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Pelecogyra (Mollusca) from the Early Ordovician of the Montagne Noire, France --Manuscript Draft--

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Corresponding Author:	Jan Ove Ebbestad, PhD Uppsala University Uppsala, Sweden
First Author:	Jan Ove Ebbestad, PhD
Order of Authors:	Jan Ove Ebbestad, PhD Bertrand Lefebvre, PhD Jean-Paul Kundura Marie-Hélène Kundura
Abstract:	<p>A new occurrence of the onychochilid mollusc <i>Pelecogyra</i> is reported from the late Floian Landeyran Formation (<i>Apatokephalus incisus</i> Biozone) in the Montagne Noire, southern France, where it is associated with the two tergomyans <i>Carcassonnella courtessolei</i> and <i>Thoralispira laevis</i>, and a mollusc indet. with a low cap-shaped shell. Flattened specimens of <i>T. laevis</i> in the same formation may be misinterpreted as specimens of <i>Pelecogyra</i>. Morphologically the Montagne Noire specimens compare with <i>Pelecogyra fezouataensis</i> from the late Tremadocian Fezouata Formation (<i>Araneograptus murrayi</i> Biozone) in Morocco and are tentatively referred to this species. Each occurrence of <i>Pelecogyra</i> is from one or two localities only, but separated in time. They differ further in the deeper facies, association with <i>Carcassonnella</i> and <i>Thoralispira</i>, and non-gregarious occurrence in Montagne Noire compared to the shallower facies, lack of other molluscs and gregarious occurrence in the Fezouata Formation. In the Lower Ordovician, <i>Pelecogyra</i>, <i>Carcassonnella courtessolei</i>, the rare <i>C. vizcainoi</i> and <i>Thoralispira laevis</i> are taxa that occur only in Montagne Noire and the Anti-Atlas, while <i>Lesueurilla prima</i> also occurs in the Prague basin of the Czech Republic. Contrary to other faunal elements, like echinoderms and trilobites, these genera seem to have a wide environmental tolerance and are long ranging taxa. The main occurrence of the three key taxa <i>Carcassonnella</i>, <i>Thoralispira</i> and <i>Lesueurilla</i> in the Montagne Noire is in the lower part of the La Maurerie Formation (<i>Taihungshania miqueli</i> acme Zone), while the same taxa appear just slightly later in Morocco (<i>?Cymatograptus protobalticus</i> Biozone). Migration to the Anti-Atlas during the early Floian seems to have been possible during a period of general faunal exchange. <i>Pelecogyra</i> may either have migrated from the Anti-Atlas to Montagne Noire during the same interval or possibly during the late Floian as indicated by shared faunal elements between these two regions at that time.</p>
Suggested Reviewers:	<p>Daniel Vizcaino, PhD daniel.vizcaino@wanadoo.fr He is an expert on the Montagne Noire fauna and stratigraphy</p> <p>Muriel Vidal, PhD Universite de Bretagne Occidentale muriel.vidal@univ-brest.fr Dr Vidal has worked on the right stratigraphic level in both Montagne Noire and Morocco</p> <p>Björn Kröger, PhD Senior curator, Finnish Museum of Natural History bjorn.kroger@helsinki.fi Dr Kröger knows the stratigraphy of both Montagen Noire and Morocco and works on molluscs</p> <p>Jiri Frýda, PhD</p>

	Czech University of Life Sciences Prague bellerophon@seznam.cz Professor Frýda is a world leading expert on early molluscs
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1 ***Pelecogyra* (Mollusca) from the Early Ordovician of the Montagne Noire,**
2 **France**

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4 Jan Ove R. Ebbestad^a, Bertrand Lefebvre^b, Jean-Paul Kundura^c, Marie-Hélène Kundura^c

5
6 ^aMuseum of Evolution, Uppsala University, Norbyvägen 16, 75236 Uppsala, Sweden

7 ^bLaboratoire de Géologie de Lyon, UMR CNRS 5276, bât. Géode, Université Lyon 1,

8 Campus de la Doua, 2, rue Dubois, 69622 Villeurbanne cedex, France

9 ^c13, villa du Pré, 91860 Epinay-sur-Sénart, France

10

11 Corresponding author. E-mail addresses: Jan-Ove.Ebbestad@em.uu.se,

12 joebbestad@hotmail.com (J.O.R. Ebbestad).

13

14 Abstract

15 A new occurrence of the onychochilid mollusc *Pelecogyra* is reported from the late Floian

16 Landeyran Formation (*Apatokephalus incisus* Biozone) in the Montagne Noire, southern

17 France, where it is associated with the two tergomyans *Carcassonnella courtessolei* and

18 *Thoralispira laevis*, and a mollusc indet. with a low cap-shaped shell. Flattened specimens of

19 *T. laevis* in the same formation may be misinterpreted as specimens of *Pelecogyra*.

20 Morphologically the Montagne Noire specimens compare with *Pelecogyra fezouataensis*

21 from the late Tremadocian Fezouata Formation (*Araneograptus murrayi* Biozone) in

22 Morocco and are tentatively referred to this species. Each occurrence of *Pelecogyra* is from

23 one or two localities only, but separated in time. They differ further in the deeper facies,
24 association with *Carcassonnella* and *Thoralispira*, and non-gregarious occurrence in
25 Montagne Noire compared to the shallower facies, lack of other molluscs and gregarious
26 occurrence in the Fezouata Formation. In the Lower Ordovician, *Pelecogyra*,
27 *Carcassonnella courtessolei*, the rare *C. vizcainoi* and *Thoralispira laevis* are taxa that occur
28 only in Montagne Noire and the Anti-Atlas, while *Lesueurilla prima* also occurs in the Prague
29 basin of the Czech Republic. Contrary to other faunal elements, like echinoderms and
30 trilobites, these genera seem to have a wide environmental tolerance and are long ranging
31 taxa. The main occurrence of the three key taxa *Carcassonnella*, *Thoralispira* and *Lesueurilla*
32 in the Montagne Noire is in the lower part of the La Maurerie Formation (*Taihungshania*
33 *miqueli* acme Zone), while the same taxa appear just slightly later in Morocco
34 (?*Cymatograptus protobalticus* Biozone). Migration to the Anti-Atlas during the early Floian
35 seems to have been possible during a period of general faunal exchange. *Pelecogyra* may
36 either have migrated from the Anti-Atlas to Montagne Noire during the same interval or
37 possibly during the late Floian as indicated by shared faunal elements between these two
38 regions at that time.

