Diez *et al.* (2010).

Remarks. H.W. Kozur and J. Lepper (in Kozur & Weems 2010) first defined *Hornestheria sollingensis* as a new species, providing the following parameters: total carapace valve length between 3.0–3.8 mm, total height between 1.95–2.85 mm, length/height ratio values between 1.3–1.66 (Kozur & Weems 2010). The morphotype of the specimens in the present study identified as *H. sp. aff. H. sollingensis* (Figures 2–6) differ from *H. sollingensis* Kozur et Lepper in their larger size and wider range of the height/length ratio values. Additionally, the larval carapace valve (= “free umbonal area” in Kozur & Weems 2010: p. 397) of *H. sollingensis* is smaller than that of *H. sp. aff. H. sollingensis*. In accordance to the general description of the genus *Hornestheria* by Kozur & Weems (2010), the presence of a radial

element on the larval carapace valve of *H. sp. aff. H. sollingensis* cannot be clearly observed, except for two individuals (collection numbers DA21/03/02/80, DA21/03/02/81; Figure 2B–E). Problematically, in most specimens the small larval carapace valve seems to be poorly preserved and the umbonal area has been almost without exception affected by deformation (i.e., sedimentary compaction). Generally, large sample sets — preferably including layers of mass occurrence (see Figure 2A) — need to be analysed, in order to better understand the full spectrum of preservation variability found in specimens attributable to *Hornestheria*.

When the radial sculpture cannot be clearly seen on the larval carapace valves, both *H. sollingensis* Kozur et Lepper (in Kozur & Weems 2010) and *H. sp. aff. H. sollingensis* (the present study) are morphologically reminiscent of both *Euestheria albertii albertii* (in the sense of Kozur *et al.* 1993; formerly designated as “*Isaura minuta albertii* (Voltz, 1835)” by Reible 1962) and *Euestheria albertii mahlerselli* Kozur et Lepper (in Kozur & Weems 2010). By comparison with the literature, *E. albertii albertii* (figured by Kozur *et al.* 1993: figs. 3.1–3.2) shows a more rounded shape, whereas *E. albertii mahlerselli* (figured by Kozur *et al.* 1993: figs. 3.4, 3.6; for references to further figures see the synonymy list in Kozur & Weems 2010: p. 391) shows a more elongated shape than *H. sp. aff. H. sollingensis*. Additionally, *E. albertii albertii* and *E. albertii mahlerselli* have the strongest carapace valve convexity in the umbonal area, whereas in *H. sp. aff. H. sollingensis* it is more or less at the centre of the carapace valve.

***Hornestheria*? Morphotype 1**

(Figures 8, 9)

300 **Material.** DA21/03/04/01, DA21/03/04/02, DA21/03/04/07-1a, DA21/03/04/07-2a,
301 DA21/03/04/07-1c, DA21/03/04/07-2c, DA21/03/04/07-1d, DA21/03/04/10, DA21/03/04/11,
302 DA21/03/04/12-1, DA21/03/04/12-2, DA21/03/04/13a, DA21/03/04/13b.

303

304 **Description.** Carapace valves very large and round in shape; dorsal margin straight, very
305 short to short; larval carapace valve very small; position of the umbo anterior to slightly
306 submedial and inframarginal to slightly marginal; anterior and posterior margins sharply
307 curved to very sharply curved; points of maximum curvature of the anterior margin located
308 median-dorsal to median-ventral, in the posterior margin median-ventral, and in the ventral
309 margin median-anterior; ventral margin is often indented in its median-posterior area.

310

311 **Dimensions.** Height (H) of the carapace valve between 4.9–7.8 mm; length (L) of the
312 carapace valve between 6.0–9.9 mm; $0.76 < H/L < 0.87$; dorsal margin length (l) between 2.7–
313 4.6 mm; $0.38 < l/L < 0.56$; larval carapace valve height (h) between 0.3–0.9 mm;
314 $0.05 < h/H < 0.16$; up to 55 growth lines, 5–7 growth lines/1 mm towards growth direction; all
315 measurements based on 10 valves plus counterparts.

316

317 **Occurrence.** Punta Negra 2 site; uppermost Unit C; Aegean (Diez *et al.* 2010), lower Anisian
318 (lower Middle Triassic).

319

320 **Remarks.** The use of open nomenclature at the species level is preferred for this set of
321 specimens, due to the small sample available for study. This careful practice follows previous
322 clam shrimp studies by Schneider *et al.* (2005: p. 11) and Schneider & Scholze (2018: p. 369),

in order to prevent the creation of new definitions for what may prove to be synonymous species. A formal species diagnosis for *Hornestheria*? Morphotype 1 should be made only when more congeneric material from a wider study area is available.

Large clam shrimps identified as “*Dictyonatella* sp.” (Żyła *et al.* 2013: figs. 5A, B) and “cf. *Dictyonatella*” (Soussi *et al.* 2017: figs. 13A, B) from the upper Lower Triassic–Middle Triassic of Poland and Tunisia, respectively, have a rounded shape similar to *Hornestheria*? Morphotype 1. According to Kozur (1982), the genus *Dictyonatella* has, among other characteristics, an ornamentation on the growth bands represented by a coarse reticulation and a recurvature of posterior growth lines below the dorsal margin. These two characteristics clearly differ from the generally small reticulated ornaments of *Hornestheria* sensu lato and its non-concave recurvature in the posterodorsal margin of the carapace valve. Notably, in *Hornestheria*? Morphotype 1, a recurved posterodorsal margin is absent.

Shen *et al.* (2002) described “*Euestheria (Magniestheria) truempyi*” from the basal Olenekian (basal upper Lower Triassic), which has a large size and a rounded carapace valve shape similar to the *Hornestheria*? Morphotype 1. Additionally, a minute reticulated ornamentation noted by Shen *et al.* (2002: plate 2, fig. 2) resembles that of *H. sp. aff. H. sollingensis* (Figure 7). “*Euestheria (Magniestheria) truempyi*” of Shen *et al.* (2002), however, shows pronounced concentric ribs in the umbonal and central areas of the carapace valves, whereas the growth bands in all the specimens of the present study are both narrower and their convex curvature is less intense, lacking pronounced concentric ribs.

More recently, Scholze *et al.* (2020: fig. 9E) described a Lower Triassic clam shrimp fauna from the Jialingjiang Formation in southwestern China, which also contained a species designated preliminarily as *Magniestheria* sp. aff. *Magniestheria subcircularis* (Chernyshev, 1934). Its size, shape, and the position of points of maximal curvature of the outer margins of the carapace valve are similar to those of *Hornestheria*? Morphotype 1 (Figures 8, 9), but the

umbo of *M. sp. aff. M. subcircularis* is located in a more submedial position. Additionally, the strongest convexity of the carapace valves, in lateral view, is located in the umbonal area in the case of *Hornestheria?* Morphotype 1, whereas in *M. sp. aff. M. subcircularis* it is located in the central area of the carapace valve.

***Hornestheria?* Morphotype 2**

(Figures 10, 11)

Material. DA21/03/04/04a, DA21/03/04/06, DA21/03/04/07-1b, DA21/03/04/07-2b, DA21/03/04/08, DA21/03/04/09.

Description. Carapace valves very large and elongated oval to oval in shape; dorsal margin slightly curved to curved, very short to long; larval carapace valve very small; position of the umbo submedial and marginal to supramarginal; anterior and posterior margins sharply curved to very sharply curved; points of maximum curvature of the anterior and posterior margins located median or slightly median-dorsal, and in the ventral margin median-anterior; the ventral margin is concavely indented in the median-posterior region of the carapace valve.

Dimensions. Height (H) of the carapace valve between 3.2–4.9 mm; length (L) of the valve between 5.3–7.5 mm; $0.57 < H/L < 0.71$; dorsal margin length (l) between 3.0–4.0 mm;

0.48<l/L<0.70; larval carapace valve height (h) between 0.2–0.9 mm; 0.06<h/H<0.2; often between 25–30 growth lines; all measurements based on 6 valves.

Occurrence. Punta Negra 2 site; uppermost Unit C, Aegean (Diez *et al.* 2010), lower Anisian (lower Middle Triassic).

Remarks. The genus name is written with a question mark, because neither its characteristic radial sculpture in the umbonal area nor microstructures (ornamentation) of the carapace valves could be clearly identified, possibly due to the imperfection of their preservation. Instead of a formal species name, open nomenclature is applied to this distinctive carapace valve morphology. This morphotype co-occurs with the above described *Hornestheria?* Morphotype 1 (Figures 8, 9). The latter mentioned morphotype reaches greater total carapace valve height values than *Hornestheria?* Morphotype 2 (Figures 10, 11). It also differs from *Hornestheria?* Morphotype 2 in having a more rounded shape.

Hornestheria? Morphotype 2 is of larger size than both *H. sollingensis* sensu stricto and *H. sp. aff. H. sollingensis* (Figures 2–6). The large carapace valves of *Hornestheria?* Morphotype 2 resemble similarly sized clam shrimps, such as “*Isaura minuta albertii*” (see Reible 1962: plate 7-fig. 7) or *E. albertii albertii* (see Kozur *et al.* 1993: fig. 3), but differ from them in both its concavely recurved ventral margin and the morphology of the umbo.

Indeterminate clam shrimps

Punta Roja site. Clam shrimps occur rarely in the Punta Roja site in the lower part of Unit B (upper Olenekian(?)–lower Anisian). So far, the sample from this site is limited to three individuals (specimen numbers DA21/03/01/01a, DA21/03/01/01b, DA21/03/01/02; Figure 12A–D) that possess the following characteristics (with semi-quantitative measurements based on both microscope line drawings and attempted line drawing reconstruction of fragments): small to medium-sized carapace valves ($L=2.3\text{--}3.5\text{ mm}$; $H=1.6\text{--}2.6\text{ mm}$), rounded in shape ($0.57 < H/L < 0.74$); dorsal margin straight, short to long ($l=1.6\text{--}1.9\text{ mm}$; $0.51 < l/L < 0.70$); larval valve very small ($h=0.1\text{--}0.5\text{ mm}$; $0.04 < h/H < 0.19$); position of the umbo submedial and inframarginal; anterior and posterior margins sharply curved to very sharply curved; points of maximum curvature along the anterior margin located medial to slightly medial-dorsal, in the posterior margin medial, and in the ventral margin medial to slightly medial-posterior; about 13–19 growth lines.

