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The ultimate Pulchelliidae (Ammonoidea, upper Barremian)

Les ultimes Pulchelliidae (Ammonoidea, Barrémien supérieur)

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Abstract

Pulchelliidae are one of the most important ammonite groups for the Barremian biostratigraphy, and its last species *Gerhardtia provincialis* was deemed to be an end of lineage with no descendants. However, presence of Pulchelliidae was mentioned several times in levels clearly assigned to the *Hemihoplites feraudianus* Interval Horizon, while this family was deemed to be extinct in the *G. provincialis* Subzone; these specimens have never been depicted or described. The description of the both two antidimorphs of *Gerhardtia ultima* sp. nov., discovered in several sections of southeastern France, fills this gap. In terms of evolution, this ultimate species continues the channeling initiated by *G. sartousiana* and *G. provincialis* with the setting up of the over deepening of the ventral furrow, which widens in order to occupy its entire width between the peripheral structures in *G. ultima* sp. nov. In parallel, the peripheral structures are attenuated, the ornamentation disappears on the flanks, and the adult size decreases together with the wide opening of the umbilicus. This hyperpaedomorphic tendency (neoteny and progenesis) occurs suddenly at the end of the lineage, at

26 the same time *G. ultima* sp. nov. is under dramatic quantitative rarefaction, announcing the
27 complete and definitive disappearance of the Pulchelliidae.

28

29 **Keywords:** Ammonites; Barremian; Pulchelliidae; Evolution; End of lineage; Vocontian
30 Basin

31

32 **Résumé**

33 Les Pulchelliidae sont l'un des groupes d'ammonites les plus importants pour la
34 biostratigraphie du Barrémien, et leur dernière espèce connue, *Gerhardtia provincialis*, est
35 reconnue comme étant une fin de lignée sans descendant. Cependant, la présence de
36 Pulchelliidae a été mentionnée à plusieurs reprises dans des niveaux clairement assignés à
37 l'Horizon d'intervalle à *Hemihoplites feraudianus*, alors que cette famille est censée avoir
38 disparu dans la Sous-zone à *G. provincialis* ; ces spécimens n'ont jamais été figurés ni décrits.
39 La description des deux antidimorphes de *Gerhardtia ultima* sp. nov., découverts dans
40 plusieurs coupes du Sud-Est de la France, complète cette lacune. Sur le plan évolutif, cette
41 espèce ultime poursuit la canalisation initiée par *G. sartousiana* et *G. provincialis* avec le
42 surcreusement du sillon ventral, qui s'élargit de façon à occuper toute la largeur de la zone
43 ventrale entre les structures périphériques chez *G. ultima* sp. nov. En parallèle, les structures
44 périphériques sont atténuées, l'ornementation disparaît sur les flancs et la taille adulte décroît
45 en même temps que l'ombilic s'ouvre. Cette tendance hyper-paedomorphique (néoténie et
46 progénèse) s'exprime brutalement à la fin de la lignée, en même temps que la raréfaction
47 quantitative spectaculaire de *G. ultima* sp. nov. qui annonce la disparition complète et
48 définitive des Pulchelliidae.

49

50 **Mots-clefs:** Ammonites ; Barremien ; Pulchelliidae ; Evolution ; Fin de lignée ; Bassin
51 Vocontien

52

53 **1. Introduction**

54 Pulchelliidae Douvillé, 1890 are one of the most important ammonite groups for the
55 Barremian biostratigraphy. In a previous work about the refinement of the upper Barremian
56 biostratigraphic zonal scheme based upon ammonites, Bert et al. (2008, p. 4) mentioned the
57 presence of the Pulchelliidae *Gerhardtia* aff. *provincialis* (d'Orbigny, 1850) in levels clearly
58 assigned to the *Hemihoplites feraudianus* Interval Horizon, while this family was usually
59 deemed to be extinct in the *G. provincialis* Subzone (Vermeulen, 2002, p. 188; 2005 - Table
60 1). This observation was used, conjointly with the stratigraphic repartition of the
61 Hemihoplitidae Spath, 1924, to argument the status of the previously *H. feraudianus* Zone to
62 the subzonal rank within the *G. sartousiana* Zone. This point of view was adopted in the
63 works of the Kilian Group (Reboulet et al., 2009); it has the advantage of keeping the limit
64 between the *G. sartousiana* and *Imerites giraudi* zones to an important faunal turnover
65 (disappearance of Pulchellidae and Hemihoplitinae Spath, 1924, proliferation of
66 Heteroceratidae Spath, 1922), which has also the benefit to correspond to a sequential change
67 (transgression, Arnaud, 2005).

68 Specimens of the genus *Gerhardtia* Hyatt, 1903 were also reported in Spain in levels more
69 recent than the *G. provincialis* Subzone (Hoedemaeker & Leereveld, 1995, fig. 2-11;
70 Company et al., 2004), however they seem extremely rare and no specimen has ever been
71 figured, which led Vermeulen et al. (2013, p. 10, and then 2014, p. 16, and then again 2016, p.
72 20) to estimate that the presence of Pulchelliidae in the *H. feraudianus* Subzone is “highly
73 improbable and may result from erroneous determinations or from harvests in condensed
74 beds”. Indeed, in his revision work on this family, Vermeulen never reported any

75 Pulchelliidae more recent than the species *G. provincialis*, which he considered to be “an end
76 of lineage” (2002, p. 191). The most recent specimen he reported among his whole works
77 comes from bed 284 of the Vergons section (2002, p. 188; equivalent to the bed LOU/142 in
78 Bert et al., 2023), i.e. immediately above the very fossiliferous level from the *G. provincialis*
79 Interval Horizon (LOU/138–140) and far below the *Hemihoplites astarte* Interval Horizon in
80 the context of the South Vocontian Basin (SE France).

81 The aim of the present work is to fill this gap in featuring for the first time specimens of
82 Pulchelliidae clearly dated from the *H. feraudianus* Subzone and the extreme top of the *G.*
83 *provincialis* Subzone, where the Pulchelliidae are supposed to be absent, and to ensure their
84 description. Their morphological originality compared to the typical *G. provincialis*, from
85 which they appear to be descended, leads us to propose the new taxon *Gerhardtia ultima* sp.
86 nov.

87

88 **2. Geological setting**

89 The Vocontian Basin (Paquier, 1900 - Figure 1), in southeastern France, is a large subsident
90 intracratonic area characterized by pelagic sedimentation deposited during the Mesozoic Era
91 at the extreme northwestern Tethys (Alpine Ocean). The basin is bounded to the north, west
92 and south by a series of platforms. The Barremian of the Vocontian Basin shows an almost
93 regular alternation of marlstones and limestones in decimetric to metric beds.

