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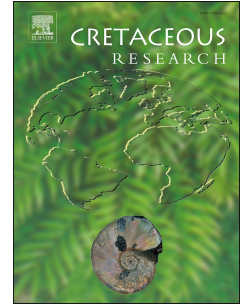
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# Journal Pre-proof

Can the intraspecific laws of variation be used as a predictive model for understanding species with insufficient data? The example of the early Heteroceratidae in their evolutionary context (heteromorph ammonites, Tethys upper Barremian)



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#### Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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1       **Can the intraspecific laws of variation be used as a predictive model for**  
2       **understanding species with insufficient data? The example of the early**  
3       **Heteroceratidae in their evolutionary context (heteromorph ammonites,**  
4       **Tethys upper Barremian)**

5  
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7  
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15  
16       **Highlights**

- 17       • The ‘laws’ of intraspecific variability in ammonites are used as a predictive tool  
18       • Phyletic reconstruction is proposed for the early *Heteroceras* (upper Barremian)  
19       • Evolutionary patterns and process of the early Heteroceratidae are studied  
20       • 2 new species of *Lazarinicerias* are introduced  
21       • Stratigraphic canvas for the Vocontian upper Barremian is refined

22  
23       **Abstract**

24       The generalized ‘laws’ of intraspecific variability in ammonites are used as a predictive tool  
25       to define the limits of poorly known species of the early Heteroceratidae (*Lazarinicerias*,

26 heteromorph ammonites), based on the construction of the *Heteroceras* theoretical model of  
27 variation. The methodology is described and the model is confronted with the  
28 palaeontological data. The discussion of the results shows that the variability observed for  
29 *Lazarinicer* takes up most of the continuous variation of the theoretical model. To minimize  
30 bias, particular attention was paid to the strict stratigraphic control of the raw data (8 sections  
31 studied). Thus, and for the good application of the theoretical model, the stratigraphic canvas  
32 and the systematics of the groups studied were refined and discussed: (1) the abandonment of  
33 the *Gerhardtia sartousiana* Zone is proposed in favor of the new *Camereiceras limentinum*  
34 Zone; (2) *Heteroceras astierianum*, *Heteroceras tardieui* and *Martelites bifurcatus* are  
35 rehabilitated; and (3) *Lazarinicer heterostylia* sp. nov. and *Lazarinicer lhaumeti* sp. nov.  
36 are introduced while *Lazarinicer astierianum* is redefined. Once the theoretical model of  
37 the variation has been obtained, it was then possible to propose phylogenetic reconstruction  
38 hypotheses using the cladistic tool crossed with the stratigraphic data, used to study the  
39 evolutionary patterns and processes of the group. The results show that: (1) *Lazarinicer* is  
40 unambiguously a Heteroceratidae despite the absence of the early helical coiling; (2)  
41 *Lazarinicer* originates within the *Toxancyloceras*; (3) Ancyloceratidae is a paraphyletic  
42 taxon; (4) evolution of the studied group is expressed by changes in adult size, heterochronies  
43 and innovations.

44

45 **Keywords:** heteromorph ammonites; intraspecific variability; predictive theoretical model;  
46 phylogenetic reconstruction; evolution; stratigraphy.

47

## 48 1. Introduction

49

50 The existence of a number of rules conditioning the intraspecific variability in ammonites is  
51 now well established (e.g. de Baets et al., 2013, 2015 and references). However, it is  
52 sometimes difficult to clearly identify this phenomenon in species for which there are no  
53 sufficiently representative samples of their population, which leads to the temptation to fall  
54 into the typological approach with the risk of many undesirable biases (Marchand and  
55 Dommergues, 2008).

56 In some cases of similar occupation of the morphological space for phylogenetically related  
57 ammonite taxa, the recently generalized ‘laws’ of intraspecific variability (Bert, 2019) could  
58 theoretically allow the development of a predictive tool. Such possibility is enhanced by the  
59 fact that morphologies that would not be explained by these laws are considered improbable  
60 (Courville and Crônier, 2005, p. 947; Courville, 2011) for epigenetic reasons (Courville and  
61 Crônier, 2003, p. 539). Thus, for a given phyletic lineage, if the variability of at least one  
62 species is sufficiently well known, the generalization of the ‘laws’ of intraspecific variability  
63 could make it possible to identify the limits of another close species with insufficient data,  
64 while considering the potential modulation by extrinsic factors (environmental changes). This  
65 possibility would circumvent, at least partially, sampling biases. The example of the early  
66 Heteroceratidae Spath, 1922 (upper Barremian) lends itself well to this exercise.

67  
68 The old conceptions placing the genus *Heteroceras* d’Orbigny, 1850 in the vicinity of  
69 Hauterivian ammonites (*Crioceratites* Léveillé, 1837, *Neocomitidae* Salfeld, 1921,  
70 *Cruasiceras* Busnardo, 1970 or *Aegocrioceras* Spath, 1924) are no longer relevant (see  
71 Delanoy, 1997, p. 177 for historical account). Similarly, the proposal by Vašíček and  
72 Wiedmann (1994) to consider *Eoheteroceras* Vašíček and Wiedmann, 1994  
73 (Leptoceratoidinae Thieuloy, 1966) as a strain of the genus *Heteroceras* has already been  
74 discussed and rejected by Delanoy (1997, p. 177). For the latter author, the first *Heteroceras*