39

40 Keywords: Onychochilidae, Mimospirida, *Carcassonnella*, *Lesueurilla*, *Thoralispira*,
41 Fezouata biota

42

43 **1. Introduction**

44 *Pelecogyra* is a striking, large sinistrally coiled mollusc hitherto known only from the Lower
45 Ordovician Fezouata Formation of Morocco (Ebbestad and Lefebvre, 2015). The peculiar
46 low spired conch has three rapidly expanding whorls, a large rounded planar aperture, and a

47 fairly thin shell with simple growth lines. The taxon is also the only known Tremadocian
48 member the Family Onychochilidae Koken in Koken and Perner, 1925. All known Moroccan
49 specimens are preserved dorso-ventrally compressed to some degree, and found originally
50 only at Oued Beni Zoli (locality Z-F5) in the Zagora area of Central Anti-Atlas, but then also
51 in a laterally equivalent site about 1.2 km to the west (Kouraïss et al., 2015). Both sites
52 include sediments encompassing the *Araneograptus murrayi* graptolite Biozone (late
53 Tremadocian). *Pelecogyra* occurs with a diverse assemblage of trilobites, echinoderms and
54 other fauna, but no other gastropods or tergomyans. Accompanying gastropod and tergomyan
55 molluscs higher in the Fezouata succession are *Carcassonnella courtessolei* (Yochelson,
56 1982) and *Thoralispira laevis* (Thoral, 1935), species otherwise only found in the Montagne
57 Noire (Horný, 1997; Ebbestad, 2016). *Lesueurilla prima* (Barrande in Perner, 1903) is also in
58 common between Morocco and France, and is a taxon recognized in the Lower Ordovician
59 and Middle Ordovician of western mid-to high latitude peri-Gondwana areas (Ebbestad,
60 2016; Ebbestad et al., 2016 and references therein). These three genera are here treated as
61 signature taxa that may be helpful in understanding the faunal exchange between peri-
62 Gondwana areas.

63 Recently, four specimens of *Pelecogyra* were discovered in the lower part of the
64 Landeyran Formation (late Floian) near Le Foulon in the Montagne Noire (southern France),
65 where they occur with an abundant and relatively diverse fauna (Vizcaïno et al., 2001) (Fig.
66 1). This is the first occurrence of *Pelecogyra* outside Morocco and the species is attributed
67 to *P. cf. fezouataensis* Ebbestad and Lefebvre from Morocco. The age, preservation,
68 associated fauna, and ecology differ between the two, which is discussed in this paper along
69 with the implications for the correlation and faunal exchange with the Fezouata Formation in
70 the Anti-Atlas of Morocco.

72 2. Geological setting and material

73 The Montagne Noire, in the southern part of the highland region of Massif Central, is
74 composed of a complex series of tectonic units and nappes (Demange, 2001). Cambrian and
75 younger sediments are found on each side of a central area with gneisses and schists, and are
76 divided into the northern and southern Montagne Noire areas (Fig. 1). In the southern
77 Montagne Noire, the thick, dominantly siliciclastic Lower Ordovician succession consists of
78 six formations (Fig. 2). The traditional levels and ‘faunizones’ originally defined by
79 Courtessole et al. (1981, 1982, 1985, 1991) in this area were at best inaccurate and poorly
80 defined because they partly reflected biofacies rather than ranges (Vizcaïno and Álvaro,
81 2003; Tortello et al., 2006 and references therein). A detailed biostratigraphic framework was
82 recently established for this succession (Fig. 2), based on trilobite ranges and zones across the
83 lithofacies (Vizcaïno and Álvaro, 2003; Tortello et al., 2006). Many of these trilobite taxa can
84 be used for regional correlations, and in particular, with the Lower Ordovician of the Anti-
85 Atlas, Morocco (Martin et al., 2016). More traditional index taxa (e.g. acritarchs, conodonts,
86 graptolites) are rare and/or restricted to some units, and generally in need of revision (Barrois,
87 1892, 1893; Thorall, 1935; Dean, 1966; Vizcaïno et al., 2001; Serpagli et al., 2007).

88 Specimens of *Pelecogyra* were found west of Les Sources du Foulon, situated near the
89 southern bank of the Orb river, about 1300 m east of Lugné, municipality of Cessenon-sur-
90 Orb, Hérault, southern France (locality CS 34, Fig. 1). This site corresponds to locality λ32 of
91 Dean (1966) and CS 34 of both Babin et al. (1982, fig. 4) and Tortello et al. (2006, appendix).
92 In the last 20 years, detailed, level by level excavations carried out in that locality by two of
93 the authors (JPK and MHK) yielded a rich and diverse macrofauna, comprising bivalves,
94 brachiopods, conulariids, echinoderms, graptolites, trilobites and various other taxa. The four
95 specimens of *Pelecogyra* were found in 2004, 2009 and 2012, and must be considered as
96 rare at this site.

97 The locality west of Les Sources du Foulon consists of a 10 meter thick section of
98 homogeneous fissile mudstones, within the *Apatokephalus incisus* trilobite Biozone (lower
99 part of the Landeyran Formation, late Floian; Fig. 2). Around 20 species of trilobites were
100 recorded from this site (Dean, 1966; Vizcaïno et al., 2001; Tortello et al., 2006; Kundura,
101 2015). Many trilobites are preserved as entire specimens, indicative of relatively sudden
102 burial events in otherwise quiet, distal depositional conditions (Dean, 1966). The lower part
103 of the Landeyran Formation is considered to represent offshore, muddy deposits in a
104 generally deepening sequence (Vizcaïno and Lefebvre, 1999; Vizcaïno et al., 2001). Detailed
105 sampling in the site west of Les Sources du Foulon revealed a *Colpocoryphe–Asaphellus–*
106 *Ampyx* dominated trilobite assemblage, whereas *Apatokephalus* seems to be restricted to
107 some horizons only, within this interval. The *Pelecogyra* specimens occur in two such
108 horizons, where the trilobite fauna shows its highest diversity, including rare elements such
109 as *Foulonia*, *Niobe*, *Ogygiocaris*, *Pliomerops* and *Selenopeltis* (Kundura, 2015).

110

111 3. Systematic palaeontology

112 Montagne Noire specimens described herein belong to the Kundura collection, and are
113 deposited in the Muséum National d'Histoire naturelle, Paris, France (MNHN). The type
114 material of Moroccan *Pelecogyra* illustrated here for comparison purposes belongs to the
115 Reboul collection, and is deposited in the Muséum d'Histoire naturelle de Marseille, France
116 (MHNM).