94 The studied sections in the southern part of the basin (GRY, LAC and MOR) are located near
95 the Barremian stratotype (Angles, Alpes de Haute-Provence department). If glauconite is
96 present in bed A/165 of the Angles stratotype as scattered dots in the matrix and coating in
97 contact with some fossils, in any case this bed shows no condensation as it is clearly dated
98 from the *Hemihoplites feraudianus* Interval Horizon alone. It is also important to precise that
99 the sections GRY, LAC and MOR show neither no condensation nor trace of glauconite in

100 any of the levels studied for the present work. Two other sections were studied at the edge of
101 the Provençal platform (Var and Alpes-Maritimes departments), where sedimentation is less
102 regular, with the presence of glauconite in some beds (sections BG6 and SA).

103

104 Most of the field work was made in the protected perimeter of the Geological National Nature
105 Reserve of Haute-Provence that ensures the conservation of the exceptional geological
106 heritage of this territory under French protective laws (see Bert et al., 2022).

107

108 **2.1. Section GRY**

109 This section has already been published and figured by Bert et al. (2013, text-fig. 5). The
110 specimen of *Gerhardtia ultima* sp. nov. studied in the present work (DBT.AW76) from bed
111 GRY/903a is the one quoted as *G. aff. provincialis* in the equivalent of bed LAC/252 by Bert
112 et al. (2008, fig. 4; see below).

113

114 **2.2. Section LAC**

115 The section was previously described and figured by Bert et al. (2008, fig. 4). The *Gerhardtia*
116 *ultima* sp. nov. DBT.BC69 comes from the thick bed LAC/244b immediately below the *H.*
117 *astarte* Interval Horizon and above the *G. provincialis* acmeic Interval Horizon (LAC/239).

118

119 **2.3. Section MOR**

120 This section was studied and figured by Delanoy (1997, fig. 136). The specimen of
121 *Gerhardtia ultima* sp. nov. DBT.AW88 comes from the bed MOR/184. This bed marks the
122 base of the *H. feraudianus* Interval Horizon and is characterized by the presence of numerous
123 specimens of the index species.

124

125 **2.4. Section BG6**

126 The locality of Le Bourguet (St Pierre) was reported by Cotillon (1971, p. 92) who only
127 featured a very synthetic section (fig. 25; p. 95) where the *Hemihoplites* Spath, 1924 are
128 present in unit 23. The section BG6 is not the one studied by Cotillon, but we recognized
129 perfectly the unit 23 with *Hemihoplites* (bed BG6/119 in Figure 2), which provided the
130 specimen DBT.BI69. This platform section has several beds where the presence of glauconite
131 is evident, and some of them are condensed without being polyzonal. This is the case, for
132 example of bed 103, which condenses the entire *Kotetishvilia compressissima* Zone into a
133 small thickness (13 cm). Bed 119 also shows glauconite, but more diffusely; it ends with a
134 hard-ground with *Rhizocorallium* Zenker, 1836. Locally, a highly reworked level at the base
135 of the overlying marls is rich in fragments of phosphatized ammonites (*Martelites* sp.) with a
136 glauconitic patina. The bed 119 is divided into two subsets whose lithology is slightly
137 different. The lower subset is a cream or orange limestone, weakly glauconitic, with biogenic
138 calcitic filaments (typically, fragments of ammonite or brachiopod shells). This level, in
139 addition to the specimen of *Gerhardtia ultima* sp. nov. studied in the present work, delivered
140 *Hemihoplites astarte* (Fallot & Termier, 1923) (Figure 3). The upper subset is more irregular,
141 even sometimes absent. It is rich in glauconite, in particular in contact with fossils; it
142 delivered *Hemihoplites feraudianus* (d'Orbigny, 1841) (Figure 4). By their slightly different
143 faunas, but both belonging to unit 23 of Cotillon, and their differential conservation, it is clear
144 that the two subsets of bed 119 do not have quite the same age at the level of the interval
145 horizon. The lower level is dated from the *H. astarte* Interval Horizon, and the upper from the
146 *H. feraudianus* Interval Horizon.

147

148 **2.5. Section SA**

149 The SA section has already been described (Vermeulen & Bert, 1998; Bert & Delanoy, 2000,
150 fig. 1). It belongs to the Arc de Nice structure and it is the thinnest section studied in the
151 present work. Several beds are highly condensed (polyzonal); this is particularly the case of
152 bed 25, rich in glauconite, which yielded the specimen of *Gerhardtia ultima* sp. nov.
153 DBT.BC82, and which condenses part of the upper Barremian (*Toxancyloceras vandenheckei*
154 and *Camereiceras limentinum* zones).

155

156 3. Material and methods

157 **Acronyms.** RHP = Geological National Nature Reserve of Haute-Provence (Digne-les-Bains,
158 France); ICZN = International Code of Zoological Nomenclature; FAD = First Appearance
159 Datum; [m] and [M] are respectively for micro- and macroconches.

160

161 3.1. Material

162 The present work focuses on extremely rare Pulchelliidae at the top of the *G. provincialis*
163 Subzone and the basis of the *H. feraudianus* Subzone. The fossil material studied was bed-by-
164 bed sampled in the sections described above. This material is curated by a public institution
165 (RHP).

166 For the measurements the following abbreviations respectively mean: D=diametre; H=whorl
167 height; W=whorl width; U=umbilic size; N/2=number of ribs per half-whorl.

168

169 3.2. Stratigraphy

170 The biostratigraphic framework used here is the one proposed by the I.U.G.S Lower
171 Cretaceous ammonite working group, the Kilian Group (Reboulet et al., 2018; Szives et al.,
172 2023). Additionally, we also consider the use of the interval horizons introduced by Bert et al.

173 (2008), Bert & Delanoy (2009) and Bert et al. (2010, 2011, 2018 and 2023), and the proposals
 174 made by Bert et al. (2023) for the *Camereiceras limentinum* Zone, resumed in the Table 1.

175

176 **Table 1.** Biostratigraphic framework of the upper Barremian, according to the Standard
 177 Tethys ammonite zonation completed with the use of the interval horizons. In red are the
 178 levels that yielded *Gerhardtia ultima* sp. nov.