75 suddenly appear at the top of the *Hemihoplites feraudianus* Subzone, in the  
76 *Pseudoshastrioceras autrani* Interval Horizon, with large-sized forms that would offer little  
77 variation, including their ornamentation (sic). However, the origin of the Heteroceratidae is  
78 still not resolved, even if we accept the great ornamental and sutural proximity between  
79 *Moutoniceras* Sarkar, 1955 and *Heteroceras* already underlined by Kilian (1888), Sarkar  
80 (1955), Kakabadze (1967) and Vermeulen (1997, 2005). This latter author (1998, 2006)  
81 reported the existence of specimens of *Heteroceras* in the *Gerhardtia sartousiana* Zone  
82 (lower part of the zone and *Gerhardtia provincialis* Interval Horizon), which reduces the  
83 important stratigraphic hiatus between the last *Moutoniceras* and the first *Heteroceras*.  
84 However, these finds have never been confirmed and no helical part of the juvenile whorls  
85 of the shell was ever reported. Finally, without any argument, Vermeulen et al. (2016, p. 18)  
86 proposed that the genus *Moutoniceras* would become extinct just in the *Gassendiceras*  
87 *alpinum* Subzone (“population related to *M. moutonianum*” [sic] - upper Barremian), whilst  
88 they assumed that “the most primitive known population of the genus *Moutoniceras* to the  
89 genus *Heteroceras*” appears in the same Subzone. Bert et al. (2018) have since shown the  
90 direct link between the last *Moutoniceras eigenheeri* (Vermeulen, 2003) and the first  
91 *Toxancyloceras canuti* Bert, Bersac, Juarez-Ruiz and Hughes, 2018, and have explained their  
92 evolutionary relationships, which have made it possible to consolidate the classification of  
93 *Moutoniceras* among the Ancyloceratidae Gill, 1871 from which they originated. Until  
94 proven otherwise, there are no *Moutoniceras* beyond the lower Barremian boundary. There is  
95 therefore no longer any argument to propose a direct origin of the *Heteroceras* among the  
96 *Moutoniceras*.

97 The recent discovery of a number of very rare specimens of *Lazarinoceras* Vermeulen,  
98 Lepinay and Mascarelli, 2011 (this work) sheds new light on the question of the origin of the  
99 Heteroceratidae. To date, the samples do not present sufficiently representatives of their

100 original populations, which do not allow the use of the statistical tool to identify their  
101 contours. However, there is a good knowledge of the variation of more recent species of  
102 Heteroceratidae well described in the literature (Delanoy, 1997).

103  
104 One of the aims of this work is therefore to use the ‘laws’ of intraspecific variability as a  
105 predictive tool to try to reconstruct the image of the theoretical variation of the early  
106 Heteroceratidae. To minimize bias, error of interpretation or the risk of diacronism between  
107 the specimens collected, which are very few in number, particular attention was paid to the  
108 strict stratigraphic control of the raw data. Once the theoretical model of the variation has  
109 been obtained, it was then possible to propose phylogenetic reconstruction hypotheses using  
110 the cladistic tool and to study the evolutionary patterns and processes of the group.

111

## 112 **2. Geological setting**

113

114 The Vocontian Basin (Paquier, 1900 - Figure 1), in southeastern France, is a large subsident  
115 intracratonic area characterized by pelagic sedimentation deposited during the Mesozoic Era,  
116 between the Triassic (late Hercynian orogeny) and the Late Cretaceous (start of the Alpine  
117 orogeny). This basin was a diverticulum of the Alpine Ocean, at the extreme northwestern  
118 Tethys, bounded to the north, west and south by a series of platforms. The Barremian of the  
119 Vocontian Basin shows an almost regular alternation of marlstones and limestones in  
120 decimetric to metric beds under relative diagenetic stability in a context of climatic change at  
121 the stage level (Bodin et al., 2005), with some occasionally more pronounced variations,  
122 which could have sometimes impacted ammonite evolution (see Bert and Bersac, 2013 - such  
123 environmental stress could also probably induced the ‘turrilate event’ described below in  
124 chapter 9.3). Despite of this, the overall conditions could be considered relatively stable

125 without any major event on the studied period (the Faraoni level occurs in the top Hauterivian  
126 and the OAE1a starts later in the lower Aptian - Arthur et al., 1980; Cecca et al., 1994). In the  
127 southern part of the Basin, along the Provençal platform, the area of the Barremian stratotype  
128 (near the village of Angles, in the Alpes de Haute-Provence department) and the neighboring  
129 localities present numerous outcrops of usually good quality with continuous sedimentation  
130 and high-quality palaeontological records (Bert et al., 2008).

131  
132 All the field sections studied in the present work belong to the protected perimeter of the  
133 Geological National Nature Reserve of Haute-Provence that ensures the conservation of the  
134 exceptional geological heritage of this territory under French protective laws (see Bert et al.,  
135 2022). Many sections were surveyed and studied there, allowing to follow the succession of  
136 ammonite fauna with great precision. Some of these sections have provided representatives of  
137 the rare genus *Lazarinicerias* studied in the present work, in a detailed stratigraphic context.  
138 For the sake of conservation of the sites, their exact location is not specified here, with the  
139 notable exception of the Barremian stratotype. They are available on request from the authors.

140

## 141 **2.1. Section A\***

142

143 Section A\* (N.43.94125, E.6.543843) is complementary to the Barremian historical stratotype  
144 of the Angles road (section A) of which it is a part (west hill of the stratotype section). It has  
145 been already described and figured by Bert (2012, 2014a) and partially by Bert et al. (2018).  
146 Unlike the historic roadside section, in A\* the basis of the *Camereiceras limentinum* Zone  
147 (new, this work) is very well exposed with the *Camereiceras limentinum* Interval Horizon,  
148 easy to spot due to its particular lithology and the presence of its index species: it is made up  
149 of two thick and compact beds that are well identifiable in the topography (beds A\*/157-2 and

150 158); note the characteristic presence of cherts in the bed A\*/157-2. This bundle is  
151 immediately overcome by a more marly sedimentation episode (beds A\*/159–163-3). The bed  
152 A\*/162 represents the *Gerhardtia provincialis* Acmeic Interval Horizon with many  
153 representatives of the index species. For the present work, *Lazarinicerias heterostylia* sp. nov.  
154 was yielded in the bed A\*/160-2 with *Gerhardtia sartousiana* (d’Orbigny, 1841), which  
155 corresponds to the top of the *G. sartousiana* Acmeic Interval Horizon. Note the presence of  
156 *Lazarinicerias ebboi* (Delanoy, 2003) in the bed A\*/149-4 (*Toxancyloceras vandenheckei*  
157 Subzone).