117

118 Class Gastropoda Cuvier, 1797

119 Superfamily Clisospiroidea Miller, 1889

120 Family Onychochilidae Koken in Koken and Perner, 1925

121

122 **Remarks.** Based on functional considerations Linsley and Kier (1984) established
123 Paragastropoda, a new class of presumed untorted molluscs with sinistrally coiled shells. As
124 constructed, the class was already from the start considered paraphyletic (Linsley and Kier,
125 1984, p. 247). Within their Order Orthostrophina, they included the pelagilleids and within
126 their Order Hyperstrophina, they included hyperstrophic macluritids, onychochilids,
127 clisospirids and tentatively even euomphalids. While onychochilids and clisospirids are
128 considered closely related (Horný, 1964; Peel, 1986), subsequent studies on protoconch
129 development have shown that macluritids and euomphalids are not related to these and that
130 Paragastropoda does not seem to have any zoological validity (Frýda, 1999, 2012 and
131 references therein; Frýda and Rohr, 2006; Frýda et al., 2008), thus leaving only onychochilids
132 and clisospirids in the original Hyperstrophina. Onychochilids and clisospirids were placed as
133 two families in the Suborder Mimospirina by Dzik (1983), distinguished mainly by the height
134 of the shell and the nature of the aperture, and both were united in the Superfamily
135 Onychochiloidea Koken in Koken and Perner, 1925 (as Onychochilacea), by Linsley and
136 Kier (1984). As pointed out in Ebbestad and Lefebvre (2015), because of the reduction of the
137 concept of the Order Hyperstrophina (containing only the Suborder Mimospirina with
138 Onychochilidae and Clisospiridae), Mimospirina Dzik, 1983, has priority and should be
139 raised to the level of order. However, Bouchet et al. (2005, 2017) did not use Mimospirina
140 and united the two families in the Superfamily Clisospiroidea Miller, 1889 (having priority
141 over the Onychochiloidea), containing sinistrally coiled taxa with sinistrally coiled
142 protoconchs. They followed Knight et al. (1960) and included the Subfamily Progalerinae
143 Knight, 1956, which have a dextral shell, but a sinistral protoconch, in the Clisospiridae.

144 The Mimospirina, as presently understood, are constructionally near the original
145 concept of Dzik (1983), who considered these taxa to be hyperstrophic dextral gastropods
146 (sinistral shell, dextral configuration of the body), although the sinistral coiling alone is not a
147 proof of hyperstrophy (Yochelson, 1984; Peel and Horný, 1996; Frýda and Rohr, 2006); they
148 could be sinistral orthostrophic taxa (sinistral shell, sinistral configuration of the body). It still
149 leaves the question, whether these taxa were torted or untorted, i.e. gastropods or not.
150 Ebbestad and Lefebvre (2015) placed the new genus *Pelecogyra* in the Family
151 Onychochilidae within the class Paragastropoda Linsley and Kier, 1984, tacitly considering it
152 as an untorted mollusc. However, the umbilical side and nature of the aperture is unknown in
153 this genus, which does not allow a detailed appreciation of the functional morphology.
154 Members of the Onychochilidae are broadly accepted today as gastropods (Bouchet et al.,
155 2005, 2017; Frýda, 2012), although not within the Archaeogastropoda (Frýda, 1999, 2001,
156 2012). A broader analysis of the numerous and disparate members of this group (see Fryda
157 and Rohr, 1999; Ebbestad and Lefebvre, 2015, table 1) may shed light on this problem.
158 Nevertheless, as a consequence of morphological uncertainties and the eroded concept of the
159 Paragastropoda, the previous opinion on *Pelecogyra* by Ebbestad and Lefebvre (2015) is
160 reconsidered and the placement of the genus within Onychochilidae as a gastropod is
161 followed herein, adhering to the classification in Bouchet et al. (2005, 2017). The inclusion of
162 Cambrian pelagiellids in the class Pargastropoda by Linsley and Kier (1984) and its
163 implications is not considered herein, as this is an entirely different discussion.

164

165 Genus *Pelecogyra* Ebbestad and Lefebvre, 2015

166

167 **Type species:** By monotypy, *Pelecogyra fezouataensis* Ebbestad and Lefebvre, 2015, p.
168 430, figs 3–5, from the Lower Ordovician, late Tremadocian *Araneograptus murrayi*
169 graptolite Zone, Fezouata Formation, at the Quaternary terrace of Oued Beni Zoli (Z-F5),
170 west of Jbel Bou- Dehir, about 17 km N of Zagora, in central Anti-Atlas, Morocco.

171

172 *Pelecogyra cf. fezouataensis* Ebbestad and Lefebvre, 2015

173 Figs 3B, 4A–J

174

175 **Locality and horizon:** West of Les Sources du Foulon, Cessenon-sur-Orb municipality,
176 Hérault, southern France, *Apatokephalus incisus* trilobite Biozone, lower part of the
177 Landeyran Formation (late Floian).

178

179 **Material:** Four specimens (Kundura collection, MNHN.F.A71806– MNHN.F.A71809),
180 mostly preserved as tectonically deformed internal moulds. One specimen
181 (MNHN.F.A71808) retains patches of shell.

182

183 **Remarks:** Although the Le Foulon specimens are slightly deformed and poorly preserved
184 they can be compared closely with *Pelecogyra fezouataensis* from Morocco (Fig. 3A). This
185 taxon was recently described by Ebbestad and Lefebvre (2015), and although a redescription
186 is not needed some features of the Montagne Noire specimens are highlighted for
187 comparison. The largest specimen (MNHN.F.A71808, Figs 3B, 4F) is about 2 cm wide,
188 compared to the maximum 2.7 cm of the Moroccan material. This largest Montagne Noire
189 specimen is however tectonically shortened and it would have originally approached the size

190 of the largest Moroccan individual (see also Fig. 4I). Shell patches in MNHN.F.A71808
191 appear wrinkled, as seen also in Moroccan specimens, but the fine growth lines cannot be
192 seen in the Le Foulon specimens (Fig. 4H). Similarly, the irregular bands preserved on
193 internal moulds of Moroccan specimens are not present in the French specimens (Fig. 4A, D,
194 E). In both Le Foulon and Oued Beni Zoli specimens, the similar shape and large size of the
195 protoconch suggest that larvae were non-planktotrophic. Although dorso-ventrally flattened,
196 specimen MNHN.F.A71806 shows some degree of the curvature of the shell in both the
197 penultimate and last whorl (Fig. 4B, C). The edge of the aperture is flat to the sediment, with
198 a small marginal edge on the internal mould. This compares well with the Moroccan species
199 (compare Fig. 4A, D, E with Ebbestad and Lefebvre, 2015, fig. 3B).

200 The Moroccan *Pelecogyra fezouataensis* was originally known from more than 50
201 specimens, all from the same locality. The fossils are generally well-preserved and
202 undisturbed by tectonics. Typically several specimens occur together and a certain range in
203 size is evident. A size range is also evident for the Montagne Noire specimens. However,
204 they do not show evidence of being gregarious, which could be related either to their rarity or
205 lack of sorting and transport in the deeper water setting. They also differ from Moroccan
206 specimens in co-occurring with specimens of *Carcassonnella courtessolei* and *Thoralispira*
207 *laevis* (Fig. 4J, 5D) (see also sample list in Horný and Vizcaíno, 1995, p. 39).