Stages		Zones	Subzones	Interval Horizons	
BARREMIAN	upper	<i>Imerites giraudi</i>	<i>Pseudocrioceras waagenioides</i>		
			<i>Martelites sarasini</i>		
			<i>Imerites giraudi</i>	<i>Heteroceras emerici</i> <i>I. giraudi</i> <i>I. dichotomus</i>	
		<i>Camereiceras limentinum</i>	<i>Hemihoplites feraudianus</i>	<i>Pseudoshasticrioceras autrani</i>	
				<i>P. bersaci</i>	
				<i>P. magnini</i>	
			<i>H. feraudianus</i>		
			<i>H. astarte</i>		
			<i>G. provincialis</i>	<i>G. provincialis</i> Acmeic <i>G. provincialis</i> FAD	
		<i>Camereiceras limentinum</i>	<i>G. sartousiana</i> Acmeic		
			<i>C. limentinum</i>		
		<i>Toxancyloceras vandenheckei</i>	<i>Gassendiceras alpinum</i>	<i>C. marchandi</i>	
				<i>C. breistrofferi</i>	
				<i>G. alpinum</i>	
			<i>T. vandenheckei</i>		<i>T. vandenheckei</i>
					<i>T. canuti</i>

179

180 4. Descriptive palaeontology

181 Class Cephalopoda Cuvier, 1798

182 Order Ammonoidea Agassiz, 1846

183 Suborder Ammonitina Hyatt, 1889

184 Superfamily Endemocerataceae Vermeulen, 1996

185 Family Pulchelliidae Douville, 1890

186 Subfamily Pulchelliinae Douville, 1911

187 Genus *Gerhardtia* Hyatt, 1903

188 Type-species: *Gerhardtia galeatoides* (Karsten, 1856). *G. galeatoides* was considered as a
189 junior synonym of *G. sartousiana* (d'Orbigny, 1841) by Vermeulen & Lahondère (2008, p.
190 102).

191

192 *Gerhardtia ultima* sp. nov.

193 [Fig. 5](#)

194 **Derivation of name.** Related to the phyletic position of the species, at the end of the phylum
195 formed by *Gerhardtia*.

196 **Zoobank Record.** LSID urn:lsid:zoobank.org:act:54A99172-82AC-4118-8CA5-
197 AFAA16741A42

198 **Holotype.** Specimen DBT.BC69 ([Figure 5f–h](#)).

199 **Type locality.** The section LAC near Saint-André-les-Alpes (southeastern France - [Figure 1](#)).

200 **Type horizon.** The bed LAC/244b of the type section (see [Bert et al., 2008](#), fig. 4).

201 **Geographic distribution.** Species currently known only in southeastern France, in both
202 basinal and platform areas. Specimens of *Gerhardtia* were reported from Spain in levels more
203 recent than the *G. provincialis* Subzone ([Hoedemaeker & Leereveld, 1995](#); [Company et al.,](#)
204 [2004](#)); as they were not depicted, it would be interesting to check if they could belong to *G.*
205 *ultima* sp. nov., which would extend the known distribution of the species.

206 **Stratigraphic distribution.** The species is present in the *H. astarte* (or a little before
207 according to the type specimen) and *H. feraudianus* interval horizons only (see [Table 1](#)).

208 **Diagnosis.** Dimorphic species of small adult size (macroconch and microconch around D=40
209 and 20 mm respectively). Shell discoid, compressed, relatively involute; in the microconch,
210 very wide umbilicus and low whorl height on the body chamber ($U/D > 0.30$). Whorl section
211 high in the macroconch, with a maximum thickness towards the middle of the flanks. At least

212 two growth stages: (1) nearly smooth inner whorls with very evanescent ribs faintly visible at
 213 the umbilical rim; peripheral structures particularly thin and close together at the top of the
 214 flanks; ventral zone clearly over deepened across its entire width. (2) On the macroconch,
 215 reinforced ornamentation on the second part of the living body-chamber; peripheral structures
 216 forming an almost continuous ridge bordering the deepened ventral furrow; on the
 217 microconch, ornamentation reinforced mainly on the peri-umbilical edge (wedge-shaped).
 218 The main specific features is the aspect of the ventral area, where the over deepening occupy
 219 the entire ventral groove between the peri-ventral edges.

220 **Material studied.** Five specimens: 3 from the basinal area (DBT.AW76 [bed GRY/903b];
 221 DBT.AW88 [bed MOR/184]; DBT.BC69 [bed LAC/244b]), and the both two last from the
 222 platform area (DBT.BI69 [bed BG6/119] and DBT.BC82 [bed SA/25]).

223 **Measurements.** See [Table 2](#).

224 **Table 2. Measurements of the specimens.** All measures are in mm.

Specimens	D	H	W	U	H/D	W/H	U/D	U/H	N/2
DBT.AW76	16.18	6.68	-	5.64	0.41	-	0.35	0.84	27
DBT.AW88	-	17.76	-	-	-	-	-	-	-
DBT.BC69 (holotype)	40.80	18.46	9.78	7.82	0.45	0.53	0.19	0.42	24
DBT.BI69	31.34	17.20	10.00	4.30	0.55	0.58	0.14	0.25	-
DBT.BC82	19.82	7.50	8.94	6.04	0.38	1.19	0.31	0.81	8

225

226 **Description of the specimens.** Of the 5 specimens studied, the holotype is the largest ([Figure](#)
 227 [5f-h](#)). Its last suture lines are approximate, which makes it possible to consider this specimen
 228 as an adult. The development is almost complete with a body chamber of almost half a whorl.
 229 Specimen DBT.AW88 ([Figure 5k-l](#)), although very incomplete, is of comparable size
 230 (measured on H); it is a fragment of an adult body chamber with what can be interpreted as a
 231 peristomal rim. Specimen DBT.BI69 ([Figure 5i-j](#)) could be a juvenile or an incomplete adult,

232 the sutures not being visible. Specimen DBT.AW76 (Figure 5a) very clearly shows its
233 complete adult body chamber of almost 2/3 whorl; its very high U/H ratio (>0.30), in
234 connection with a clear opening of the umbilicus, could accredit that it may be a microconch.
235 The same for the specimen DBT.BC82 (Figure 5b–e), which is particularly well preserved.
236 This latter specimen has a particular ornamentation on the body chamber, erased from the
237 mid-flanks; however, wedge-shaped ribs on the umbilical rim and especially the very
238 distinctive shape of the ventral area are diagnostic characters of *G. ultima* sp. nov.
239 The shell is discoid, most often compressed and relatively involute, except for the presumed
240 microconch whose uncoiled last whorl makes the shell frankly evolute. The section of the
241 whorls is very high with a maximum thickness towards the middle of the flanks, which are
242 slightly convex; microconch specimen DBT.BC82 is a notable exception with its very
243 rounded subquadratic depressed section (W/H=1.19; robust morphology and different
244 conservation with internal mold preservation in thickness), while the postmortem compression
245 of the other microconch (DBT.AW76) does not allow to know its width. Due to the very
246 significant covering of the whorls, the ontogeny is only partially accessible. On the presumed
247 macroconch, at least two stages of growth are known:

248 - The visible part of the phragmocone and half of the adult body chamber appear
249 almost smooth, the ribbing being much attenuated. Very evanescent ribs are faintly visible at
250 the umbilical edge. The rest of the ornamentation is mainly expressed at the top of the flanks,
251 in the form of the peripheral structures described by Vermeulen (i.e. the termination of the
252 ribs in the peri-ventral zone) for the other species of Pulchelliinae Douvillé, 1911 and in
253 particular in *Gerhardtia* (Vermeulen, 2002, fig. 18; see Figure 6). These structures are here
254 particularly thin and close together, which gives a finely crenellated appearance to the peri-
255 ventral margin. The ventral zone is clearly over deepened over its entire width and its bottom

256 is slightly concave (Figure 5g), which has the effect of turning the peripheral structures into
257 two well individualized carina (Figure 5g).