158

## 159 **2.2. Section G33**

160

161 This section was described and figured by Delanoy (1994, 1997) under the name ‘Vergons 1  
162 (VER 1)’. Unfortunately, it was not possible to correlate all the beds recognized by this  
163 author, and a new survey with renumbering of the beds was necessary (here G33, Fig. 2). On  
164 the one hand, this allowed to establish a more complete succession towards the bottom of the  
165 series, and on the other hand to remove the invisibilities of the ‘VER 1’ log. Thus, the new  
166 G33 survey allows stratigraphic observations under the *Hemihoplites astarte* Interval Horizon  
167 (the chert bed labeled 100 in the both logs) and allows to recognize the *G. sartousiana*  
168 Acmeic Interval Horizon, the *G. provincialis* First Appearance Datum (FAD) Interval  
169 Horizon and the *G. provincialis* Acmeic Interval Horizon in the best conditions. This latter  
170 (bed G33/93) delivered a fragmentary specimen of *Lazarinicerias heterostylia* sp. nov. very  
171 comparable to the one harvested at G12.

172

## 173 **2.3. Section LAC**

174



175 The section, in the vicinity of the town of Saint-André-les-Alpes, was described and figured  
176 by Bert et al. (2008) and Bert (2014a). The *Camereiceras breistrofferi* Interval Horizon  
177 concerns the beds LAC/224-226, and maybe starts at bed LAC/121, which yielded a fragment  
178 of the index species. As for the section A\*, the *C. limentinum* Interval Horizon is very well  
179 individualized by its lithology (beds LAC/230–233) with cherts in bed LAC/230, and the  
180 abundant presence of its index species. For the present work, three specimens of  
181 *Lazarinicerias astierianum* (d'Orbigny, 1850) were collected respectively in beds LAC/221,  
182 230a and 232.

183

#### 184 **2.4. Section G5**

185

186 Mentioned by Delanoy (2003) because it yielded several specimens of *Toxancyloceras*  
187 Delanoy, 2003, this section was figured and formally described by Bert et al. (2018). Due to  
188 its proximity with the historical Angles road stratotype, the section G5 is very similar to A\*,  
189 but does not exceed the middle part of the *G. alpinum* Subzone. The bed G5/91 yielded  
190 several specimens of *Toxancyloceras bangilae* (Vermeulen, Damay and Lepinay, 2015),  
191 immediately in the stratigraphic continuity of *Toxancyloceras vandenheckei* (Astier, 1851)  
192 (beds G5/86–89). *T. canuti* (beds G5/84–85) and *Moutoniceras eigenheeri* (beds G5/78–82)  
193 are also well represented.

194

#### 195 **2.5. Section G12**

196

197 The section G12 was figured and described for the first time by Bert et al. (2013). It belongs  
198 to a series of outcrops located near sections G5 and G33. The lower upper Barremian is well  
199 exposed, especially the *T. vandenheckei* and *C. limentinum* (new, this work) zones. The bed

200 G12/310 [immediately above the bed G12/309 with *Gassendiceras alpinum* (d'Orbigny,  
201 1850)] delivered a specimen of *Lazarinicerias lhaumeti* sp. nov.; and the bed G12/331  
202 delivered a fragment of *Lazarinicerias heterostylia* sp. nov. with a poorly preserved specimen  
203 of *Gerhardtia* sp. Despite the fact that the *C. limentinum* Zone (new, this work) in this section  
204 is slightly reduced compared to the neighboring ones (G5 to the north and G33 to the south),  
205 the bed G12/331 could be assigned to the *G. provincialis* Acmeic Interval Horizon according  
206 to its lithology: it is situated at the top of the more marly sedimentation episode, which  
207 usually follows the *C. limentinum* Interval Horizon.

208

## 209 **2.6. Section LOU**

210

211 The section LOU has already been described and partially figured by Delanoy (1997). As for  
212 the 'VER 1' section, it was not possible to fully recognize the published succession on the  
213 field, in particular in its lower part, and a new survey was necessary (Fig. 3). It was thus  
214 possible to complete the log downward, to the beds immediately underlying the thick bundle  
215 of the *C. limentinum* Interval Horizon, which is here highly developed and forms a small cliff  
216 of difficult access (beds LOU/116–128). The chert bed is recognized in the lower part of the  
217 cliff (LOU/118). Above, the more marly sedimentary episode of the *G. sartousiana* Acmeic  
218 Interval Horizon is also perfectly recognizable. It should be noted that this section is the most  
219 dilated of the whole studied area for the interval between the *C. limentinum* and *H. astarte*  
220 interval horizons, comparable to the neighboring section of the Oratoire de la Gardette studied  
221 by Vermeulen (2002, fig. 17). For the present work, the bed LOU/137 delivered an almost  
222 complete specimen of *Lazarinicerias heterostylia* sp. nov.

223 Delanoy (1997) pointed out an interesting fact with the juxtaposition of the Aptian marlstones  
224 almost immediately above the *Hemihoplites feraudianus* Interval Horizon. This configuration

225 actually concerns only a much localized part of the site, probably resulting from erosion by an  
226 old erosive channel; at a very short distance (a few tens of meters to the north, beyond a syn-  
227 /post-depositional fault) the normal succession shows the entire limestone series up to the  
228 basal Aptian with *Deshayesites* Kasansky, 1914.

229

## 230 **2.7. Section CBL**

231

232 Located in the vicinity of Moriez, this section is mentioned here for the first time. It was  
233 surveyed in the Asse de Moriez area, at a short distance from the village. The section ranges  
234 from the *T. vandenheckei* to the *Imerites giraudi* zones, with a good development of the *C.*  
235 *limentinum* Zone (new, this work), which is partly showed in Figure 4. As for the previous  
236 sections described, the thick bundle corresponding to the *C. limentinum* Interval Horizon is  
237 perfectly recognizable with cherts at its base (CBL/168) and the perfectly clear presence of  
238 the index species. It is topped by the more marly sedimentary episode of the *G. sartousiana*  
239 Acmeic Interval Horizon. Two specimens of *L. astierianum* were collected respectively at the  
240 base (CBL/168) and at the top (CBL/170) of the *C. limentinum* Interval Horizon.