208 Another hitherto undescribed taxon from the Montagne Noire also occurs in the
209 Landeyran Formation at the Le Foulon site (Fig. 5E, F). It has a low cap-shaped shell, where
210 the sloping side has been pushed inwards and deformed the fossil. Maximum width of an un-
211 deformed specimen would be around 10 mm. The aperture is planar and with a broadly
212 circular outline. The pointed apex projects a bit, but does not overhang the margin of the
213 shell, with a subapical surface that curves sharply towards the margin. Preservation does not
214 allow a precise determination of this specimen, nor is it possible to determine whether it is a

215 gastropod or a tergomyan mollusc. Yochelson (1982) described two broadly similar taxa
216 from the La Maurerie Formation as *Archinacella* sp. and *A. cf. A. ovata* Barrande in Perner,
217 1903 (now *Barrandicella* Peel and Horný, 1999), but those have an apex closer to or
218 overhanging the margin. Horný (1995) described the enigmatic cap-shaped mollusc
219 *Solandangella* from the Foulon Formation, but this differs from the younger cap-shaped
220 specimen from Le Foulon in being larger, having a more sub-central and less pointed apex
221 with a less inclined apical slope. The internal mould of *Solandangella* possesses a distinct
222 muscle-scar pattern, but muscle scars are not preserved in the Le Foulon indet. specimen.
223 Two specimens of *Carcassonnella courtessolei* are found in close association, next to the
224 indet. specimen (Fig. 5B).

225 Possible misidentifications of *Pelecogyra* may occur within the Montagne Noire
226 material. A flattened specimen of the tergomyan *Thoralispira laevis* (Thoral, 1935), about 2.5
227 cm across, is preserved in shale at Les Rocs Nègres (locality CV 12, Fig. 1), in the upper part
228 of the Landeyran Formation (*Hanghungolithus primitivus* trilobite Biozone). This being a
229 tergomyan mollusc, where the aperture is taken to be posterior, it is the left lateral side that is
230 preserved (Fig. 5C). Fine comarginal growth lines are visible on the surface, curving slightly
231 abaperturally towards the dorsal part of the shell; the median dorsum itself is not preserved.
232 Horný and Vizcaïno (1995) erected the genus based on abundant material in the Montagne
233 Noire area, ranging from the Saint-Chinian through to the Landeyran formations. Specimens,
234 such as the one shown herein, are rare in shales, but common in concretions in the lower half
235 of the Landeyran Formation (Horný and Vizcaïno, 1995). The flattened left lateral side of the
236 shell broadly resembles the shell of *Pelecogyra*, albeit coiling the wrong way. However,
237 flattened specimens of *Thoralispira* preserved with their right lateral side could potentially be
238 misidentified as *Pelecogyra*. Specimens tentatively identified as *Carcassonnella*

239 *courtessolei* occur at Les Rocs Nègres locality (JPK pers. obs.) and probably represent the
240 youngest documented occurrence of *C. courtessolei* in the Montagne Noire.

241

242 **4. Discussion**

243 4.1. Gastropods and tergomyans in the Lower Ordovician of the Montagne Noire and the
244 Anti-Atlas

245

246 Modern descriptions of gastropod and tergomyan molluscs from the Montagne Noire were
247 given by Yochelson (1982), Horný and Vizcaino (1995) and Horný and Peel (1996). They
248 range from the Saint-Chinian Formation through to the Landeyran Formation. With the
249 addition of *Pelecogyra* and the undetermined cap-shaped shell mentioned herein, 16

250 gastropod or tergomyan taxa are known (Fig. 2). *Carcassonnella courtessolei* and

251 *Thoralispira laevis* are the dominant taxa throughout the entire succession, co-occurring in
252 the lowest part with the widely distributed *Peelerophon oehlerti* (Bergeron, 1889).

253 *Thoralispira* sp. occurs in sandstone levels of the Cluse de l'Orb Formation, while other

254 molluscs of the *Taihungshania shui landeyranensis* trilobite Biozone are found in the shaly
255 sequence of the Setso Shale. *Lesueurilla prima* also has a long, though discontinuous, range,

256 extending from the La Maurerie Formation to the Landeyran Formation. In the lower part of
257 its range, it co-occurs with the rare, but distinct *Carcassonnella vizcainoi* Horný and Peel,

258 1996, as well as with *C. courtessolei* and *T. laevis*. Associated fauna places these occurrences
259 in the *Taihungshania miqueli* acme trilobite Zone (Babin et al., 1982, table 1). This interval

260 shows the highest diversity of gastropods and tergomyans in the Lower Ordovician of the

261 Montagne Noire (Fig. 2).

262 *Pelecogyra* occurs in the Landeyran Formation (*Apatokephalus incisus* Zone) in the upper
263 part of the succession, associated with both *C. courtessolei* and *T. laevis*. The entire
264 succession in which these molluscs range is nearly 1300 m thick, covering the latest
265 Tremadocian and the Floian, which gives a very long range for some of the key taxa. Most of
266 the occurrences discussed herein are associated with calm, distal settings typical of the
267 raphiophorid biofacies (Saint-Chinian Formation, base of the La Maurerie Formation and the
268 Landeyran Formation), as shown by the occurrence of *Ampyx priscus*. On the other hand, the
269 presence of these mollusks also in the shallower, more proximal settings of both the Cluse de
270 l'Orb and Foulon formations (where raphiophorids are absent, and more proximal trilobite
271 assemblages are occurring) does not support any close relationship between these taxa and
272 any particular sedimentary setting, bathymetry or trilobite biofacies.

273 The distribution of gastropods and tergomyans in the Lower Ordovician Fezouata Formation
274 of Anti-atlas, Morocco is in many respects similar to that in the Montagne Noire (Horný,
275 1997; Ebbestad, 2016), although the range of the three key taxa *Carcassonnella*, *Thoralispira*
276 and *Lesueurilla* differs and are much more restricted in the Anti-Atlas area (Fig. 2). The
277 hitherto recognized diversity in the Anti-Atlas is as well lower, with only seven species
278 known (Fig. 2). The distribution pattern seen in the Anti-Atlas may be affected either by
279 environmental conditions and/or sampling bias.

280 A large number of specimens of *T. laevis* are known from various localities of the Fezouata
281 Formation (Horný, 1997; Ebbestad, 2016). For occurrences of *Thoralispira*, Horný (1997)
282 listed Destombes localities 34, 983, 1540, 1572, 1621 and 1682, of which the first was
283 equalled to locality F-Z26 in Ebbestad (2016) within the ?*Cymatograptus protobalticus*
284 graptolite Biozone. It would mean an increased range downwards of this taxon, not reflected
285 in Ebbestad (2016, fig. 2), where only stratigraphically constrained specimens from locality
286 Z-F25 were included. Both *C. courtessolei* and *L. prima* are associated with *T. laevis* at these

287 localities (Horný 1997). However, the various Destombes localities are far apart and difficult
288 to date, although associated fauna suggest a Floian age for all of them. The age uncertainty is
289 reflected in Fig. 2, where tentative extended ranges upwards for the three key taxa are
290 indicated.