258 - On the second part of the body chamber, the ornamentation is clearly reinforced and
259 the ribs become visible along their entire length (DBT.BC69), or only from the upper half of
260 the flanks (DBT.AW88). They are straight on the lower half of the flanks and sometimes
261 wedge-shaped near the umbilical rim (Figure 5f). On the upper third of the flanks the ribs
262 become proverse, falciform and show their maximum vigor. They are not sharp, except at the
263 peri-ventral zone where their limit with the ventral furrow forms a true ridge. Compared to the
264 previous stage, the ribs are wider there, which only partially reduces the impression of a
265 double carina (Figure 5h). The peristome seems preserved on specimen DBT.AW88 (Figure
266 5k): it is simple, slightly sinuous with a slight lateral and ventral expansion.

267 The presumed microconch repeats these stages, with the exception that the peri-umbilical
268 wedge-shaped ribs are clearly more pronounced in the last part of the body chamber, until
269 they form the start of rib bundles clearly visible in specimen DBT.AW76 (Figure 5a).
270 Specimen DBT.BC82 (Figure 5b–e) is slightly different and represents the robust morphology
271 of the species. The ornamentation on the phragmocone is well marked and thick (with the
272 exception of the smooth inner whorls), whereas it is more effaced on the upper flanks on the
273 body chamber. This can be possibly interpreted as a continuous variation of the ‘secondary
274 erasing of ornamentation’ type (see Bersac & Bert, 2012, p. 235 and fig. 14 - ‘variability of
275 type 2’).

276 **Systematic discussion.** The specimens collected belong unambiguously to the genus
277 *Gerhardtia*, of which they respect the diagnosis (following the conception of Vermeulen who
278 revised this group; 1999, 2002). More specifically, their general morphology is close to the
279 slender morphology of this genus, with the exception of the very robust specimen DBT.BC82.

280 Compared with *G. sartousiana* (and its minor synonym *G. galeatoides*) and *G. provincialis*,
281 the adult size of *G. ultima* sp. nov. seems to be smaller, particularly in the presumed
282 macroconchs (D=40 mm versus 50–55 mm), even if we exclude the Colombian
283 representatives of these species, which can reach a relatively larger size than the specimens
284 from the Vocontian Basin (up to exceeding D=80–90 mm). On the other hand, there is no
285 information concerning the presumed microconchs of these species, dimorphism having not
286 been taken into account by Vermeulen, even if we can consider that with D<20 mm,
287 specimens DBT.AW76 and DBT.BC82 are in all cases very small for adult Pulchelliidae.

288 The shape of the ventral area of *G. ultima* sp. nov. is discriminating compared to the other
289 *Gerhardtia* species. In *G. sartousiana*, it is flat and forms a furrow framed by the lateral
290 structures, but without any over deepening (Figure 6a); in *G. provincialis*, there is an over
291 deepening restricted only to the middle of the furrow (Figure 6b). In *G. ultima* sp. nov., the
292 over deepening occupies the entire width of the ventral groove, giving a morphology that is
293 apparently quite similar to that of *G. sartousiana*, but with higher lateral-ventral ridges. At the
294 same time, the lateral structures are simplified and lose their angulations, adopting a spatulate
295 morphology, or even disappearing altogether. The ribs are also much narrower and denser in
296 *G. ultima* sp. nov., whereas in the other species they are usually very wide, particularly on the
297 body chamber. However, on the phragmocone of the most slender specimens of *G.*
298 *provincialis* (see Vermeulen, 2002, pl. 52, figs. 1-4; pl. 53, figs. 3-4, 6-8), the ornamentation
299 may be particularly thin but is always well marked, unlike in *G. ultima* sp. nov., which is
300 almost smooth on the flanks (with the exception of the robust microconch morphology as
301 exemplified by specimen DBT.BC82). Furthermore, the ornamentation of *G. sartousiana* and
302 *G. provincialis* does not form the almost continuous carination on the periventral area.

303 Specimen DBT.AW88 (Figure 5k-l), with its smooth zone in the lower half of the flanks on
304 the body chamber, combined with the falciform appearance of the ribs in the upper part of the

305 flanks, shows a certain affinity with the older species *Kotetishvilia brevicostata* (Kotetishvili,
306 1980) (base of the *C. limentinum* Zone). However, in the latter, the double periventral carina
307 is perfectly continuous and lacks the lateral structures seen in *G. ultima* sp. nov.

308

309 **5. Discussion**

310 There is no doubt that *Gerhardtia ultima* sp. nov. is original, both stratigraphically, since it
311 occurs in levels where Pulchelliidae are deemed to have disappeared (Vermeulen et al. 2013,
312 p. 10; 2014, p. 16; 2016, p. 20), and morphologically because of its ornamental features and
313 especially the appearance of its ventral area.

314 Taking these elements into account, it is possible to describe the last evolutionary patterns of
315 *Gerhardtia*. The transition from *G. sartousiana* to *G. provincialis*, as recognised by
316 Vermeulen (1999; 2002), is materialised by the establishment of the ventral over deepening,
317 which appears progressively, first inconspicuously within populations (*G. provincialis* FAD
318 Interval Horizon), then more systematically (*G. provincialis* Acmeic Interval Horizon - [Figure](#)
319 [6a–b](#)). In *G. ultima* sp. nov., this over deepening widens to occupy the entire ventral groove
320 between the peripheral structures ([Figure 6c](#)). At the same time, the peripheral structures
321 attenuate, giving the ribs a spatulate appearance. The smooth stage and the ornamentation
322 increasingly thin and approximate on the flanks (with the exception of the robust morphology)
323 is a feature only seen in the very inner whorls of *G. sartousiana* and *G. provincialis*. This
324 trend, combined with the reduction in the adult size of *G. ultima* sp. nov., and its earlier
325 umbilical opening, suggest an evolutionary pattern of the hyper-paedomorphosis type (in the
326 sense of Dommergue et al., 1986 = combination of neoteny and progenesis). This hyper-
327 paedomorphosis seems to have occurred only at the very end of the lineage formed by *G.*
328 *sartousiana* -> *G. provincialis* -> *G. ultima* sp. nov., in an abrupt manner. It is legitimate to
329 think that the abruptness of this phenomenon on the geological time scale (punctuated event)