241

## 242 **2.8. Section TN1**

243

244 This section has never been described and is shown here for the first time (Fig. 5). Its  
245 lithology substantially differs from the other sections studied because of its position in the  
246 more proximal part of the Vocontian Basin at the bottom of the slope (distal hemipelagic  
247 domain). TN1 is located at the south of the Blieux syncline, in the Chiran-Mourre de Channier  
248 tectonic unit, which overlies the Chasteuil-Talloire unit to the south. This is one of the  
249 overlapping scales that forms the SW bend of the tectonic Arc de Castellane (Laurent et al.,

250 2000). This palaeogeographic position explains the particular dilation of the TN1 section  
251 compared to the other sites studied, more pelagic, as well as the presence of growth faults.  
252 The thickness of the limestone beds is constantly greater there, with certain deposit  
253 anomalies; some zone boundaries are currently not well characterized pending for more data.  
254 An interesting feature is the presence of 3 chert levels in the lower part. The intermediate one  
255 (TN1/163) is remarkable for its continuity and also because it yielded a rich ammonite fauna  
256 from the *C. limentinum* Interval Horizon, including a specimen of *L. astierianum*. The upper  
257 chert level (TN1/165) is included in a very irregular bed, which consists of poorly defined  
258 subsets that can reach a 2 m thickness with substantial lateral variations (slump). The basis of  
259 this 'bed' provided *G. sartousiana*, while it is immediately topped by the beds of the *H.*  
260 *feraudianus* Interval Horizon, here, highly developed (TN1/166–171 or 177?). It is possible  
261 that the missing horizons are present in the particular bed TN1/165 as slipped packets. The  
262 presence of cherts at this level could possibly be correlated to the classic chert bed of the *H.*  
263 *astarte* Interval Horizon usually visible in the more distal part of the Vocontian Basin.  
264 Finally, the sedimentary discontinuity, which usually closes the limestone formation in  
265 contact with the Aptian marls, is older here (TN1/200), dated of the basis of the *I. giraudi*  
266 Zone, whereas it is lower Aptian in the other more pelagic sections (Cotillon et al., 2000).

267

### 268 **3. Material and methods**

269

#### 270 **3.1. Material**

271

272 The present work focuses on the discovery of new material of the extremely rare early  
273 Heteroceratidae belonging to the genus *Lazariniceras*. The fossil material studied was bed-by-  
274 bed sampled in the sections described above, near the Barremian stratotype (the area between

275 Angles-Barrême-Castelane in the Alpes de Haute-Provence department, southeastern France).  
276 This material is curated by a public institution (RHP - see chapter 3.4 for the institutional  
277 acronyms).

278 Additionally, the type-specimen of *L. astierianum* (in the d'Orbigny's collection at the  
279 MNHN), from the Escragnolles section (Alpes Maritimes department, southeastern France),  
280 was also studied. Some specimens of *L. ebboi* were also examined for comparison: the type  
281 specimen figured by Delanoy (2003, pl. 4, fig. 1), the specimen figured by Bert (2017, pl. 2,  
282 fig. E) and the unpublished specimen DBT.04007-A\*/149-4.BI68 from the Barremian  
283 stratotype near Angles.

284

### 285 **3.2. Measurements**

286

287 The specimens are fragmentary most of the time, with sometimes different morphologies or  
288 part of the shell preserved (spiral part; straight shaft = proversum; bend of the hook = flexus;  
289 return of the hook = retroversum - Fig. 6), which prevents any biometrics and complicates  
290 comparisons with the measurements. The following indicative measurements were made:  
291  $L_p$ =length of the preserved proversum;  $D_{sp}$ =diameter of the preserved spiral part;  $H$ =whorl  
292 height at  $D_{sp}$  or  $L_p$ ;  $W$ =whorl width at  $D_{sp}$  or  $L_p$ ;  $U_{sp}$ =umbilicus diameter at  $D_{sp}$ ;  
293  $W/H$ =relative height; \* in the tables means that the corresponding measure is estimated.

294

### 295 **3.3. Method for the comprehension of the species limits and their variation**

296

297 The extreme rarity and the often very fragmentary state of the specimens of early  
298 Heteroceratidae in the *T. vandenheckei* and the lower part of the *C. limentinum* zones does not  
299 make it possible to apprehend their intraspecific variability in an objective or quantifiable

300 way, which, in case of significant variation, usually leads to typological biases (see Marchand  
301 and Dommergues, 2008). However, this variation is a constant among the ammonites, even if  
302 it is not always expressed with the same intensity or according to the same modalities.

303 It has already been shown that adult size and ornamentation can vary greatly in heteromorph  
304 ammonites, and especially in Ancyloceratidae and Heteroceratidae (Delanoy, 1997; Bersac  
305 and Bert, 2020). Several recent works have made it possible to theorize intraspecific  
306 variability in ammonites, including heteromorphs, and to identify a certain number of general  
307 constants, or ‘laws’ (Bert 2014a,b, 2019; De Baets et al., 2015; Bert et al., 2021), which  
308 would theoretically allow the possibility of anticipating variation to help for a better  
309 understanding of the species limits. With appropriate caution, it is thus possible to propose  
310 hypotheses concerning the variation in *Lazarinicerias* using a model based on a close taxon.