Punta Negra 1 site. Two clam shrimps carapace valves were collected from the Punta Negra 1 site, in the base of Unit C, of lower Anisian (Aegean; Diez *et al.* 2010) age. In both individuals, the outline of the carapace valves is incomplete; specimen DA21/03/03/02 (Figure 12E, F) appears to be strongly compressed by diagenesis; specimen DA21/03/03/01 (Figure 12G, H) is a fragment of an anterior part of a probably juvenile carapace valve.

Discussion

Taxonomic remarks on the genus Hornestheria

In lateral view, the genus *Hornestheria* often shows a low convexity with its maximal curvature located in the umbonal to central areas of the carapace valve and its umbo lying against or slightly overtopping the dorsal margin. The presence of a radial sculpture on the larval carapace valve represents an important taxonomic characteristic; however, its degree of development is quite variable (Kozur & Weems 2010). This might be a consequence of taphonomic variability, i.e. variable compression could flatten out that feature when the carapace is not well-supported by sediment beneath during the early diagenesis. The radial sculpture seems to be well preserved in only a few of the specimens figured by Kozur & Weems (2010: fig. A2), showing a generally high morphologic variability. This is also true for the material in our present study, wherein such a radial structure cannot be clearly observed in most specimens of *Hornestheria*? Morphotype 1 and *Hornestheria*? Morphotype 2, due to the only moderately good preservation seen in the larval carapace valve areas. Therefore, *Hornestheria*? is written with a question mark in order to indicate that this variability is a problem at our current state of knowledge, which does particularly account for these two morphotypes. More data on well-preserved specimens are required, which would also involve making a detailed re-study of either the *Hornestheria* type material of Kozur & Weems (2010) or new material from its type locality, in order to better understand the undeformed larval carapace valve morphology of this genus.

Other species with radial sculptures on their larval carapace valves were discussed by H.W. Kozur and J. Lepper (in Kozur & Weems, 2010: p. 395), including *Protomonocarina* spp. Shen (in Chang *et al.* 1976). Among these species, one individual of *Protomonocarina sinensis* figured in Chang *et al.* (1976: plate 14, fig. 6) showed a radial rib running from the umbo towards the ventral margin of the carapace valve, which agrees with the taxonomic range of the genus *Protomonocarina* Tasch, 1962. The other species, *P. carinata* Shen (in Chang *et al.* 1976: plate 15, figs. 1, 2), *P. oblonga* Shen (in Chang *et al.* 1976: plate 15, figs. 11, 12), *P. ziguiensis* Shen (in Chang *et al.* 1976: plate 15, figs. 3–7), *P. hubeiensis* Shen (in

Chang *et al.* 1976: plate 15, figs. 8, 9), *P. buzhuangheensis* Shen (in Chang *et al.* 1976: plate 15, fig. 10), and *P. xiangxiensis* Shen (in Chang *et al.* 1976: plate 15, fig. 13), were assigned to the genus *Hornestheria* by Kozur & Weems (2010), based on the presence in those species of a radial sculpture on their larval carapace valves. These species of *Protomonocarina* spp. can be readily differentiated from *H. sp. aff. H. sollingensis* (Figures 2–6) by the relatively smaller sizes of the larval carapace valve and the radial sculpture of the latter species. Additionally, values for total carapace valve length and height of *Protomonocarina* spp. sensu Shen (in Chang *et al.* 1976) range between 1.9–2.9 mm and 1.2–1.8 mm, respectively; these dimensions are distinctly smaller than those of *H. sp. aff. H. sollingensis*.

In contrast to specimens of *H. sp. aff. H. sollingensis* (Figures 2–6), specimens of both *Hornestheria?* Morphotype 1 (Figures 8, 9) and *Hornestheria?* Morphotype 2 (Figures 10, 11) are less well-preserved, showing a mixture of brownish carapace fragments and sedimentary imprints or moulds. Microstructures are present in *Hornestheria?* Morphotype 2 but cannot be clearly seen or imaged (Figure. 11C, D), which is most likely a consequence of its poor preservation. Therefore, an open nomenclature is preferred instead of a formal species name for these specimens, even though *Hornestheria?* Morphotype 1 and *Hornestheria?* Morphotype 2 probably represent new taxa. Both of these carapace valve morphologies are known from a single stratigraphic horizon at the same fossil site (i.e., Punta Negra 2), so they are here separated into two different forms because of the consistently observed differences in the carapace valve morphology of each of these morphotypes. In particular, *Hornestheria?* Morphotype 1 (Figures 8, 9) has a rounded shape, whereas *Hornestheria?* Morphotype 2 (Figures 10, 11) is much more elongated. This might be an expression of sexual dimorphism; it is known from other studies of fossil clam shrimps that sexual dimorphism can be recognised within a single population by the presence of two carapace forms (e.g., Astrop *et al.* 2012; Weems & Lucas 2015). By comparison with the literature, similarly high degrees of shape variation are known from other late Olenekian–early Anisian clam shrimp species, such

as *E. albertii mahlerselli*. According to H.W. Kozur and J. Lepper (in Kozur & Weems 2010: p. 392), this differentiation is based on the length (L)/height (H) ratio values of the carapace valves, resulting in the definition of a slender morphotype ($L/H=1.57-1.74$) and a stout morphotype ($L/H=1.11-1.44$). Another example of a high degree of carapace valve shape variation representing a differentiation into two morphotypes is *H. sollingensis* Kozur et Lepper (in Kozur & Weems 2010), as shown in the photographs of the type material: round carapace valves (see Kozur & Weems 2010: figs. A2.1, A2.4) represent a stout morphotype, whereas elongated-oval carapace valves represent a slender morphotype (see Kozur & Weems 2010: figs. A2.3, A2.5–2.7).

In analogy to these examples of slender and stout morphotypes, one may assume that the assemblage of *Hornestheria*? Morphotype 1 and *Hornestheria*? Morphotype 2 specimens represents a monospecific fauna, which is composed of a morphologically highly variable species that could be differentiated by its total carapace valve height (H)/total carapace valve length (L) ratio values into a stout morphotype (= *Hornestheria*? Morphotype 1; $0.76 < H/L < 0.87$) and slender morphotype (= *Hornestheria*? Morphotype 2; $0.57 < H/L < 0.71$). The stout morphotype would be characterized by both larger total carapace valve sizes and a more round shape. Generally, separation into slender and stout morphotypes seems to be a well-established practice for describing high morphological variability in clam shrimps (e.g., Astrop *et al.* 2012; Weems & Lucas 2015). As exemplified by *Magniestheria mangaliensis* (Jones, 1862) from Lower Triassic deposits of the Buntsandstein Group in Germany (e.g., Kozur & Seidel 1983a; Scholze *et al.* 2015, 2016), the presence of slender and stout morphotypes within a single species can be best recognized by studying large numbers of specimens within single layers of mass occurrences. In the best case, both morphotypes occur in a single population in direct association on a bedding plane. The latter has not been possible to observe in most slabs of the present study, due to both a low amount of available specimens within layers of mass occurrences and the predominantly moderate to poor

preservation of *Hornestheria*? Morphotype 1 and *Hornestheria*? Morphotype 2 specimens. Consequently, both forms are treated as two separate morphotypes by using open nomenclature at the species level owing the rather limited state of knowledge at present.

Implications for biostratigraphy

The sedimentary succession in the wider study area is interrupted by a widespread hiatus at the Permian–Triassic transition. The onset of this stratigraphic gap in the upper Permian has been identified on the Balearic Islands (e.g., Rosell *et al.* 1988), and has been suggested to range upward approximately to the early Olenekian or locally even up to the early Anisian (e.g., Linol *et al.* 2009). This gap is also present in the Iberian Ranges (e.g., López-Gómez *et al.* 2012) and other neighbouring regions in the western peri-Tethys (Bourquin *et al.* 2011). On Mallorca, such a gap has not been recognised so far, because the uppermost part of the Permian sequence and the lowermost part of the Triassic sequence do not crop out anywhere on the island (Calafat 1988; Gómez-Gras 1993). Previous works have dated the herein called units B–D as lower Anisian (Diez *et al.* 2010), but an upper Olenekian age cannot be excluded for (part of) Unit A. Records of conifer cones and other plant remains from Unit B reveal a flora similar to that of the Grès à Voltzia Formation of the Vosges, and this was considered to be an indicator for an Anisian age (Álvarez-Ramis *et al.* 1995; Grauvogel-Stamm & Álvarez Ramis 1996; Gall & Grauvogel-Stamm 2005). Our new data on clam shrimp occurrences on Mallorca generally support assumptions on an uppermost Olenekian–Anisian age for this sequence of strata, because index species typical of the lower Lower Triassic (Induan) were not recorded in the present study, as discussed in the following paragraphs.

Clam shrimp biostratigraphic zonation for the upper Permian–Lower Triassic transition on the northern hemisphere of the supercontinent Pangaea were initially established by Kozur & Seidel (1983b) and Kozur (1993), which became later expanded by Kozur & Weems (2010) to cover a wider time span ranging from the uppermost Permian to the lowermost Jurassic. These biozones have been critically tested (e.g., Becker 2015; Scholze *et al.* 2016) and partially refined, based on new data from multiple stratigraphic intervals of different regions (e.g., Weems & Lucas 2015; Sell 2018; Scholze *et al.* 2019). Recently published studies on new finds of Lower Triassic clam shrimps, such as from European Russia (Scholze *et al.* 2015), Germany (Scholze *et al.* 2016), Jordan (Scholze *et al.* 2017), and southwestern China (Scholze *et al.* 2020), have been summarized by Schneider & Scholze (2018) and Schneider *et al.* (2020).