291 The confirmed extended range downwards of *T. laevis* is plotted in Fig. 2 herein, thus
292 matching those of taxa *C. courtessolei*, *C. vizcainoi* and *L. prima* within the ?*Cymatograptus*
293 *protobalticus* graptolite Biozone. The occurrence of *C. vizcainoi* Horný and Peel, 1996 at
294 locality Z-F26 (Ebbestad 2016), may be of importance as it has a restricted occurrence in
295 Montagne Noire (Horný and Peel, 1996), while the three key taxa extend also up into the
296 ?*Baltograptus jacksoni* Zone and possibly higher. *Peelerophon* would be expected in the
297 Fezouata Formation but has not yet been recognized. *Pelecogyra* occurs stratigraphically
298 low in the unit, and is not found with other gastropods or tergomyans. The entire succession
299 in which these molluscs range is about 370 m thick, and the associated trilobite assemblage,
300 including taxa like *Ampyx priscus* and *Colpocoryphe*, reflects the distal raphiophorid
301 biofacies (Martin et al., 2016).

302

303 4.2. Correlation between Montagne Noire and the Anti-Atlas area

304 In the Lower Ordovician, *Pelecogyra*, *Carcassonnella courtessolei*, *C. vizcainoi* and
305 *Thoralispira laevis* are taxa that only are reported from Montagne Noire and the Fezouata
306 Formation in the Anti-Atlas, while *Lesueurilla prima* also occurs in the Prague basin of the
307 Czech Republic and the Middle Ordovician of Iran (Ebbestad et al., 2016). These key taxa are
308 therefore potentially of interest to understand the correlation and faunal exchange between
309 the two areas in the Lower Ordovician.

310 Gastropod or tergomyan molluscs have been collected from the middle Tremadocian La
311 Dentelle Formation (JPK, pers. obs.), but the stratigraphically oldest Ordovician gastropod
312 and tergomyan molluscs identified in the literature in the Montagne Noire appear in the
313 *Euloma filacovi* trilobite Biozone in the Saint-Chinian Formation. Tremadocian conodonts of
314 the *Paltodus deltifer deltifer* conodont Subzone are known in the lower part of the underlying
315 *Shumardia (C.) pusilla* trilobite Biozone (Álvarez et al., 2007; Serpagli et al., 2007). This zone
316 is just below the *A. murrayi* graptolite Biozone (Bergström et al., 2004), where *Pelecogyra*
317 is found in the Fezouata Formation, and according to Fortey (2011) zonal graptolites of this
318 type occur in the upper Saint-Chinian Formation in France. In both known Moroccan
319 occurrences, *Pelecogyra* is abundant but without associated remains of the other key
320 mollusc taxa.

321 Fortey (2011) also reported *Tetragraptus akzharensis* from the *Taihungshania miqueli* acme
322 trilobite Zone in Montagne Noire, a species associated with the upper subdivision of *T.*
323 *phyllograptoides* graptolite Biozone (Bergström et al., 2004). The lower part of the Upper
324 Fezouata Formation encompass the ?*Cymatograptus protobalticus* graptolite Biozone, also
325 corresponding to the upper subzone of the *T. phyllograptoides* graptolite Biozone (Bergström
326 et al., 2004). Thus, the main co-occurrence of *C. courtessolei*, *C. vizcainoi* (rare), *T. laevis*,
327 and *L. prima* at the base of the ~400 m thick La Maurerie Formation and within the
328 *Taihungshania miqueli* acme trilobite Zone, appears close to that of the lower range of these
329 molluscs in the Upper Fezouata Formation, in the ?*Cymatograptus protobalticus* graptolite
330 Biozone, although the Moroccan occurrences seem a bit younger.

331 The zonal fossil *Taihungshania* in Montagne Noire is absent in the Fezouata Formation,
332 which suggests that faunal exchanges with this part of Morocco were restricted at least until
333 the latest Tremadocian (Martin et al., 2016). This is also reflected in a high relative
334 endemicity of both echinoderms and trilobites in the shallower depositional settings of the

335 late Tremadocian (Lefebvre et al., 2016; Martin et al., 2016). In contrast, endemicity of
336 echinoderms and trilobites is lower in the early Floian, coinciding with a general
337 transgressive trend and deeper facies (Lefebvre et al., 2016; Martin et al., 2016). This interval
338 is also where the main distribution of gastropod and tergomyan molluscs is found (Fig. 2).
339 The trilobite assemblage, including taxa like *Ampyx priscus* and *Colpocoryphe*, reflects the
340 raphiophorid biofacies (Martin et al., 2016).

341 It seems that *C. courtessolei*, *L. prima* and *T. laevis* had a relatively wide environmental
342 tolerance as they are found across a range of biofacies in the Montagne Noire. Environmental
343 preferences is clearer for e.g. trilobites and echinoderms, with some taxa restricted to the
344 distal raphiophorid biofacies in the Saint-Chinian and La Maurerie formations, then absent in
345 the shallower Cluse de l'Orb and Foulon formations, and re-appearing again in the Landeyran
346 Formation, with the return of more distal conditions (raphiophorid biofacies; Vizcaïno and
347 Lefebvre, 1999). Such a pattern is absent for the three key taxa in Montagne Noire, but a
348 wider environmental tolerance would on the other hand facilitate faunal exchange to the Anti-
349 Atlas area during the early Floian. Thus, although the main occurrences of the key taxa
350 coincide fairly well between Montagne Noire and Morocco it probably reflects a temporary
351 breakdown of faunal barriers and migration of faunas during an opportune time between the
352 two areas. As the key taxa have long ranges, their biostratigraphical value seems otherwise
353 limited.

354 Some associated trilobites (Martin et al., 2016), echinoderms (Vizcaïno and Lefebvre,
355 1999; Lefebvre et al., 2016) and bivalves (Babin, 1982; Polechová, 2016) from the
356 *?Baltograptus jacksoni* graptolite Biozone in the Fezouata Formation are as well found in the
357 Landeyran Formation in Montagne Noire (see also discussion in Lefebvre et al., 2018), but
358 Martin et al. (2016) suggested that the trilobite assemblage in Morocco was slightly older
359 than that of the Landeyran Formation. The graptolite assemblage in the lower Landeyran

360 Formation belongs with the *Pseudophyllograptus densus* graptolite Biozone (Gutiérrez-
361 Marco in Kröger and Evans, 2011), presently correlated with the late Floian *Baltograptus*
362 *minutus* graptolite Biozone (Gutiérrez-Marco and Martin, 2016), which supports the slight
363 differences in ages.