330 is correlated with the dramatic quantitative rarefaction of *G. ultima* sp. nov., which becomes
331 anecdotal in the faunal assemblages, whereas *G. provincialis* was in a much more dominant
332 position shortly before (*G. provincialis* Acmeic Interval Horizon). We might wonder how
333 much of this drastic selection is due to competition with other species versus the impact of
334 environmental variations, given that the disappearance of *Gerhardtia* occurred more or less at
335 the same time as the quantitative explosion of *Hemihoplites*, which are dominant in the *H.*
336 *feraudianus* Interval Horizon. However, such a correlation is not certain, since the two groups
337 are very different in terms of morphology (even considering only the youths) and thus
338 probably did not occupy the same ecological niche. Furthermore, the Hemihoplitinae are
339 already well represented in the faunal assemblages from the *C. limentinum* Interval Horizon,
340 which would otherwise have prevented the proliferation of *Gerhardtia* during the *G.*
341 *provincialis* Subzone.

342

343 An interesting parallel can be drawn with the evolution of the Oxfordian Peltoceratinae and
344 the transition from *Peltoceratoides* Spath, 1924 to *Gregoryceras* Spath, 1924, which also
345 represents a true punctuated event combining hyper-paedomorphosis and dramatic
346 quantitative rarefaction (Bert, 2004, p. 120–122, fig. 23; 2014, p. 279–280). The difference is
347 that *Gregoryceras* survived this morphological upheaval, which is not the case for
348 *Gerhardtia*, since the disappearance of *G. ultima* sp. nov. marks the disappearance of the
349 Pulchelliidae as a whole.

350

351 **6. Conclusion**

352 Until recently, *Gerhardtia provincialis* was considered to be an end of lineage that
353 disappeared before the end of its eponymous subzone, very shortly after its acme phase,
354 bringing with it the disappearance of the Pulchelliidae as a whole (Vermeulen, 2002; 2005).

355 The existence of Pulchelliidae had nevertheless been reported in the *Hemihoplites feraudianus*
356 Subzone as early as 1995 in Spain (Hoedemaeker & Leereveld, 1995, fig. 2-11; Company et
357 al, 2004), and more recently in France (Bert et al., 2008), but none of the reported specimens
358 had ever been figured.

359 In this work, specimens of Pulchelliidae more recent than *Gerhardtia provincialis*, present
360 until the *Hemihoplites feraudianus* Interval Horizon, are figured for the first time, filling this
361 gap. In addition to their stratigraphic distribution, their study shows that their morphological
362 originality sets them apart from the other known species of the genus and that they belong to a
363 new species: *Gerhardtia ultima* sp. nov.

364 From an evolutionary point of view, this ultimate species continues the channeling begun with
365 *G. sartousiana* and *G. provincialis* with the establishment of the over deepening of the ventral
366 furrow, which widens to occupy its entire width between the peripheral structures in *G. ultima*
367 sp. nov. (Figure 6). At the same time, the peripheral structures attenuate to give a spatulate
368 appearance to the ribs, the ornamentation fades on the flanks and becomes increasingly thin
369 and approximate (with the exception of the robust morphology), and above all, the adult size
370 decreases and the umbilicus is markedly more open. This hyper-paedomorphic trend (neoteny
371 and progenesis) occurs abruptly at the end of the lineage, at the same time as the dramatic
372 quantitative rarefaction of *G. ultima* sp. nov. heralds the total disappearance of the
373 Pulchelliidae.