According to the biozonation schema proposed by Schneider *et al.* (2020), an interval of the so-called *Euestheria gutta* Fauna (Schneider *et al.* 2020) correlates to the basal Lower Triassic (lowermost Induan). Apart from occurrences of both *Euestheria* sp. and the lowermost Triassic index species *Euestheria gutta* (Lutkevich, 1937), this fauna also includes *Palaeolimnadiopsis vilujensis* Varentsov, 1955, *Palaeolimnadiopsis* sp., and one carapace valve form morphologically resembling *Rossolimnadiopsis* Novozhilov, 1958. The latter three taxa also have records in the upper Permian (Scholze *et al.* 2019), so they slightly straddle the Permian–Triassic boundary. According to Schneider *et al.* (2020), this fauna is directly followed by the so-called *Cornia germari* Fauna of Lower Triassic (Induan) age, which is composed of its index species *Cornia germari* (Beyrich, 1857) and several radially ribbed species belonging to the genus *Estheriella* Weiss, 1875. The species of both the *Euestheria gutta* Fauna and the *Cornia germari* Fauna can be accompanied by *Magniestheria mangaliensis* (Jones, 1862), which is widely distributed during the Early Triassic (e.g., Jones 1862; Kozur & Seidel 1983a; Liu & He 2000; Goretzki 2003; Ghosh 2011; Hauschke 2014; Scholze *et al.* 2015, 2016; Chu *et al.* 2019). The studied outcrop sections on Mallorca lack all

these species characteristically found in Lower Triassic (Induan) deposits of other regions. Therefore, an age younger than Induan is inferred for the clam shrimp faunas found in the Mallorcan Unit B and Unit C; the Mallorcan clam shrimp faunas show much closer affinities with the Olenekian–Anisian interval clam shrimp faunas, specifically those designated as the *Hornestheria sollingensis* Zone and “*Magniestheria-Euestheria-Hornestheria* Fauna” by Kozur & Weems (2010) and Schneider *et al.* (2020), respectively.

According to Kozur & Weems (2010), the occurrence of *H. sollingensis* in the Solling Formation (Buntsandstein Group) in the German part of the Central European Basin is biostratigraphically indicative of the so-called *Hornestheria sollingensis* Zone within the uppermost Spathian Substage (uppermost Olenekian, uppermost Lower Triassic). Kozur & Weems (2010) also re-assigned several Anisian-aged species of the genus *Protomonocarina* from China (see Chang *et al.* 1976: p. 112–115) to *Hornestheria*. An Olenekian age for records of *Protomonocarina sinensis* in northern China was also reported by Liu & He (2000). These re-assignments extend the stratigraphic range of the genus *Hornestheria* upward from the uppermost Olenekian into the Anisian.

Other occurrences of upper Olenekian–Anisian clam shrimps were reported by Żyła *et al.* (2013) from the Samsonów Formation (Buntsandstein Group) in the Polish part of the Central European Basin, which includes an assemblage of *Dictyonatella* sp. and *Palaeolimnadia mecsekensis* Nagy, 1960. The genus *Dictyonatella* was first described by Kozur (1982) and so far is only known from Anisian occurrences in Poland (“*Dictyonatella* spp.” in Żyła *et al.* 2013: fig. 5A, B) and France (“*Palaeolimnadiopsis dictyonata*” in Reible 1962: plate 10, figs. 1–3; Gall 1971: plate IX, fig.2; which was later designated as *Dictyonatella dictyonata* in Kozur & Weems 2010). In the Grès à Voltzia Formation of the uppermost Buntsandstein Group in the French part of the Central European Basin, *Dictyonatella* is accompanied by *Palaeolimnadia alsatica* (= *Palaeolimnadia alsatica*

alsatica in Kozur & Seidel 1983a) and *Euestheria albertii* (= “*Isaura minuta albertii*” in Reible 1962). According to Kozur & Weems (2010), these species belong to the *Euestheria albertii albertii* Zone of the Bithynian Substage (middle Anisian). Further occurrences of large-sized forms morphologically similar to *Dictyonatella* were also reported from Anisian–lower Ladinian deposits in Tunisia (Soussi *et al.* 2017). The common occurrence of *Dictyonatella* in all of these deposits might suggest a biostratigraphic correlation between all of these sections in Poland, France and Tunisia, while the absence of this genus in the clam shrimp faunas from the units B and C of Mallorca studied herein suggest that the Mallorcan clam shrimp faunas are of a different age. Notably, other typical Anisian index species like *E. albertii* and *P. alsatica* are absent as well. Consequently, a slightly older age is inferred for the faunas from Mallorca studied here. For these reasons, forms similar to *H. sollingensis* are, at our current state of knowledge, considered to be indicative of an upper Spathian (upper Olenekian) to Anisian stratigraphic range.

Remarks on taphonomy

In contrast to the exceptionally well-preserved thorax, furca, and appendages of both *Palaeolimnadia alsatica* Reible, 1962 (= *P. alsatica alsatica* sensu Kozur & Seidel 1983a) (see Gall 1971: plate 7, fig. 4) and *Palaeolimnadiopsis dictyonata* Reible, 1962 (= *Dictyonatella dictyonata* sensu Kozur 1982) (see Reible 1962: fig. 8) from the Grès à Voltzia Formation in France, segments of the crustacean body are not preserved in *H. sp. aff. H. sollingensis* (Figures 2–6), *Hornestheria?* Morphotype 1 (Figures 8, 9), or *Hornestheria?* Morphotype 2 (Figures 10, 11) from the units B and C of Mallorca. The fact that the majority of observed carapace valves are preserved with intact outlines indicates that there was no significant long-distance post-mortem transport through water currents, which is consistent with the low energy conditions inferred for the deposition of the fine-grained beds

590 containing the fossils. Additionally, there is no indication of abrasion, scavenging, or
591 predation on these clam shrimp carapace valves. Occasional fragmentation of some carapace
592 valves most likely is an artefact resulting from the splitting of claystone and siltstone slabs
593 during fieldwork. This was difficult to avoid because these rocks have been pervasively
594 affected by the development of microfractures generated during diagenesis. This pervasive
595 microfracturing likely also is the cause of loss of flexibility and other carapace properties
596 during diagenesis, at which time mineral changes in the shell substance increased its
597 susceptibility to fragmentation (Monferran *et al.* 2018).

598 As known from studies of modern spinicaudatan clam shrimps, their carapace valves
599 consist of a multi-layered cuticle of chitin, which can be taxa-specifically strengthened by
600 integrating calcium carbonate minerals within them (Astrop *et al.* 2015; Hegna *et al.* 2020).
601 Microstructures (i.e., ornamentation) of the carapace valve can appear as different
602 morphologies depending on the preservation of the respective cuticle layers (Monferran *et al.*
603 2018). Accordingly, the lack of clearly observable ornaments in most of the carapace valves
604 from Mallorca studied here is interpreted to be the result of incomplete preservation or even
605 the absence of primarily mineralized outer cuticles in their respective carapace valves. As the
606 colours of clam shrimp carapace can serve as indicator for fossilization temperatures (P.
607 Tasch, cited in Monferran *et al.* 2018: p. 1062–1063), the slightly brownish coloured
608 remnants of the carapace substance in *H. sp. aff. H. sollingensis* from the Pedra Alta site (e.g.,
609 Figures 2, 4) indicate temperatures between 450°C–600°C during diagenesis. Besides heat
610 resulting from burial depth, such relatively high temperatures might also reflect a magmatic
611 heat input, possibly derived from alkaline basaltic flows that are present in the Upper Triassic
612 strata found in the Serra de Tramuntana mountains (e.g., Navidad & Álvaro 1985; Sanz *et al.*
613 2013).

Summary

The transitional upper Olenekian (upper Lower Triassic) to lower Anisian (lower Middle Triassic) deposits of the “*Buntsandstein* facies” in the Serra de Tramuntana mountains on Mallorca have yielded a clam shrimp fauna composed of *Hornestheria* sp. aff. *H. sollingensis*, *Hornestheria*? Morphotype 1, *Hornestheria*? Morphotype 2, and a few undetermined specimens. *H. sp. aff. H. sollingensis* shows finely reticulated ornamentation, in agreement with the original taxonomic description of *H. sollingensis* Kozur et Lepper (in Kozur & Weems 2010). This taxon, in comparison with literature data, shows strong morphological similarities with the group of *Euestheria albertii albertii* (Reible, 1962) and *Euestheria albertii mahlerselli* Kozur et Lepper (in Kozur & Weems 2010) in respect to their carapace valve size and shape. The taxonomically characteristic radial sculpture on the larval carapace valve region of *Hornestheria* is demonstrably well developed in very few individuals, but this is likely due, at least in part, to its generally small-sized larval carapace valve and only a moderate level of preservation due to deformation (i.e., sedimentary compaction) during diagenesis. According to both the biostratigraphic zonation schema of Kozur & Weems (2010) and the stratigraphic range of the genus *Hornestheria*, the new records of *H. sp. aff. H. sollingensis* from Mallorca indicate that these strata formed during the *Hornestheria sollingensis* Zone, corresponding to the latest Olenekian–Anisian interval.

Large-sized carapace valves, reported here on Mallorca for the first time, are designated preliminarily as *Hornestheria*? Morphotype 1 and *Hornestheria*? Morphotype 2; they show a high degree of variability in their valve shape, best expressed by the variation of the total valve height/length ratio values. This degree of variability may reflect the occurrence of either a single morphologically variable species, possibly divided into a slender and a stout morphotype, or two new species previously unknown. First results from ESEM observations suggest that there is microsculpturing on the carapace valve surface of *Hornestheria*?

Morphotype 2, but the exact geometry of the shape of these ornaments is not well-preserved in the analysed sample set.

Consequently, future studies are recommended to more completely document the full spectrum of carapace valve morphologies in *Hornestheria* from Mallorca and other regions, such as from its type area in the Solling Formation (Upper Buntsandstein) in the German part of the Central European Basin. This future study needs to include a more detailed re-study of the rather enigmatic radial sculpture on its larval carapace valve, both by reinvestigating the holotype material of *H. sollingensis* Kozur et Lepper and any other material found in the holotype region. Nevertheless, the new data presented here on clam shrimp occurrences in the studied outcrop sections on Mallorca emphasizes the great potential of clam shrimps for achieving a detailed biostratigraphy of Permian–Triassic continental deposits.