364

365 4.3. *Pelecogyra* in Montagne Noire and the Fezouata Formation

366 All four specimens of *Pelecogyra* cf. *fezouataensis* from Montagne Noire come from the
367 same locality and are well-constrained by trilobites to the *Apatokephalus incisus* trilobite
368 Biozone. Graptolites at this site suggest a placement within the *Baltograptus minutus*
369 graptolite Biozone, thus establishing a late Floian age. The depositional setting represents
370 quiet muddy deposits in an off-shore environment within a raphiophorid biofacies.

371 In Morocco *Pelecogyra fezouataensis* occurs at Oued Beni Zoli (locality Z-F5) and the
372 species was also found at a laterally equivalent site 1.2 km to the west. The sections there
373 contain a high diversity assemblage commonly associated with younger strata in the Fezouata
374 area, which lead Kröger and Lefebvre (2012) to suggest an early Floian age. This would be
375 equivalent to sections yielding *Carcassonnella courtessolei*, *C. vizcainoi*, *Lesueurilla prima*
376 and *Thoralispira laevis* (localities Z-F24 (north of Toumiat) and Z-F26 (Toumiat), of the
377 ?*Cymatograptus protobalticus* graptolite Zone, see fig. 2 in Ebbestad and Lefebvre, 2015), in
378 slightly deeper facies. However, the apparent similarities of the assemblages is attributed to
379 similar environmental settings, and the Z-F5 locality and the lateral equivalent represent the
380 late Tremadocian (Tr 3) *Araneograptus murrayi* graptolite Biozone in well-oxygenated lower
381 shoreface environments (Kouraiss et al., 2015; Martin et al., 2016). The Fezouata specimens
382 are often aligned in the troughs of ripple marks (Ebbestad, 2016) testifying to the shallower
383 settings.

384 The single occurrences of *Pelecogyra* allow no appreciation of the range of the genus in
385 either area, but besides the large time span between them there are some significant
386 differences in the two occurrences. They differ in the deeper facies, association with
387 *Carcassonnella* and *Thoralispira*, and non-gregarious association in Montagne Noire
388 compared to the shallower facies, lack of other molluscs and gregarious association in the
389 Fezouata Formation. Key mollusc taxa in Montagne Noire and the Fezouata Shale have a
390 relatively long range, as do several species of trilobites (Martin et al., 2016). But whereas e.g.
391 the trilobite assemblages clearly define environmental settings in both areas (Vizcaino and
392 Álvaro, 2003; Martin et al., 2016) the molluscs in Montagne Noire range across both distal
393 and proximal sedimentary settings; the range in the Anti Atlas as currently known is much
394 more restricted. Migration of these taxa from the Montagne Noire area may have occurred
395 during a short-lived opportune dispersal of marginal raphiophorid assemblages during times
396 of deeper facies distribution in the early Floian as discussed earlier.

397 *Pelecogyra* may represent a taxon endemic to the Anti-Atlas area in the late Tremadocian,
398 only able to migrate outside the area during the Floian. A large protoconch suggests that
399 *Pelecogyra* had non-planktotrophic larvae, generally associated with dispersal only over
400 short distances, but if the taxon had a wide environmental tolerance a wide dispersal would
401 not necessarily be precluded by a non-planktotrophic larval development (see for instance
402 Hansen, 1980; Jablonski and Roy, 2003 and references therein). It may further suggest that
403 the Montagne Noire specimens represent a distinct species through adaptive divergence,
404 although there are no apomorphic features to support this notion.

405 The exact timing of the dispersal remains unsettled, as it is possible that *Pelecogyra*
406 either migrated to Montagne Noire from Morocco in the early Floian or arrived much later.
407 The deeper facies and common occurrence of trilobite species between the older strata in
408 Morocco and the younger Landeyran Formation in Montagne Noire, could support a late

409 dispersal from Morocco during a transgressive phase. In that case, more occurrences of
410 *Pelecogyra* could be expected in the early and middle Floian of Morocco but not in
411 Montagne Noire. On the other hand, if the dispersal occurred already in the early Floian,
412 when the three key taxa *Carcassonnella*, *Thoralispira* and *Lesueurilla* appear in Morocco,
413 *Pelecogyra* would be expected to occur even in the early and middle Floian in Montagne
414 Noire. It is also a clear distance between these regions of the Gondwana margin, if the
415 tentative palaeogeographic reconstruction in Álvaro et al. (2003) is considered, which may
416 suggest that *Pelecogyra* could be expected to be found in regions that were in between the
417 Anti Atlas and Montagne Noire during the Lower Ordovician. Only further finds of the genus
418 may clarify this problem.

419

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424

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606

607 Figure captions

608 **Fig. 1.** Geographical and geological maps. **A.** Map showing the position of Montagne Noire
609 in southern France. **B.** Geological map of the southern Montagne Noire, with simplified
610 outcrop areas of Cambrian–Devonian sediments. **C.** Map showing localities discussed in this
611 paper: west of Les Sources du Foulon (CS 34) and Les Rocs Nègres (CV 12). Map in B
612 modified from Guérangé-Lozes and Burg (1990).

613

614 **Fig. 2.** Stratigraphy and ranges of known gastropod and tergomyan molluscs in the Lower
615 Ordovician of Montagne Noire, France (left) and the Fezouata Formation, Morocco (right).
616 Grey areas in the stratigraphical column from Montagne Noire represent sandstone
617 dominated units. Stippled upper range bars for *Carcassonnella* indicate tentative
618 identification. The light grey horizontal band indicates the correlation discussed in the text.
619 Modified from Vizcaïno and Álvaro (2003) with new data added here. The right column is
620 modified from Ebbestad and Lefebvre (2015). Note that some biostratigraphic boundaries
621 are placed lower compared to the lithostratigraphic column as there were some minor drafting
622 problems with the main stratigraphical figure in Vizcaïno and Álvaro (2003, fig. 2) (pers.
623 comm. Vizcaïno to BL 2019).

624

625 **Fig. 3.** Comparison of *Pelecogyra* from the Fezouata Formation, Morocco, and the
626 Landeyran Formation, Montagne Noire. **A.** *Pelecogyra fezouataensis* Ebbestad and
627 Lefebvre, 2015. Holotype, MHNM.15690.194; Fezouata Formation, Oued Beni Zoli (Z-F5),
628 Anti-Atlas, Morocco. **B.** *Pelecogyra* cf. *fezouataensis* Ebbestad and Lefebvre, 2015.
629 MNHN.F.A71808 Landeyran Formation, west of Les Sources du Foulon (CS 34), Cessenon-
630 sur-Orb, Hérault, southern France. Scale bars: 0.5 cm.