311 The model used here to identify the outline of possible variation in both *L. astierianum* and *L.*  
312 *heterostylia* sp. nov. is the *Heteroceras* model. This choice was made for the following  
313 reasons: (1) the two successive species *Heteroceras astierianum* d’Orbigny, 1851 (= *Heteroceras*  
314 *coulleti* Delanoy, 1994, see below the nomenclatural notes in chapter 7.1) and  
315 *Heteroceras tardieui* Kilian, 1888 [= *Heteroceras emericianum* (d’Orbigny, 1842) sensu  
316 Delanoy, 1997] have a general morphology and ornamentation of the shell extremely close to  
317 both *Lazarinicerias astierianum* and especially *L. heterostylia* sp. nov.; (2) their stratigraphic  
318 distribution immediately follows that of *Lazarinicerias*; (3) these last two points suggest an  
319 ancestor-descendant link between *Lazarinicerias* and *Heteroceras*, a hypothesis reinforced  
320 here by cladistic analysis (see below the Phyletic reconstruction and evolution in chapter 9);  
321 and (4) both *H. astierianum* and *H. tardieui* have the advantage of having well-known  
322 intraspecific variation since described in detail by Delanoy (1997) based on numerous  
323 specimens.

324

### 325 **3.4. Acronyms**

326

327 MNHN = National Museum of Natural history of Paris (France); RHP = Geological National  
328 Nature Reserve of Haute-Provence; ICZN = International Code of Zoological Nomenclature;  
329 FAD = First Appearance Datum; FO = First Occurrence.

330

### 331 **4. Biostratigraphy**

332

333 Apart the points about the newly proposed *C. limentinum* Zone detailed below, the  
334 biostratigraphic framework used here is the one proposed by the I.U.G.S Lower Cretaceous  
335 ammonite working group, the Kilian Group (Reboulet et al., 2018). With the need to increase  
336 precision for palaeontological and evolutionary purpose, we consider additionally the use of  
337 the interval horizons and the biostratigraphic proposals introduced by Bert et al. (2008), Bert  
338 and Delanoy (2009) and Bert et al. (2010, 2011 and 2018).

339

340 Bert et al. (2008) previously argued that the index species *G. sartousiana* mischaracterizes the  
341 basis of its eponymous zone. These authors however proposed to keep the *G. sartousiana*  
342 Zone with a downward shift of its lower limit to the FAD of *Camereiceras limentinum*  
343 (Thieuloy, 1979). Reboulet et al. (2018) did not follow this proposal to avoid confusion in the  
344 use of the *G. sartousiana* Zone with different definitions and they proposed to keep the FAD  
345 of *G. sartousiana* as the marker for the base of the Zone (first definition). Indeed, Vermeulen  
346 (2002, p. 46) had considered that *C. limentinum* appeared prior to *G. sartousiana* in the  
347 sections, and he proposed to consider the position of the *C. limentinum* Interval Horizon at the  
348 top of the *T. vandenheckei* Zone (= *Heinzia sayni* Zone). However, in their latest work dealing  
349 with upper Barremian biostratigraphy, Vermeulen et al. (2016) unambiguously extend the *G.*

350 *sartousiana* Zone to include the *C. limentinum* Interval Horizon but without using the  
351 definition proposed by Bert et al. (2008), which brings some confusion.

352 The fundamental problems with *G. sartousiana* are: (1) its parent species is not yet known  
353 (Vermeulen, 2002, p. 186 - see new elements below); and (2) its exact stratigraphic repartition  
354 is not known either. Actually, the *G. sartousiana* Zone in its current use is based on the FO,  
355 and not the FAD, of its index species. Vermeulen (2002, p. 47) moreover rightly specified that  
356 the appearance of *G. sartousiana* in the sections is very probably acmeic. Accordingly, he  
357 reported an affine specimen just above the chert bed in the Vergons area (section of the  
358 Oratoire de La Gardette, in the equivalent bed LOU/119 or 120, see Fig. 3), namely, in the *C.*  
359 *limentinum* Interval Horizon. *G. sartousiana* is in any case rare at the basis of its eponymous  
360 zone (in its current definition supported by Reboulet et al., 2018) and only becomes frequent  
361 very little before the appearance of its daughter-species *Gerhardtia provincialis* (d'Orbigny,  
362 1850).

363 Our own research shows that typical specimens of *G. sartousiana* are already present in the *C.*  
364 *limentinum* Interval Horizon, even rare. A robust specimen was even collected in the  
365 *Camereiceras marchandi* Interval Horizon at the top of the *T. vandenheckei* Zone; it shows a  
366 morphological trend close to *Heinzia sayni* Hyatt, 1903 (Fig. 7), which could be a reliable  
367 candidate as the potential parent species of *G. sartousiana*. Thus, the FAD of *G. sartousiana*  
368 is potentially located in a level not yet defined in the *G. alpinum* Subzone, which makes it  
369 unreasonable to be used as a biostratigraphic index species to define a more recent zone.

370 In order to avoid any confusion in the use of different definitions of the *G. sartousiana* Zone,  
371 we recommend here its abandonment in favor of a *C. limentinum* Zone of which the lower  
372 boundary is based on the *C. limentinum* Interval Horizon. The index species of the latter has  
373 the advantage of being perfectly defined within the evolutionary framework of the



374 Hemihoplitinae Spath, 1924 and easy to use in the field [parent species: *Camereiceras*  
375 *marchandi* (Bert and Delanoy, 2000)].

376

377 ***Camereiceras limentinum* Zone (new)**

378 **Definition of the lower boundary.** The *C. limentinum* Interval Horizon.

379 **Index species.** *Camereiceras limentinum* (Thieuloy, 1979).

380 **Reference section.** The stratotype of the Barremian near Angles (southeastern France,  
381 Vocontian Basin), more precisely the section A\* with the beds interval 156-16–167 of which  
382 the basis corresponds to the thick bundle including the chert bed recognizable in all the  
383 sections studied in the present work (the *C. limentinum* Interval Horizon). The top of the zone  
384 corresponds to the last thick bed with *Pseudoshasticrioceras autrani* Delanoy, 1998 just  
385 below the more marly sequence of the *Imerites giraudi* Zone (the *Imerites dichotomum*  
386 Interval Horizon).