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Figure Captions

Figure 1. Position of the study area, lithostratigraphy, and field photographs of outcrop sections with respective clam shrimp occurrences. **A:** Simplified geological map of the island of Mallorca with indication of the location of the study area. **B:** Lithostratigraphic framework of the Lower–Middle Triassic red-beds of Mallorca, indicating the four main units (lithostratigraphic units A–D) and the stratigraphic position of the clam shrimp-bearing horizons. The colour of each unit represents the dominant colour of the rocks that constitute it. **C–F:** Outcrop conditions of the Punta Roja site (Fig. C), Pedra Alta site (Fig. D), Punta Negra 1 site (Fig. E), and Punta Negra 2 site (Fig. F); with stars marking the respective fossiliferous horizons.

1011 **Figure 2.** Clam shrimps and plants from Pedra Alta site; upper Unit B, lower Anisian. **A:**
1012 mass-occurrence of *Hornestheria* sp. aff. *Hornestheria sollingensis* and coalified plant
1013 remains (marked with yellow arrows); DA21/03/02/80. **B:** external view on a right carapace
1014 valve of *Hornestheria* sp. aff. *Hornestheria sollingensis*. **C:** radial sculpture on the larval
1015 carapace valve (marked by red arrow), which is a diagnostic character for the genus
1016 *Hornestheria*; white arrows mark concentric growth lines in the umbonal area of the carapace
1017 valve; DA21/03/02/81. **D:** detail of Fig. A, external view on a left carapace valve of
1018 *Hornestheria* sp. aff. *Hornestheria sollingensis*; DA21/03/02/80. **E:** detail of Fig. D, showing
1019 an indistinct radial sculpture on the larval carapace valve (red arrow) and earliest growth lines
1020 (white arrows).

1022 **Figure 3.** Light microscopic photographs (Figs. A, C), line drawings, and ESEM images (D,
1023 E) of *Hornestheria* sp. aff. *Hornestheria sollingensis* from Pedra Alta site; upper Unit B,
1024 lower Anisian. **A–B:** external view on a right carapace valve (DA21/03/02/75). **C–E:** details
1025 of the same individual showing finely reticulated ornaments (highlighted by yellow dashed
1026 lines) on the growth bands.

1028 **Figure 4.** Light microscopic photographs and line drawing of *Hornestheria* sp.
1029 aff. *Hornestheria sollingensis* from Pedra Alta site; upper Unit B, lower Anisian. **A–B:**
1030 external view on a right carapace valve (DA21/03/02/72). **C:** details of the same individual
1031 showing indistinct fine ornaments on the growth bands.

1033 **Figure 5.** Light microscopic photographs and line drawing of *Hornestheria* sp.
1034 aff. *Hornestheria sollingensis* from Pedra Alta site; upper Unit B, lower Anisian. **A–B:**
1035 external view on a left carapace valve, slightly shifted against the underlying internal side of

the right carapace valve (DA21/03/02/77). **C–D:** details of the same individual showing indistinct fine ornaments on the growth bands.

Figure 6. Light microscopic photographs and line drawings of *Hornestheria* sp. aff. *Hornestheria sollingensis* from Pedra Alta site; upper Unit B, lower Anisian. **A–B:** external view on a right carapace valve (DA21/03/02/58). **C–D:** external view on a left carapace valve (DA21/03/02/78). **E–F:** external view on a left carapace valve (DA21/03/02/68).

Figure 7. ESEM image of the ornamentation on the external side of a right carapace valve of *Hornestheria* sp. aff. *Hornestheria sollingensis* from the Pedra Alta site, upper Unit B, lower Anisian; collection number DA21/03/02/72. **A:** Image taken in the central area of the carapace valve; concentric growth lines are marked by white arrows. **B:** Detail showing irregularly reticulated ornaments on the growth band.

Figure 8. Light microscopic photographs and line drawings of *Hornestheria?* Morphotype 1 from Punta Negra 2 site; uppermost Unit C, lower Anisian. **A–B:** compacted carapace in lateral view (DA21/03/04/11). **C–D:** external view on a right carapace valve (DA21/03/04/07-1a). **E–F:** internal side of a right carapace valve, appearing optically inverted through artificial shallow-angle illumination (DA21/03/04/07-2a).

Figure 9. Light microscopic photographs and line drawings of *Hornestheria?* Morphotype 1 from Punta Negra 2 site; uppermost Unit C, lower Anisian. **A–B:** compacted carapace in lateral view; rock surface was covered with adhesive (DA21/03/04/07-1d). **C–D:** external side

1060 of a left carapace valve (DA21/03/04/12-1). **E–F:** external side of a fragmented right carapace
1061 valve (DA21/03/04/13a).

1062

1063 **Figure 10.** Light microscopic photographs and line drawings of *Hornestheria?* Morphotype
1064 2 from Punta Negra 2 site, showing more or less developed concave bending of the ventral
1065 margin in the median-posterior area of the carapace valve; uppermost Unit C, lower Anisian.
1066 **A–B:** Right carapace valve, almost completely preserved as a steinkern (DA21/03/04/07-1b).
1067 **C–D:** imprint of a right carapace valve, appearing optically inverted through shallow
1068 illumination (DA21/03/04/07-2b). **E–F:** external side of a left carapace valve, overlying the
1069 internal side of the corresponding right carapace valve; both carapace valves are shifted
1070 relative to each other (DA21/03/04/08).

1071

1072 **Figure 11.** Light microscopic photograph (Fig. A), line drawing, and ESEM images (Figs. C,
1073 D) of *Hornestheria?* Morphotype 2 from Punta Negra 2 site; uppermost Unit C, lower
1074 Anisian. **A:** external view on a right carapace valve (DA21/03/04/09). **B:** Line drawing
1075 showing the positions of the ESEM images. **C–D:** irregularly (not smoothly) preserved
1076 surface; the ornamentation is not clearly detectable even under high magnification.

1077

1078 **Figure 12.** Light microscopic photographs and line drawings of indeterminate clam shrimp
1079 fragments; specimens from Punta Roja site, middle Unit B, upper Olenekian(?)–lower Anisian
1080 (Figs. A–D); and from Punta Negra 1 site, lowermost Unit C, lower Anisian (Figs. E–H). **A–**
1081 **B:** compacted fragments of the left and right carapace valves (DA21/03/01/01a). **C:**
1082 compacted carapace fragment (DA21/03/01/01b). **D:** steinkern of a right carapace valve
1083 (DA21/03/01/02). **E–F:** compacted carapace in lateral view (DA21/03/03/02). **G–H:** external
1084 view on an anterior fragment of a right carapace valve (DA21/03/03/01).