631

632 **Fig. 4.** *Pelecogyra* cf. *fezouataensis* Ebbestad and Lefebvre, 2015. Landeyran Formation,
633 west of Les Sources du Foulon (CS 34), Cessenon-sur-Orb, Hérault, southern France. **A–C.**
634 MNHN.F.A71806; Dorsal, dorsal oblique and lateral views showing curvature and profile of
635 the whorls. **D, E.** MNHN.F.A71807; dorsal oblique and dorsal views showing development
636 of aperture. **F–H.** MNHN.F.A71808; dorsal and detailed views of largest specimen showing
637 protoconch and remnants of the shell. **I, J.** MNHN.F.A71809; Dorsal view of *Pelecogyra*
638 specimen and overview showing the same specimen (right) and two associated specimens of
639 *Carcassonnella courtessolei* (left) (MNHN.F.A71810, MNHN.F.A71811). Scale bars in A–F,
640 I, J: 5 mm. Scale bars in G, H: 1 mm.

641

642 **Fig. 5.** Associated gastropods and tergomyans in the Landeyran Formation. **A.** MHNM.
643 MNHN.F.A71812; *Carcassonnella courtessolei* found on same slab as *Pelecogyra* specimen
644 in Figs 3(B), 4(F). West of Les Sources du Foulon (CS 34). **B.** MNHN.F.A71813,
645 MNHN.F.A71814; two specimens of *Carcassonnella courtessolei* from the site west of Les
646 Sources du Foulon (CS 34). Associated with the mollusc indet. in Fig. 5(E, F). **C.**
647 MNHN.F.A71815; left lateral side of flattened specimen of *Thoralispira laevis* from Les
648 Rocs Nègres locality (CV 12), Causses-et-Veyran, Hérault, southern France. **D.**
649 MNHN.F.A71816, MNHN.F.A71817; *Thoralispira laevis* (left) and *Carcassonnella*
650 *courtessolei* from the site west of Les Sources du Foulon (CS 34). **E, F.** MNHN.F.A71818;
651 Indet. cap-shaped mollusc from the site west of Les Sources du Foulon (CS 34). Scale bars: 5
652 mm.

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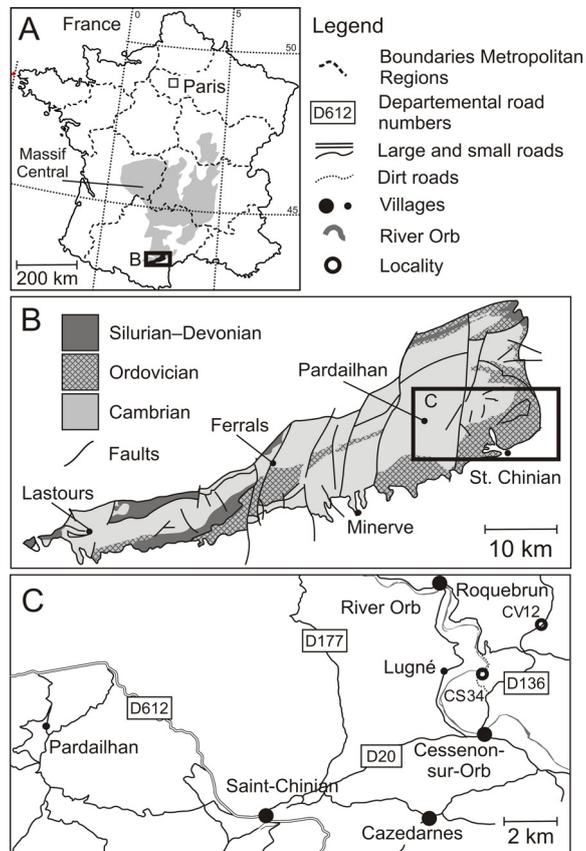


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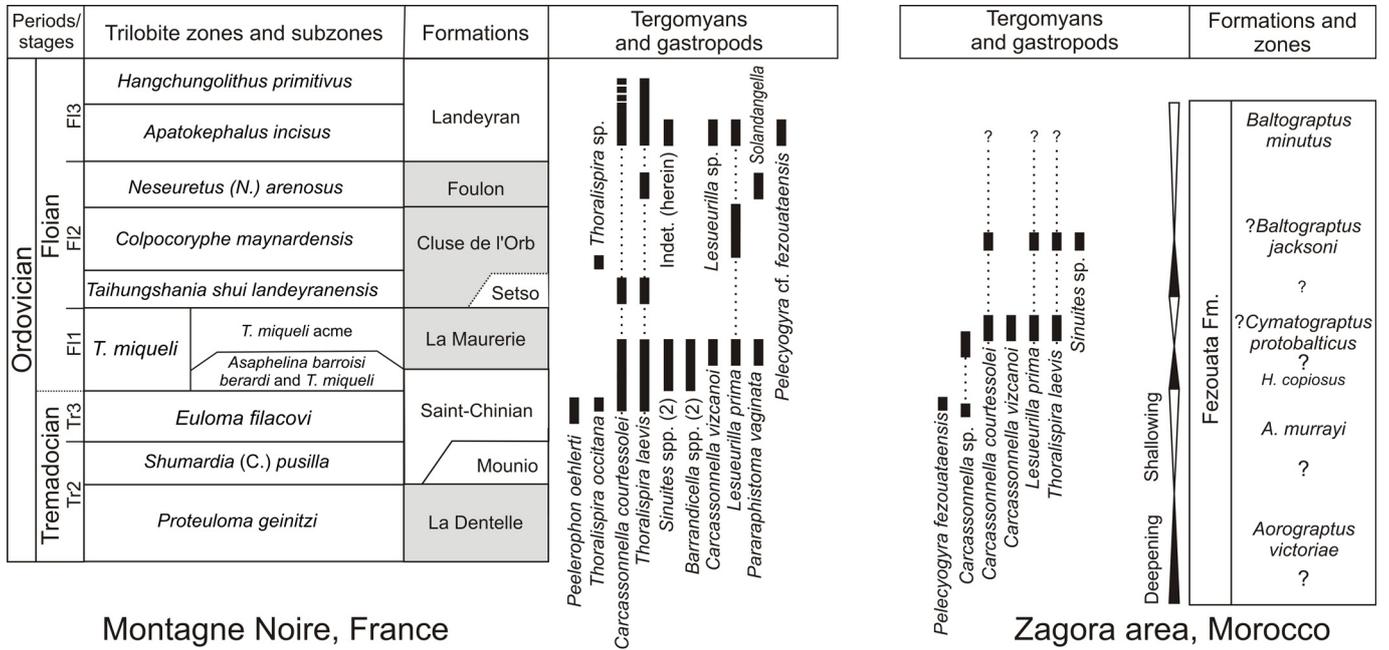