387 **Status.** *C. limentinum* is part of an evolutionary continuum in relay of species of the genera  
388 *Camereiceras* Delanoy, 1990 and *Hemihoplites* Spath, 1924, most of which being already  
389 used as biostratigraphic index of interval horizons: *Camereiceras breistrofferi* (Sarkar, 1955),  
390 *C. marchandi*, *C. limentinum*, *Hemihoplites cornagoae* Bert, Delanoy and Bersac, 2006,  
391 *Hemihoplites astarte* Fallot and Termier, 1923, and *Hemihoplites feraudianus* (d'Orbigny,  
392 1841). In this continuum, *C. limentinum* is the first species with whorls clearly in contact, its  
393 ancestors being slightly uncoiled. The *C. limentinum* Zone has the same lower limit as the *G.*  
394 *sartousiana* Zone taken in the sense of Bert et al. (2008), i.e. the FAD of *C. limentinum*, but it  
395 is not the equivalent of the *G. sartousiana* Zone in the sense of Reboulet et al. (2018). In its  
396 current use in the Vocontian Basin (based on the FO of its index species), the lower limit of  
397 the *G. sartousiana* Zone in the sense of Reboulet et al. (2018) would be located near the basis  
398 of the more marly episode overlying the thick bundle of the *C. limentinum* Interval Horizon.

399 Actually, in the strict application of its definition based on the FAD of *G. sartousiana*, the  
400 lower limit of this zone remains currently undetermined in the *G. alpinum* Subzone. This  
401 difference in conception of the *G. sartousiana* Zone, and the difficulties in defining its lower  
402 limit with certainty are sources of inevitable confusion: the new *C. limentinum* Zone is  
403 therefore proposed at least for the Vocontian Basin where it is easy to use. *C. limentinum* is  
404 frequent and easy to determine, even by non-specialists.

405 *C. limentinum* has also some, though currently limited, potentials for long-distance  
406 correlations as its presence is attested in Spain (Company et al., 2004), southeastern France  
407 (Thieuloy, 1979; Delanoy, 1990a, 1997), Tyrol (Haug, 1889), very probably in Bulgaria  
408 (Toula, 1890, see below the nomenclatural note), and probably in Morocco (unpublished  
409 data).

410 **Subdivisions.** The subdivisions proposed by Bert et al. (2008) remain unchanged. The *C.*  
411 *limentinum* Zone is divided into three successive subzones: *C. limentinum*, *G. provincialis* and  
412 *H. feraudianus* subzones.

413 **Faunal assemblage.** See Delanoy (1997), Vermeulen (2002) and Bert et al. (2008).

414 **Nomenclatural note.** By its morphological characteristics, '*Crioceras*' *suessi* Toula, 1890 is  
415 very probably a senior synonym of *Camereiceras limentinum*. It is difficult to ensure that the  
416 conditions for reversal of priority are met (ICZN, Art. 23.9), since the palaeontologists who  
417 have worked on the *Camereiceras* in general are few. The taxon of Toula was only used once  
418 in the sense of Article 23.9.6 by Dimitrova (1967, pl. 32, fig. 3) to name an incomplete  
419 specimen. If the conditions of Art. 23.9.1 are not perfectly met, it is however important to  
420 point out that '*Crioceras*' *suessi* is based on a fragmentary type specimen, not precisely  
421 located, which could, by its characteristics, belong either to the species *Camereiceras*  
422 *limentinum* (the most probable), or possibly to *C. marchandi*. Under these conditions, we  
423 propose '*Crioceras*' *suessi* to be considered as a *nomen dubium* as it should not replace the

424 taxon of Thieuloy, which is on the contrary well defined, well located stratigraphically and  
 425 abundantly cited. This solution would clearly be in line with the nomenclatural stability  
 426 promoted by point 4 of the ICZN principles and Art. 23.2.

427

## 428 5. Construction of the theoretical model and results

429

### 430 5.1. Background on the laws of intraspecific variability in ammonites

431

432 In the generalization of the ‘laws’ of intraspecific variability in ammonites (Bert, 2019), there  
 433 are currently at least 8 potential factors of variation, within discontinuous and continuous  
 434 categories. These factors may or may not be expressed simultaneously and some can covary  
 435 between each other (see the example of morphological-dependent heterochronies in Bert,  
 436 2014b). They are summarized in the Table 1.

437

438 **Table 1.** The 8 recognized factors of the intraspecific variation ‘laws’ in ammonites.

Discontinuous variability	Continuous variability
<b>Sexual dimorphism</b> (differentiation in shell size, coiling, peristome aspect, ornamentation, or combinations)	<b>Multipolar variation</b> (relation between robustness of the ornamentation, thickness of the section, height of the whorl and opening of the umbilicus)
<b>Non-sexual polymorphism</b> (can concern a particular character such as supernumerary tubercle)	<b>Heterochronies</b> (variations in the rate of development, which means in ammonites the shifting of the ontogenetic stages)
<b>Fluctuating asymmetry</b> (linked to ecological stress)	<b>Coiling variation</b> (heteromorphy)
<b>Chirality</b> (dextrality/senestria)	<b>Secondary erasing of ornamentation</b> (linked with a probable role of the environment)

439

440 **5.2. Intraspecific variation in *Heteroceras* and construction of the theoretical model for**  
 441 ***Lazarinicer***

442

443 The data and the rich descriptions and figures provided by Delanoy (1997), and our own field  
 444 data, allow surrounding the intraspecific variation of the large sized *Heteroceras* taxa (*H.*  
 445 *astierianum* and *H. tardieui*). The presence of all the possible intermediates between the  
 446 extreme morphologies leaves no doubt as to their belonging to a single population (Delanoy,  
 447 1997, p. 44–51). According to these data, it seems at first glance that *H. astierianum* shows  
 448 less variation than *H. tardieui*, but the presence of specimens of very different sizes (including  
 449 the minimum whorl height expressed at the base of the proversum) with an ornamentation that  
 450 can be very variable in the assemblages (robust/slender - Fig. 8), shows that this could be a  
 451 sampling bias. The general ‘laws’ of intraspecific variability applied to the specific case of  
 452 *Heteroceras* is developed in Table 2. This is relevant even for fragmentary specimens (Fig. 8).  
 453 This is the model applied to the *Lazarinicer* in the present work, while considering that this  
 454 genus in no way shows evidence for a helical part (see below the descriptive palaeontology  
 455 section).