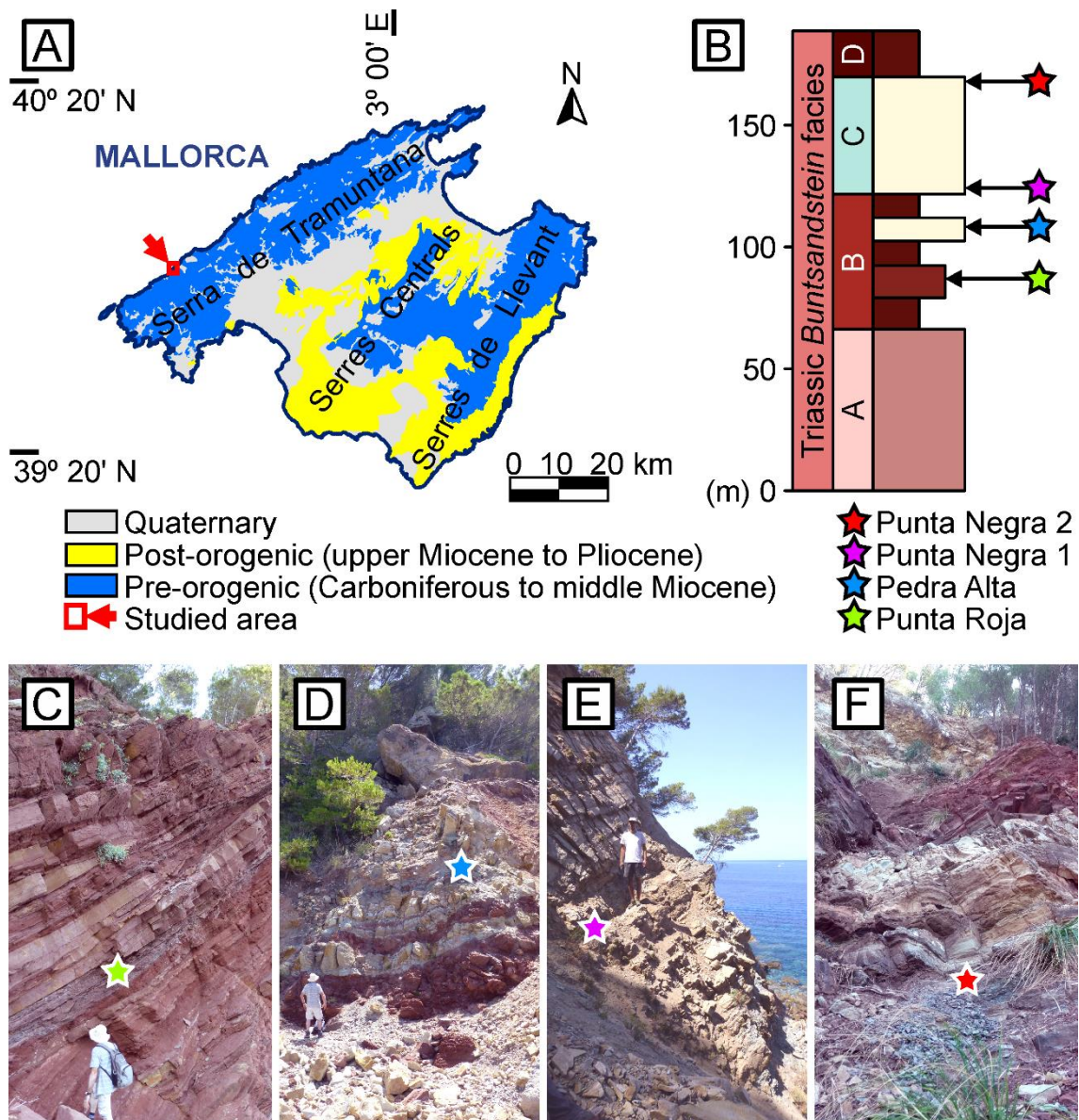
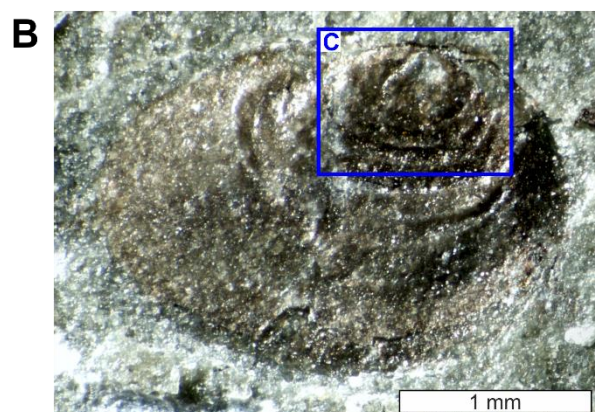
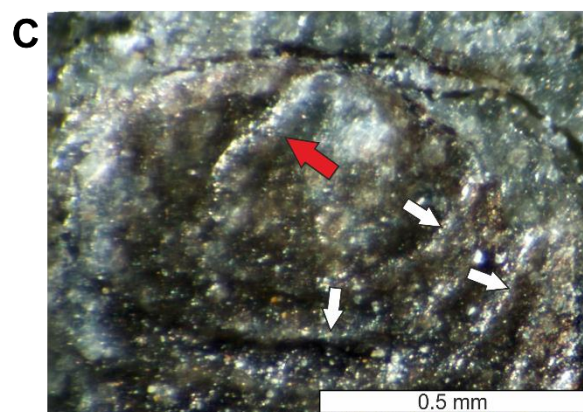
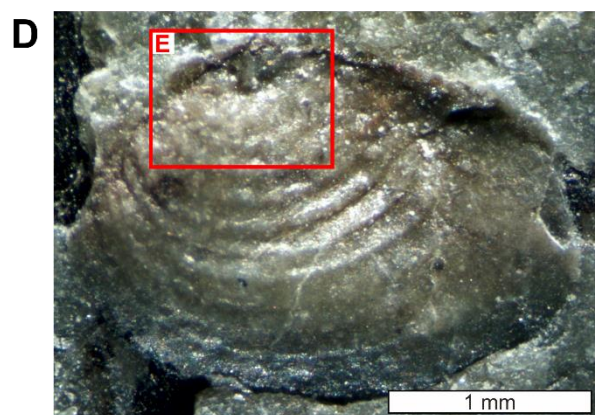
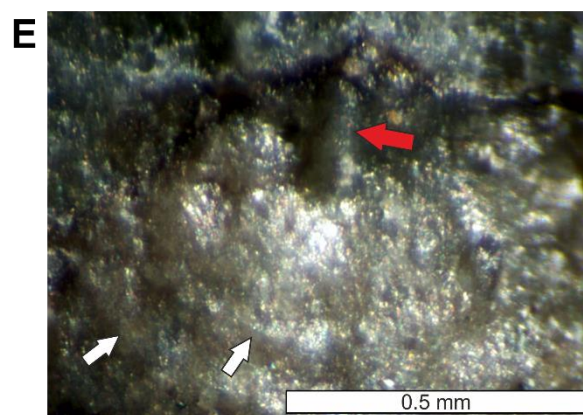
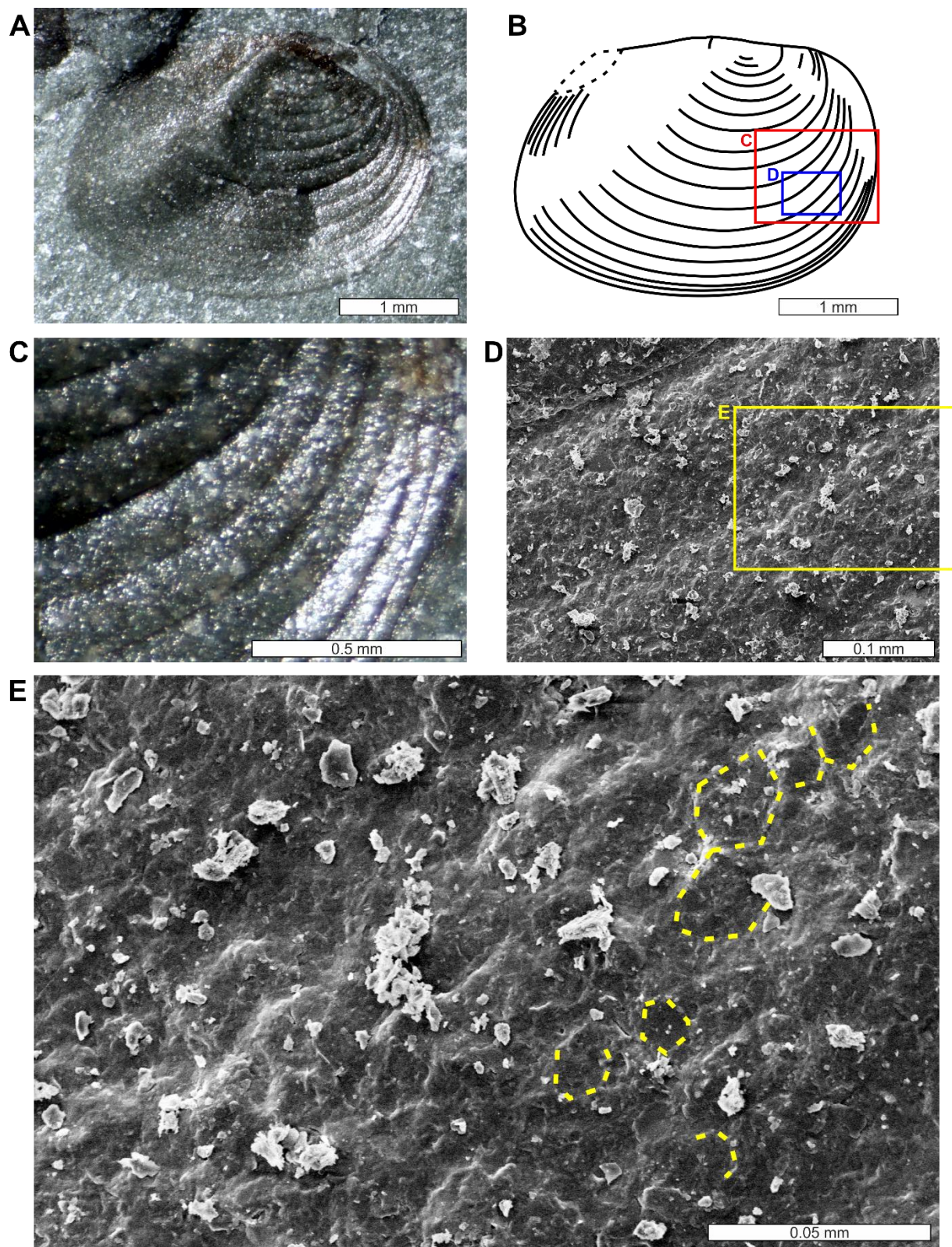


Figure 1



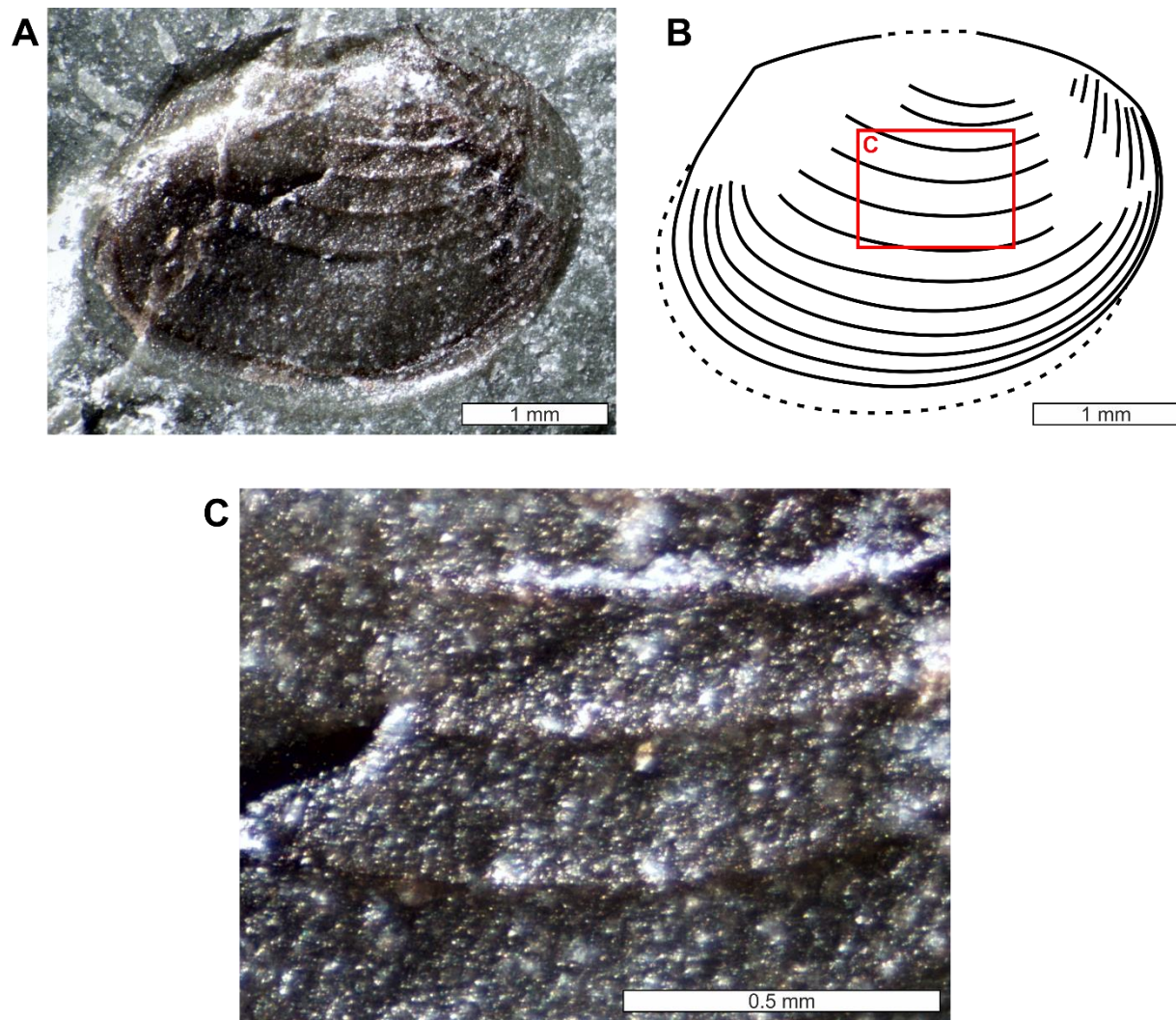
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1088 Figure 2