374

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380

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384

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386

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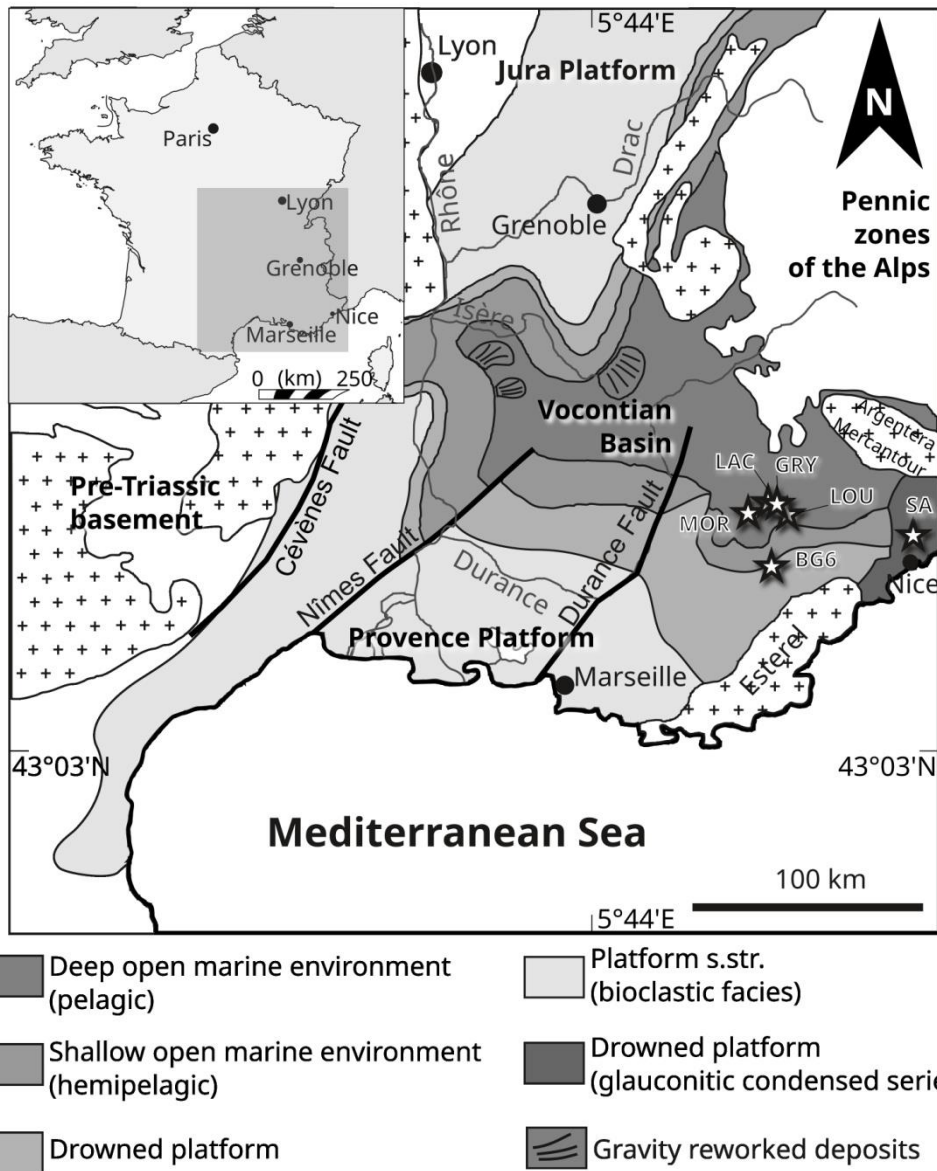
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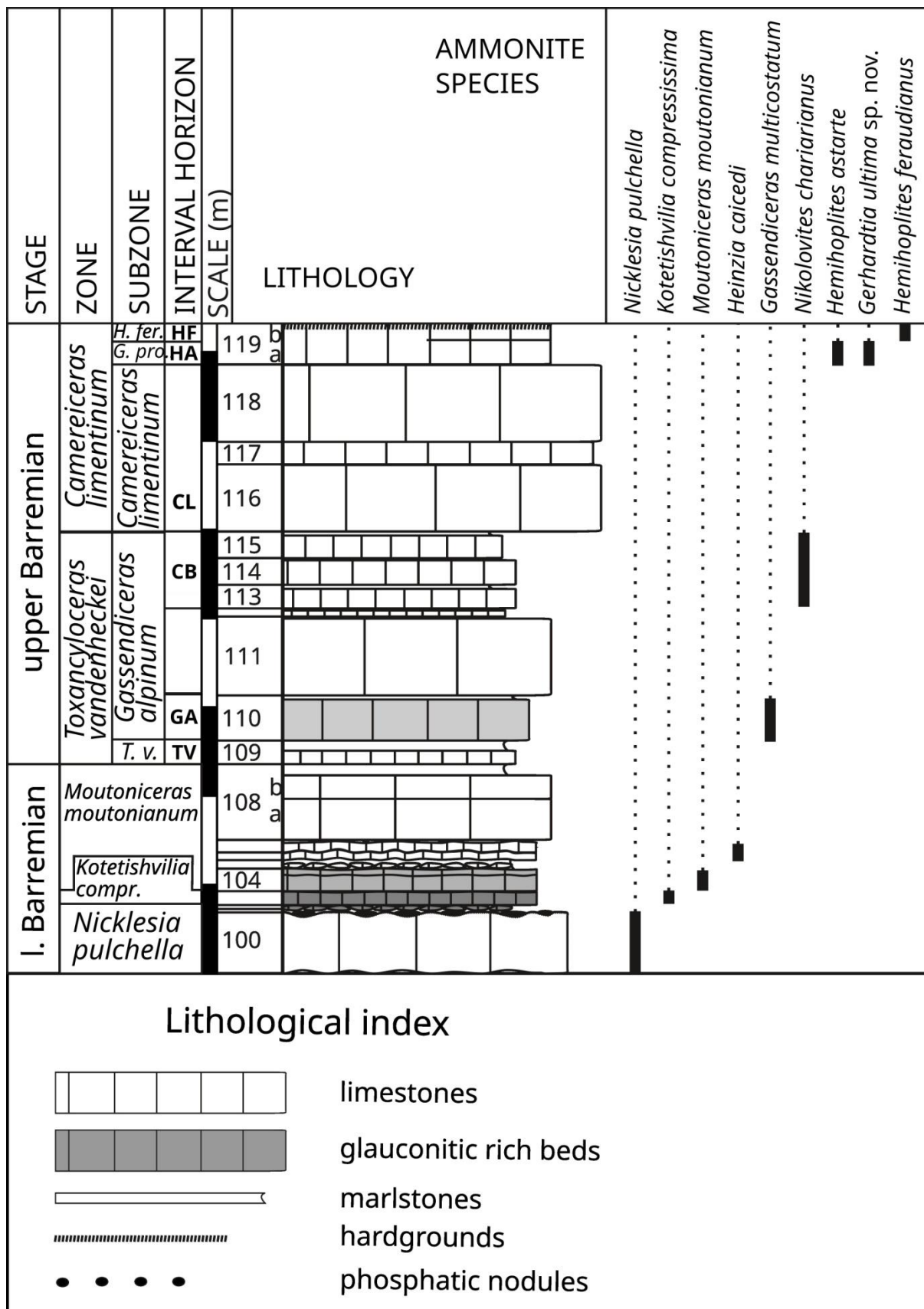
517 **Captions of the figures:**



518

519 **Figure 1.** Palaeogeographic map of the Vocontian Basin for the Barremian (southeastern
 520 France, modified after [Arnaud, 2005](#)). The stars point out the sections mentioned in the text:
 521 MOR near Moriez; LAC and GRY (near Saint-André-les-Alpes); LOU (near Vergons); BG6
 522 (near Le Bourguet); SA (near Nice).

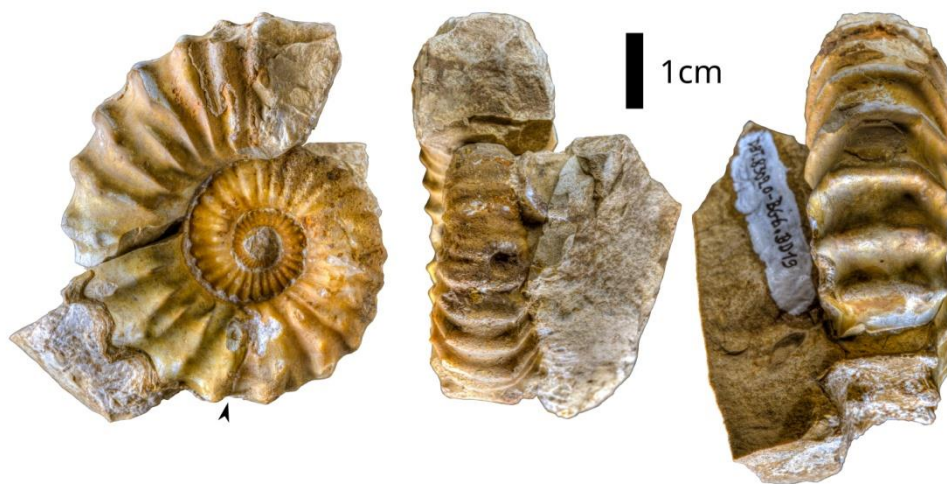
523 **Figure 1.** Carte paléogéographique du Bassin Vocontien pour le Barrémien (sud-est de la
 524 France, modifiée d'après [Arnaud, 2005](#)). Les étoiles pointent les coupes mentionnées dans le
 525 texte : MOR près de Moriez, LAC et GRY (près de Saint André-les-Alpes) ; LOU (près de
 526 Vergons) ; BG6 (près de Le Bourguet) ; SA (près de Nice).