456

457 **Table 2.** The intraspecific variability ‘laws’ applied to *Heteroceras*.

Discontinuous variability	Continuous variability
<b>Sexual dimorphism:</b> not demonstrated	<b>Multipolar variation:</b> commonly present with an inverse correlation between ornamental robustness (robust with strong and spaced ribs <i>versus</i> slender with thin and close ribs) and whorl height; a positive link between robustness of the ornamentation and size of the helical part was demonstrated (Delanoy, 1997, p. 53)
<b>Non-sexual polymorphism:</b> very rarely, a tubercle	<b>Heterochronies:</b> present with the variable length of the

<p>could be present on the helical part (Vermeulen, 1996)</p>	<p>ontogenetic stage with strong/clavate ribbing on the proversum (from the half height to the 2/3 of the proversum, even rarely the whole proversum or its lowermost part only); looks to be correlated with the size of the helical part and consequently to the overall robustness of the ornamentation (Delanoy, 1997, p. 53 and figs. 26, 30, 31, 38): ‘robust’ specimens show preferentially a longer ontogenetic stage with strong/clavate ribs in the lower part of the proversum</p>
<p><b>Fluctuating asymmetry:</b> not reported, but probably present with the particular case of the turruculate early whorls; the sudden appearance of this coiling could potentially be an extreme case of hereditary fluctuating asymmetry (see chapter 9)</p>	<p><b>Coiling variation:</b> strong, in two ways (Delanoy, 1997): (1) full size variation, with a range factor of 1.7–2.5 (total known length range respectively of 330–800 mm in <i>H. astierianum</i> and 285–500 mm in <i>H. tardieui</i>); (2) in the case of specimens with a very long proversum, it can become particularly slender in its young part, thus, considering the minimum whorl height following the helical part, it is of factor 4 with a range of 15–59 mm for <i>H. tardieui</i> (a lower value of 12.3 is reached in <i>H. astierianum</i>); (3) coiling variation with the presence of a potentially large spiral part, or not (commonly inversely correlated with the size of the helical part)</p>
<p><b>Chirality:</b> only visible in the helical part of the shell in a not quantified proportion (potentially around 50% considering the data of Delanoy, 1997)</p>	<p><b>Secondary erasing of ornamentation:</b> possible on the flexus</p>

458

459 **6. Systematic palaeontology**

460

461 Class: Cephalopoda Cuvier, 1795

462 Subclass: Coleoidea Bather, 1888

463 Superorder: Ammonoida Haeckel, 1866

464 Order: Ammonitida Haeckel, 1866

465 Suborder: Ancyloceratina Wiedmann, 1966

466 Superfamily: Ancyloceratoidea Gill, 1871

467 Family: Heteroceratidae Spath, 1922

468 Genus *Lazarinicer* Vermeulen, Lepinay and Mascarelli, 2011

469 **Type species.** *Lazarinicer* *rouvieri* Vermeulen, Lepinay and Mascarelli, 2011, junior  
 470 synonym of *Ancyloceras astierianum* d'Orbigny, 1850. In application of the ICZN (Art.  
 471 67.1.2), the name of a type species remains unchanged even if it is a junior synonym or  
 472 homonym, or a suppressed name.

473 **Specific content.** *Lazarinicer* *astierianum* (d'Orbigny, 1850), *Lazarinicer* *ebboi*  
 474 (Delanoy, 2003), *Lazarinicer* *heterostylia* sp. nov. and *Lazarinicer* *lhaumeti* sp. nov.

475

476 *Lazarinicer* *astierianum* (d'Orbigny, 1850)

477 Figs. 9–11

478 **Synonymy.**

479 v 1850b *Ancyloceras astierianus* sp. nov.; d'Orbigny, p. 101, n°632.

480 1851 *Ancyloceras astierianus* d'Orbigny, 1850; Astier, p. 442.

481 1852 *Ancyloceras astierianum* d'Orbigny, 1850; Giebel, p. 317–318.

482 1861 *Ancyloceras astierianus* d'Orbigny, 1850; Pictet and Campiche, p. 47

483 1887 *Anisoceras* n. sp. ind.; Uhlig, pl. 5, fig. 9a-c, p. 90–91.

484 v 1937 *Ancyloceras astierianus* d'Orbigny, 1850; Cottreau, p. 28–29, pl. 78, figs. 18–  
 485 19.

486 1955 *Ancyloceras astierianus* d'Orbigny, 1850; Sarkar, p. 135.

487 2007 *Ancyloceras? astierianum* d'Orbigny, 1850; Klein et al., p. 133–135.

488 2011 *Lazarinicerias rouvieri* sp. nov.; Vermeulen et al., p. 98–100, figs. 1–2.

489

490 **Holotype.** Specimen MNHN.R00846 from the d'Orbigny's collection (formerly numbered  
491 5414 - Fig. 9A–D), which corresponds to several fragments belonging to a single specimen.

492 The specimen label indicates that it is a syntype, and the Museum's website  
493 (<http://coldb.mnhn.fr/catalognumber/mnhn/f/r00846>, last accessed April 08, 2022) specifies  
494 that the holotype designation by monotypy after 2000 by Klein et al. (2007, p. 133) is abusive  
495 and that the specimen “cannot be designated or fixed as a lectotype under arts. 74.5 and 74.6  
496 of ICZN. It therefore retains its status as a syntype” (transl.).