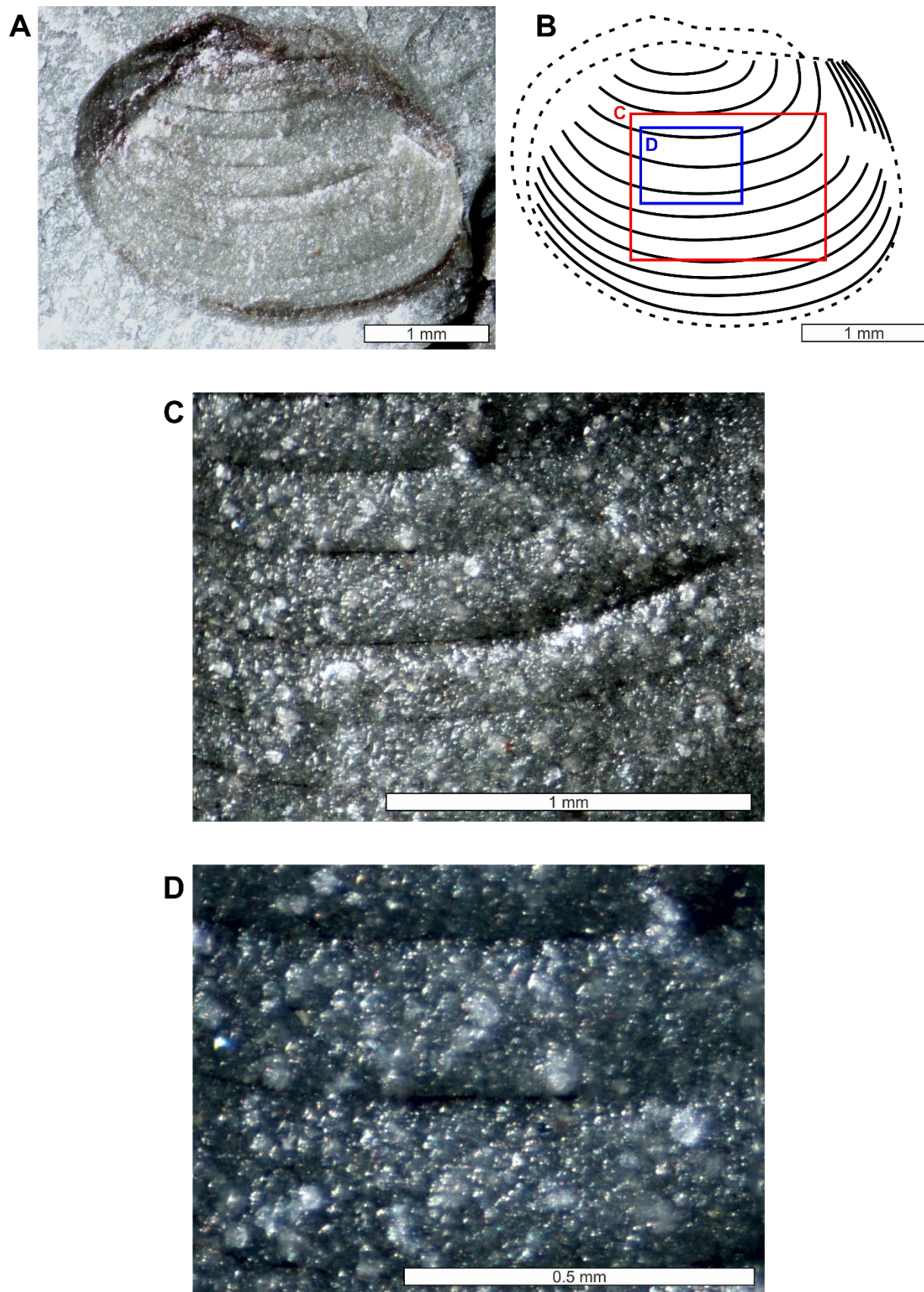
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1090 Figure 3



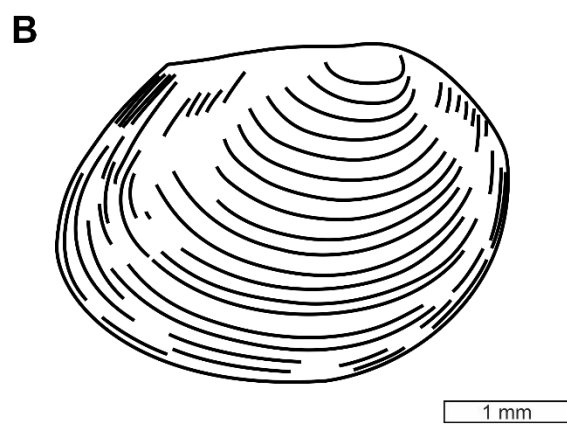
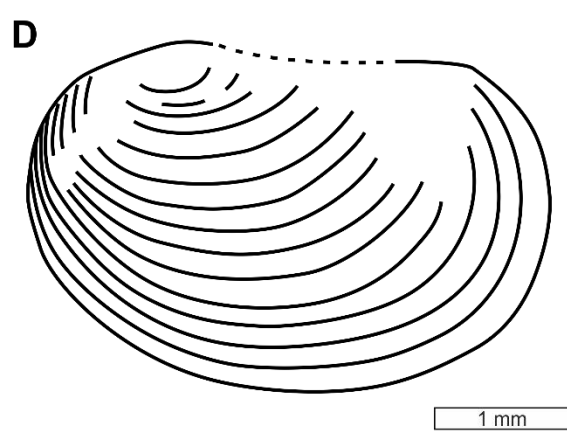
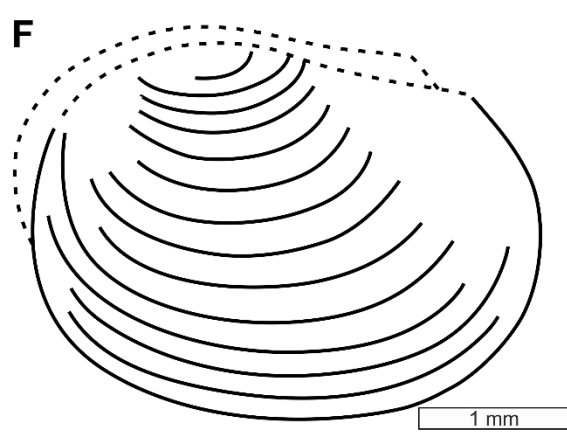
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1092 Figure 4



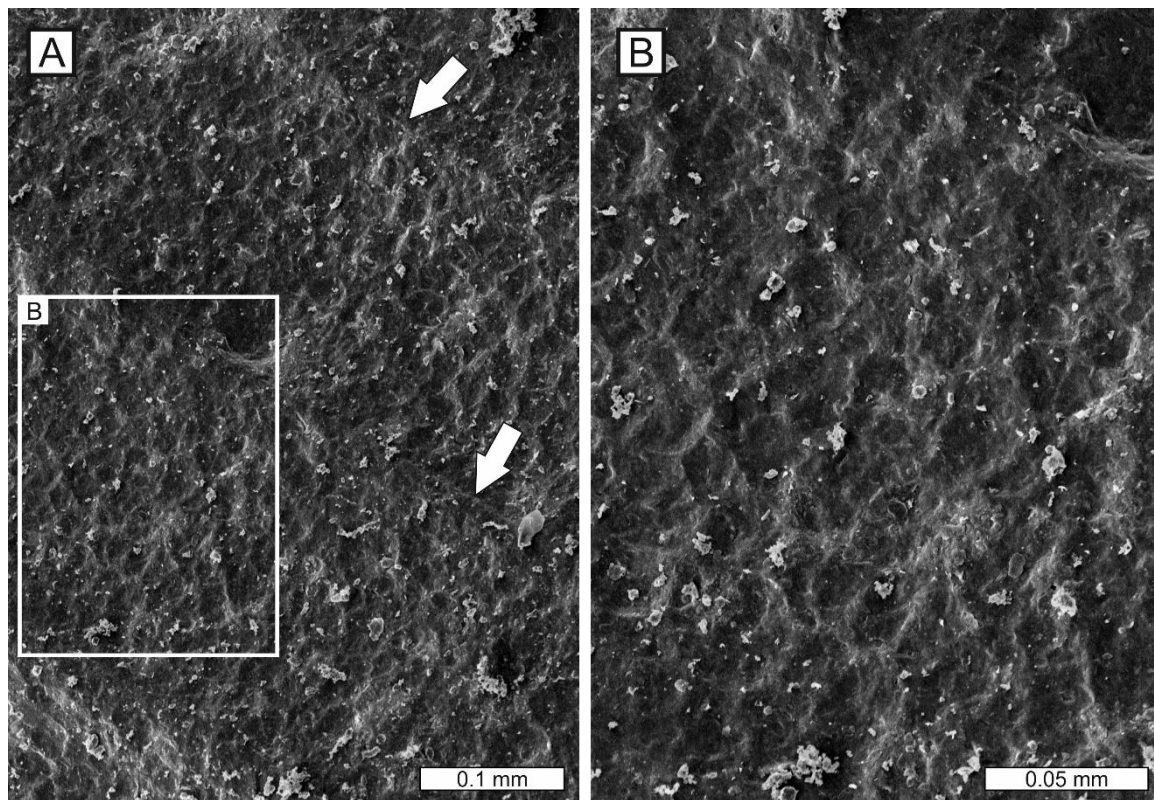
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1094 Figure 5