529 **Figure 2.** Log of the section BG6 near Le Bourguet (Var department), with the position of
530 *Gerhardtia ultima* sp. nov. and some characteristic ammonites. TV = *Toxancyloceras*
531 *vandenheckei* Interval Horizon; GA = *Gassendiceras alpinum* Interval Horizon; CB =
532 *Camereiceras breistrofferi* Interval Horizon; CL = *C. limentinum* Interval Horizon; HA =
533 *Hemihoplites astarte* Interval Horizon; HF = *Hemihoplites feraudianus* Interval Horizon.

534 **Figure 2.** Coupe BG6 près de Le Bourguet (department du Var), avec la position de
535 *Gerhardtia ultima* sp. nov. et de quelques ammonites caractéristiques. TV = Horizon
536 d'intervalle à *Toxancyloceras vandenheckei* ; GA = Horizon d'intervalle à *Gassendiceras*
537 *alpinum* ; CB = Horizon d'intervalle à *Camereiceras breistrofferi* ; CL = Horizon d'intervalle
538 à *C. limentinum* Interval Horizon ; HA = Horizon d'intervalle à *Hemihoplites astarte* ; HF =
539 Horizon d'intervalle à *Hemihoplites feraudianus*.

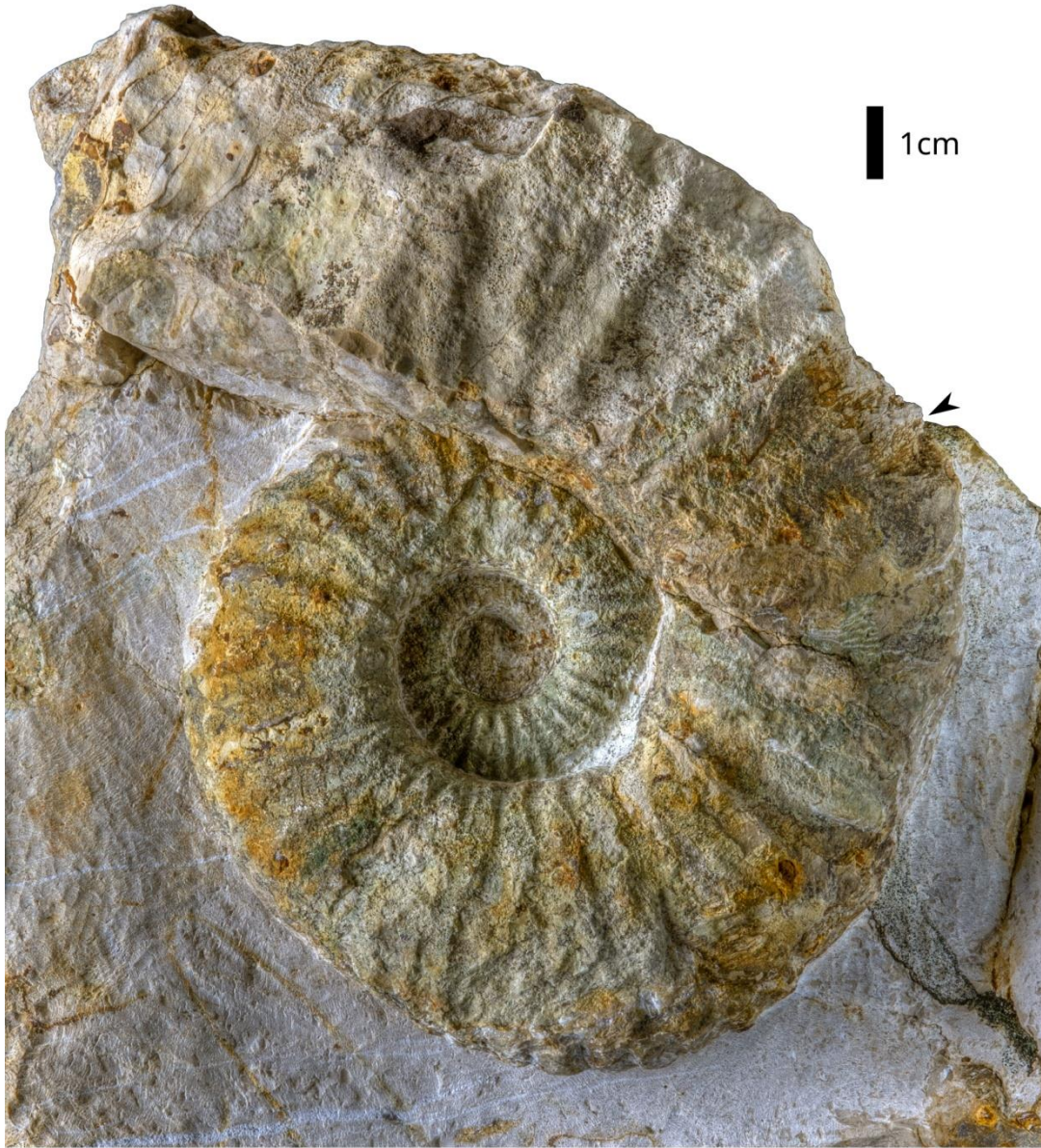
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542 **Figure 3.** *Hemihoplites astarte* [m], adult specimen n°DBT.BD19, from bed 119a of the
543 section BG6. The arrow points out the last suture.