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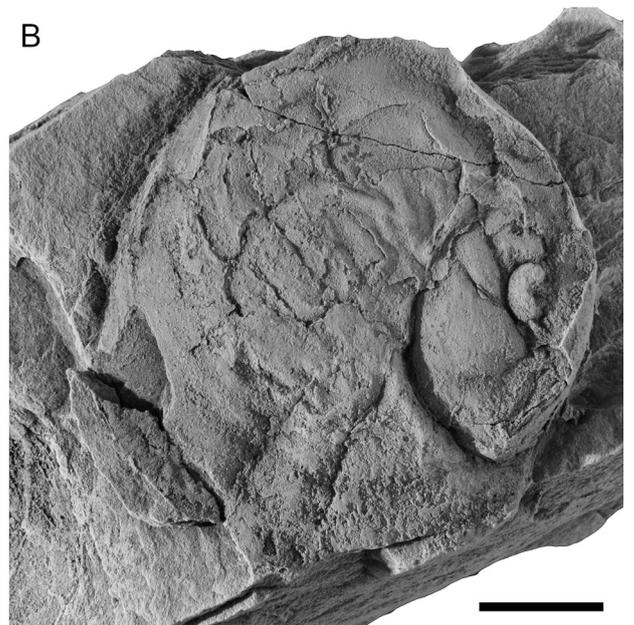
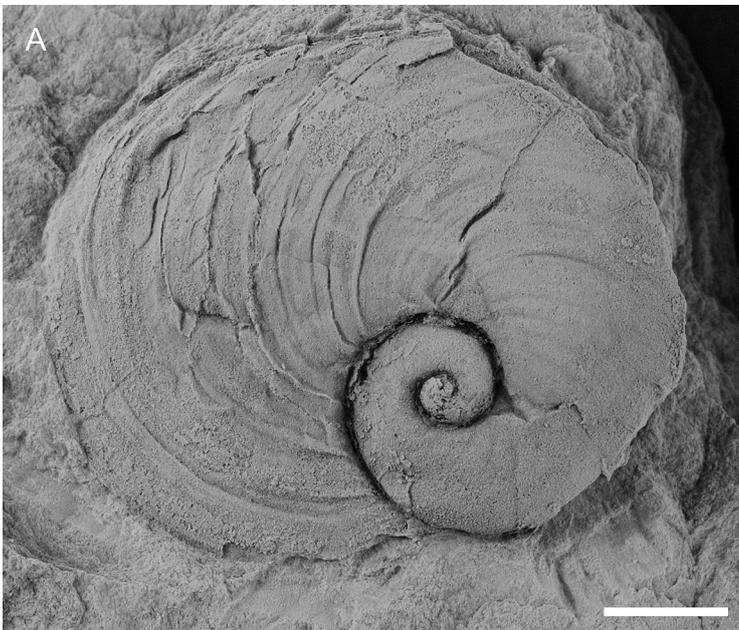


Figure-04.tif

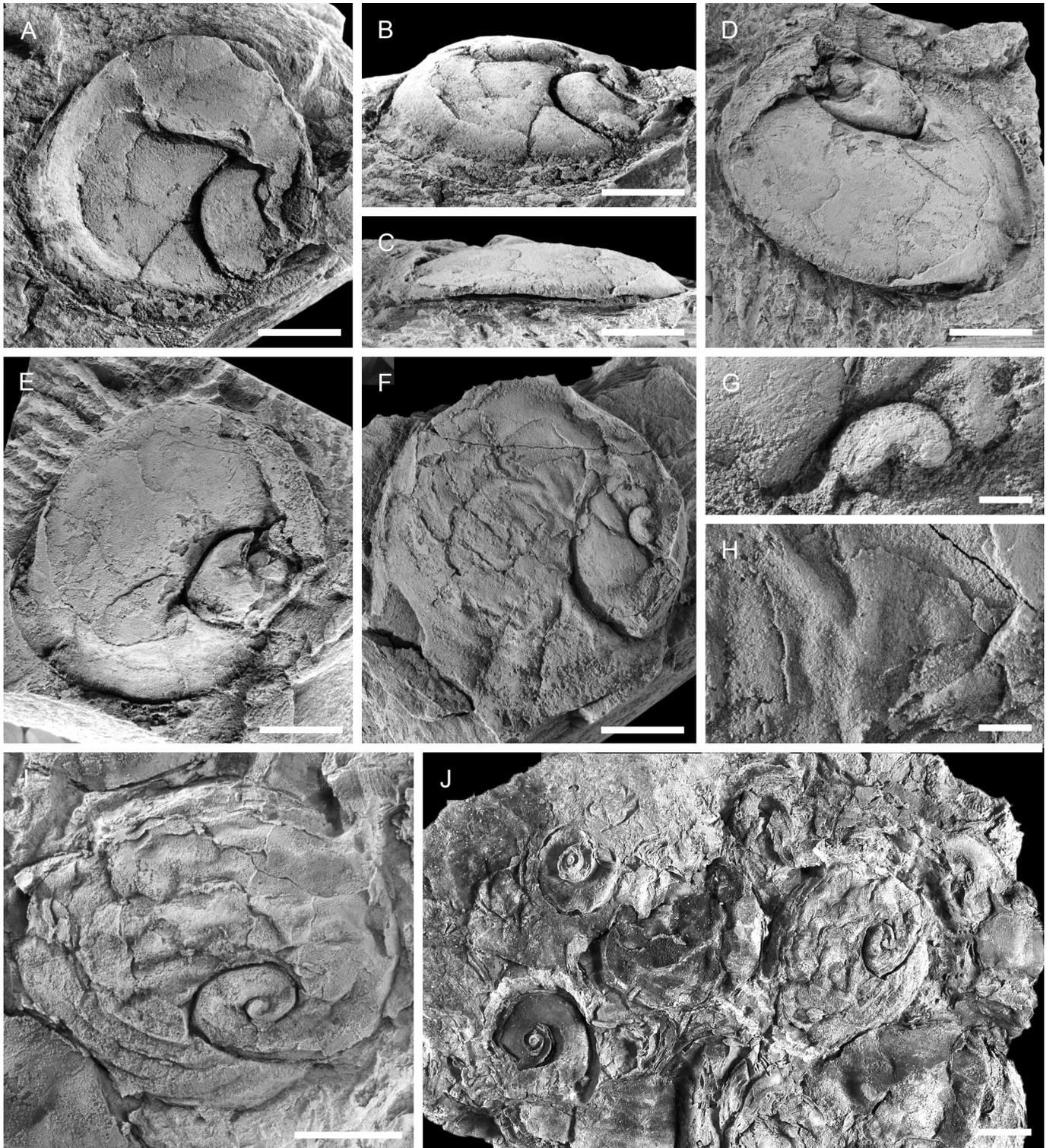


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