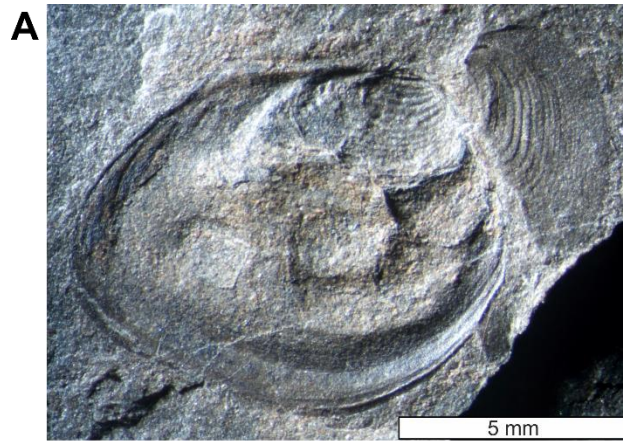
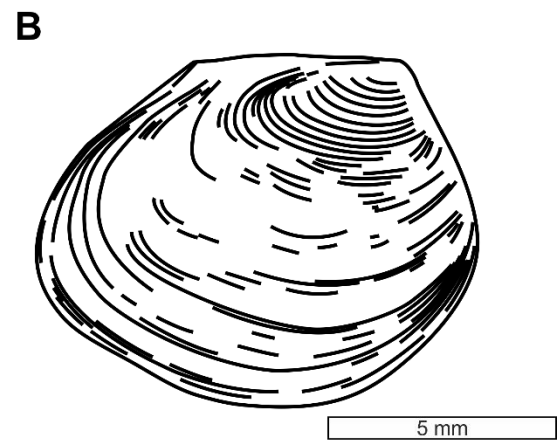
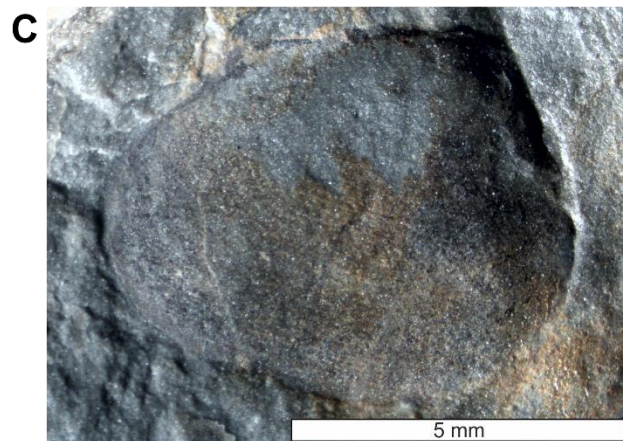
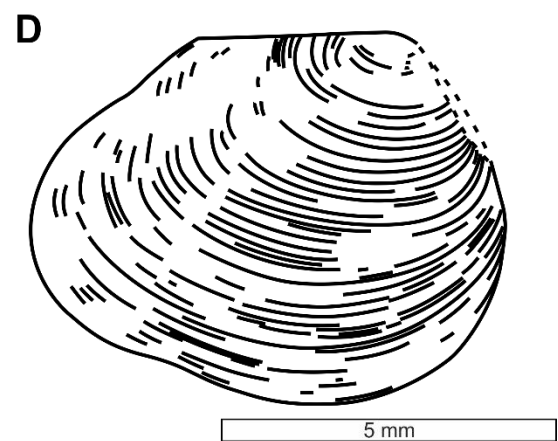
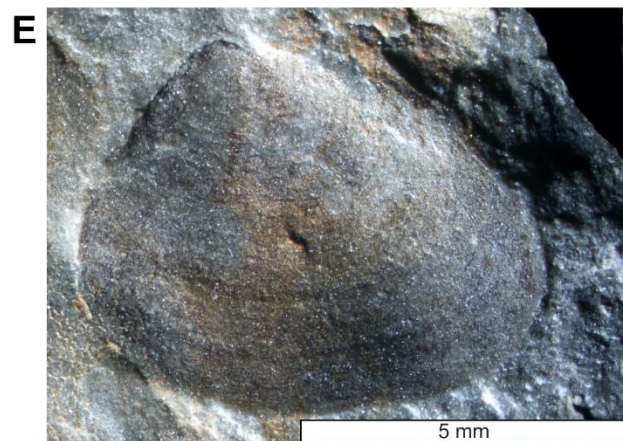
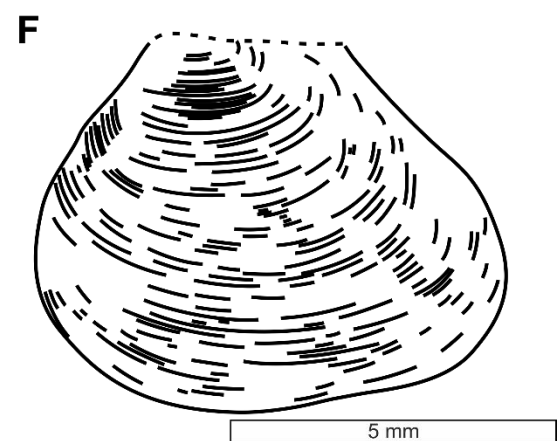
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1096 Figure 6



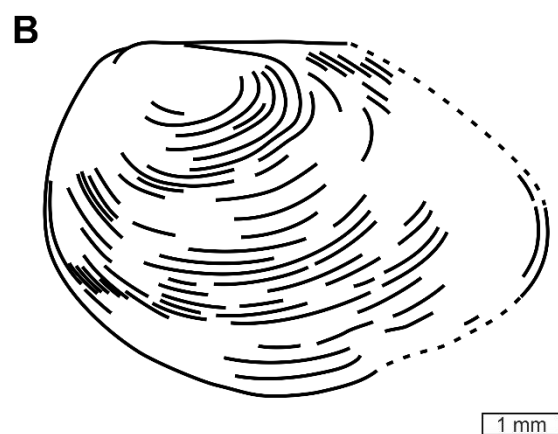
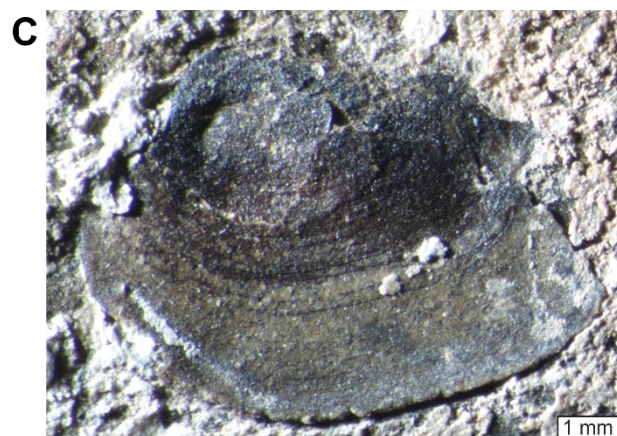
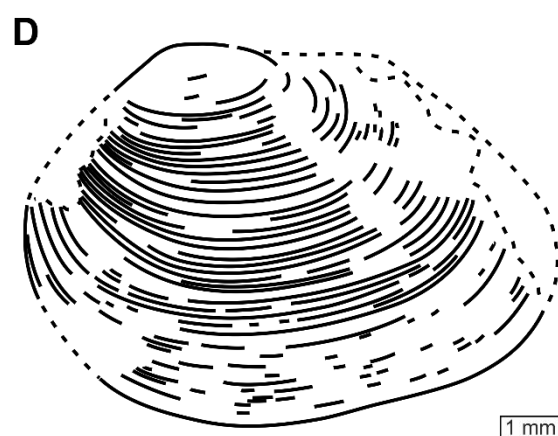
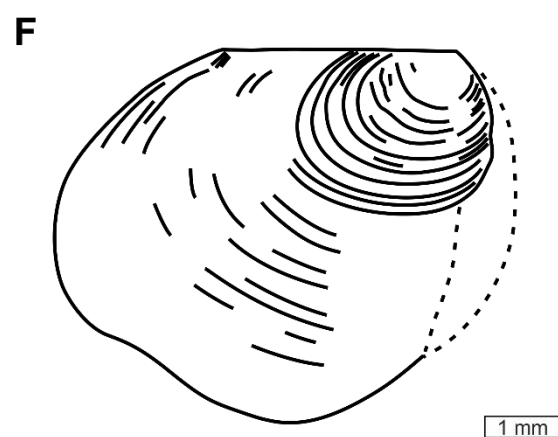
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1098 Figure 7