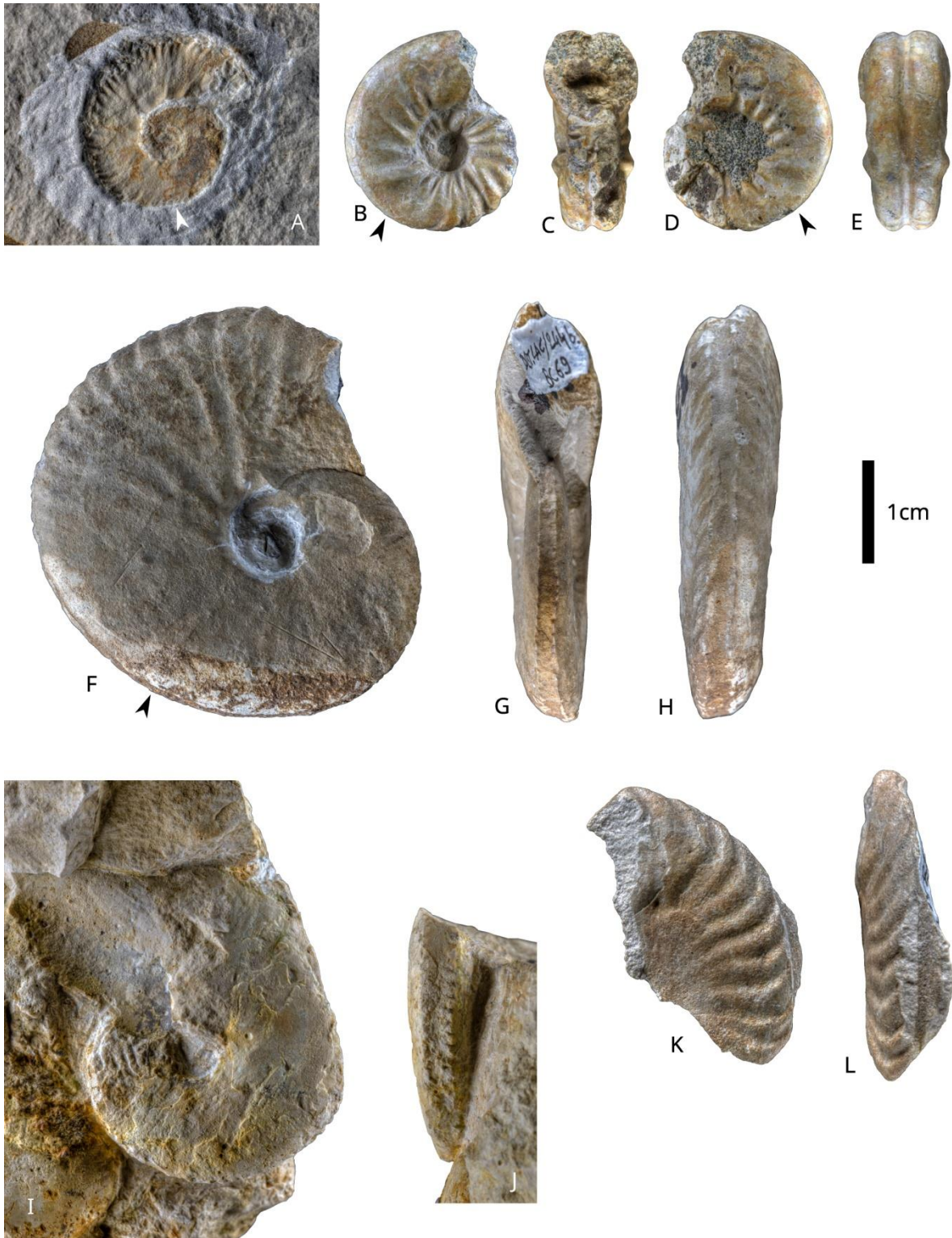
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546 **Figure 4.** *Hemihoplites feraudianus* [M], specimen n°DBT.BJ34, from bed 119b of the
547 section BG6. The arrow points out the last suture.

548 **Figure 4.** *Hemihoplites feraudianus* [M], spécimen n°DBT.BJ34, du banc 119b de la coupe
549 BG6. La flèche pointe la dernière suture.

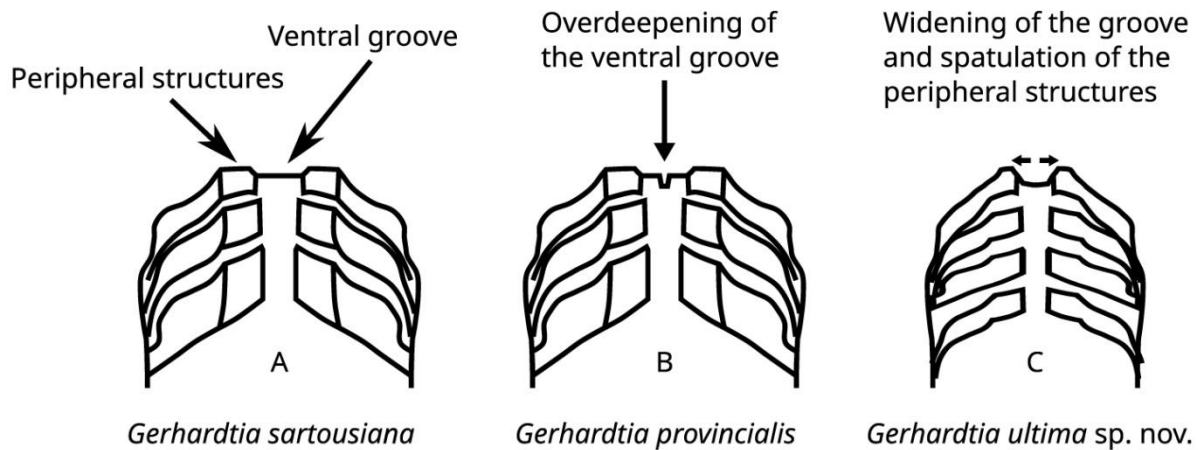
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552 **Figure 5.** *Gerhardtia ultima* sp. nov.; **A:** [m] DBT.AW76 from bed 903b of section GRY; **B–**
 553 **E:** [m] DBT.BC82 from bed 25 of section SA; **F–H:** [M] DBT.BC69 from bed 244b of
 554 section LAC; **I–J:** [M] DBT.BI69 from bed 119 of section BG6; **k–l:** [M] DBT.AW88 from
 555 bed 184 of section MOR. All the specimens at the same scale.

556 **Figure 5.** *Gerhardtia ultima* sp. nov.; **A:** [m] DBT.AW76 du banc 903b de la coupe GRY; **B–**
 557 **E:** [m] DBT.BC82 du banc 25 de la coupe SA; **F–H:** [M] DBT.BC69 du banc 244b de la
 558 coupe LAC; **I–J:** [M] DBT.BI69 du banc 119 de la coupe BG6; **k–l:** [M] DBT.AW88 du
 559 banc 184 de la coupe MOR. Tous les spécimens sont à la même échelle.
 560



561
 562 **Figure 6.** Evolution of the ventral groove and aspect of the peripheral structures of the ribs,
 563 successively in **A:** *Gerhardtia sartousiana*, **B:** *G. provincialis* and **C:** *G. ultima* sp. nov. See
 564 text for explanations.

565 **Figure 6.** Evolution du sillon ventral et de l'aspect des structures périphériques des côtes,
 566 successivement chez **A:** *Gerhardtia sartousiana*, **B:** *G. provincialis* et **C:** *G. ultima* sp. nov.
 567 Voir le texte pour les explications.