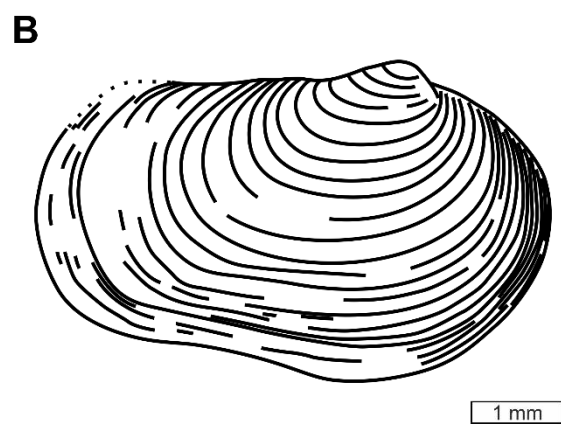
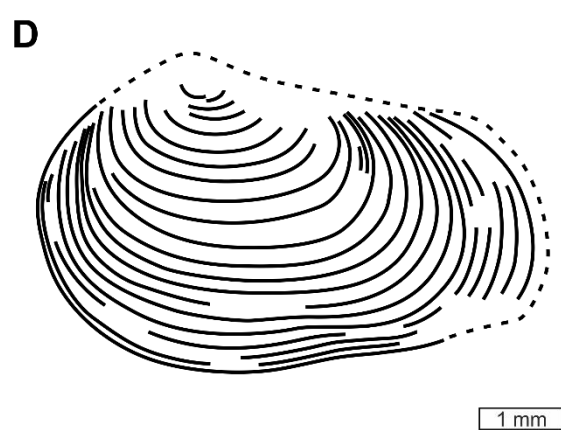
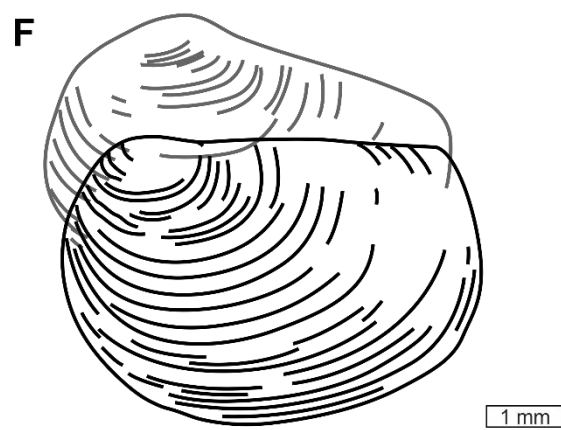
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1100 Figure 8



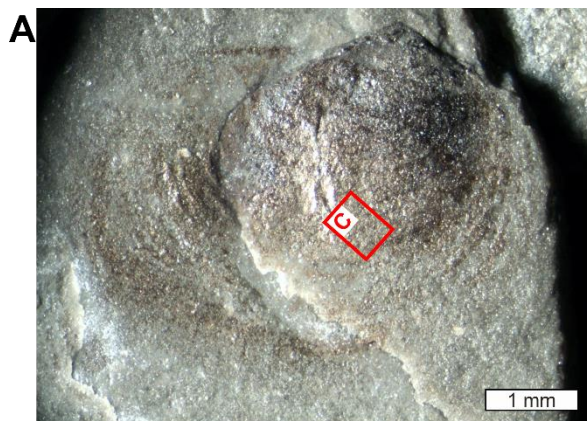
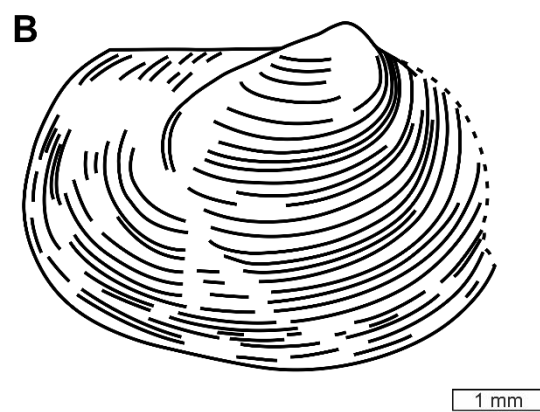
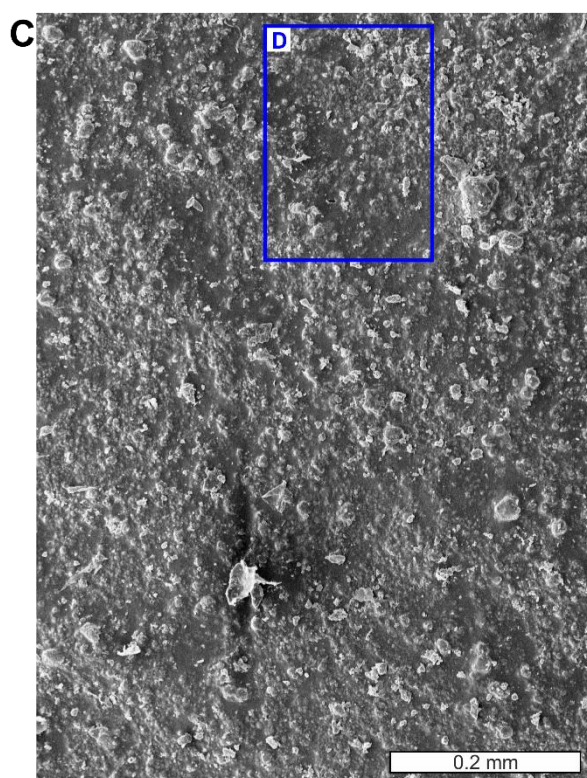
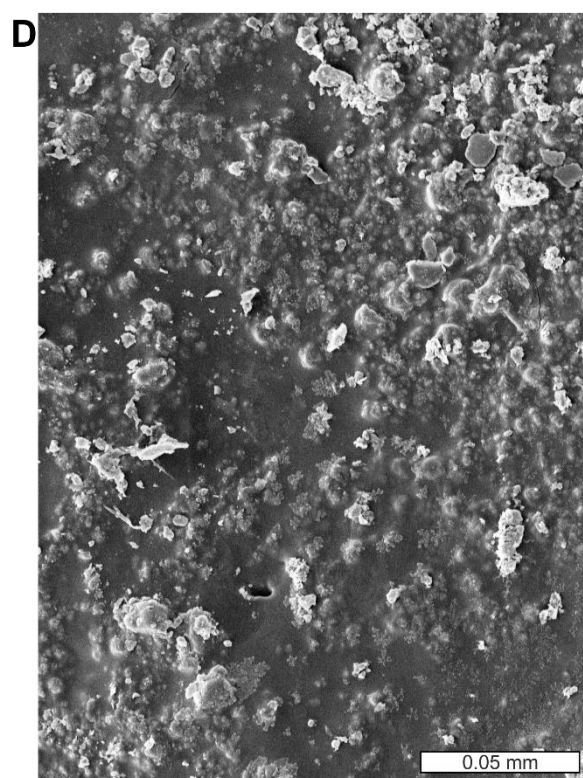
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1102 Figure 9



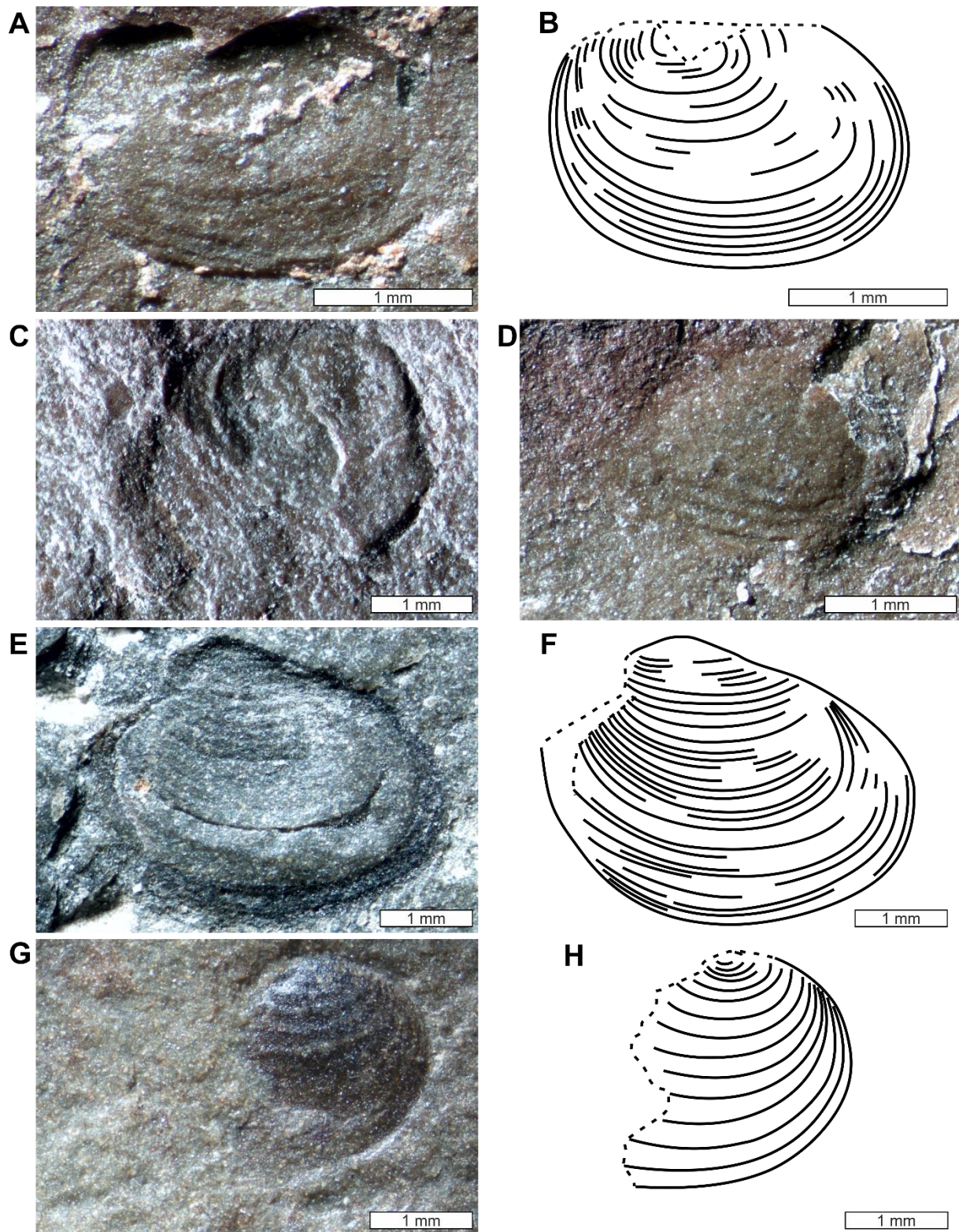
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1104 Figure 10



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1106 Figure 11



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1108 Figure 12