497 However, syntypes are specimens of a type series that collectively constitute the name-  
498 bearing type (ICZN, Art. 73.2). In the case of *L. astierianum*, there is no question of  
499 considering the different fragments as syntypes since they belong to a single and unique  
500 specimen that is easy to reassemble (Fig. 9A–D). On the other hand, even if d'Orbigny  
501 (1850b, p. 101) does not specify on how many specimens he introduced his species, it is  
502 possible to rely on the details provided by Astier (1851) and Cottreau (1937) in the  
503 application of ICZN articles 73.1.2 and 72.4.1.1 (taking into account evidence from outside  
504 the original work). Astier (1851, p. 442) indicated that d'Orbigny got the species from him  
505 and specified that another specimen was collected by Panescorse in the Clars Valley;  
506 however, there is no indication that d'Orbigny was aware of the Panescorse specimen, which  
507 could very well have been discovered after the introduction of the species in the Prodrôme.  
508 Cottreau actually mentioned only one specimen of this species, both in the d'Orbigny's  
509 collection and in its catalogue.

510 The confusion is probably due to the fact that d'Orbigny (1850b, p. 101) described the ‘hook’  
511 of the species, whereas it is absent from the only specimen in the collection, which could have

512 suggested the existence of other specimens. It is important to remind that the terminology of  
513 the different parts of the shell of ammonites in the 19th century does not correspond to the  
514 current terminology, including for the dorsal and ventral parts of the shell which are inverted  
515 (e.g. d'Orbigny, 1850a, p 277–278, 286). What d'Orbigny called 'hook' in his description  
516 actually corresponds to the proversum in current terminology (d'Orbigny, 1850a, p. 290–291),  
517 which is largely preserved on specimen MNHN.R00846. This point is confirmed by the  
518 description made by d'Orbigny himself, which agrees perfectly with this part of the shell of  
519 MNHN.R00846. The state of fossilization of the specimen ensures that the retroversum (in the  
520 current sense of this term) was not originally preserved and is not missing by accident, which  
521 was confirmed by Cottreau (1937, p 29). In our opinion, d'Orbigny only based his species on  
522 a single specimen, MNHN.R00846, which is therefore the holotype by monotypy in the  
523 application of article ICZN 73.1.2.

524 **Type locality.** Specified by Astier, who collected the holotype (1851, p. 442) in the Ravin St-  
525 Martin near Escagnolles; this section was described and figured by Vermeulen (1996).

526 **Type horizon.** Cottreau (1937) had already noticed that the matrix is a yellowish gray  
527 limestone dotted with glauconite grains, which, in the type locality, is characteristic of the  
528 Barremian deposits. Replacing *a posteriori* the specimen in the Ravin St Martin section is  
529 difficult. However, examination of the specimen, whose surface is an orange coating of  
530 alteration and whose matrix has irregular glauconitic areas, confirms its attribution to the  
531 upper part of the section, between beds 19–21 of the Vermeulen numbering (1996).

532 **Geographic distribution.** The species is currently known only in the south-east of France, on  
533 the southern margin of the Vocontian Basin and the adjoining drowned platform.

534 **Stratigraphic distribution.** From the precisely located and well dated specimens, whether on  
535 the drowned platform or in the Vocontian Basin, the species is currently known only in the  
536 *Camereiceras limentinum* Interval Horizon, at the base of the *C. limentinum* Zone (new).



537 **Emended diagnosis.** Tripartite-coiled species with whorl section higher than wide. Maximal  
 538 full size estimated to about 400 mm with a corresponding spiral part variable in size, around  
 539  $D=120\text{--}180$  mm; long proversum; unknown retroversum; large size variation (possibly from  
 540 simple to double). Ontogeny shows: (1) inner spiral (up to  $D=45\text{--}50$  mm) with the  
 541 Trituberculate Stage (main ribs alternately with smooth interribs); (2) outer spiral (up to  
 542  $D=100$  mm) with the Bituberculate Stage (umbilical and latero-ventral tubercles); (3)  
 543 Irregular monotuberculate Stage on the outermost part of the spiral and beginning of the  
 544 proversum, where tubercles become smooth; proversum with only latero-ventral  
 545 reinforcements on the ribs. Tubercles, when expressed, are always weak. Ornamentation  
 546 attenuated on the ventral part of the shell. Suture line with trifid lateral lobe.

547 **Material studied (N=7).** Six specimens are from the pelagic Vocontian Basin (DBT.04030-  
 548 TN1/163.BH04; DBT.04133-CBL/168b.BH05; DBT.04133-CBL/170.BH06; DBT.04173-  
 549 LAC/221.BI65; DBT.04173-LAC/232.BH07; DBT.04173-LAC/230a.BH08), and the  
 550 holotype (MNHN R00846) is from the drowned platform, in the Arc de Castellane. To these  
 551 specimens is added the No. AN008 very well described and figured by Vermeulen et al.  
 552 (2011) from the Comps-sur-Artuby area (Var; drowned platform).

553

554 **Table 3. Measurements of the specimens.** All measures are in mm. Due to the fragmentary  
 555 state of the specimens, the measures are given indicatively.

Specimens	Lp	Dsp	H	W	Usp	W/H
MNHN R00846	242.0	127.0	45.5	32.3	61.7	0.51
DBT.04030- TN1/163.BH04	-	165*	41.8	-	-	-
DBT.04133- CBL/168b.BH05	-	180*	41.5	33.0	-	0.80
DBT.04133-	160*	-	30.0	-	-	-

CBL/170.BH06	(two parts)					
DBT.04173-LAC/221.BI65	29.0	-	12.1	-	-	-
DBT.04173-LAC/232.BH07	220.0	-	52.3	33.0	-	0.64
DBT.04173-LAC/230a.BH08	100	-	15.8	8.3	-	0.53
AN008 (type of <i>L. rouvieri</i> taken from the original picture)	33	120	42.5	31.9	52	0.75

556

557 **Description and variation of the specimens.** All the known specimens of this species are  
558 fragmentary, but they allow getting a good idea of the shell morphology with the exception of  
559 the retroversum and the youngest whorls, which are unknown. Among the specimens in the  
560 literature, the type of the species (MNHN.R00846 - Fig. 9A–D) corresponds to a half whorl  
561 and most of the proversum, and the specimen figured by Vermeulen et al. (2011, figs. 1–2 -  
562 Fig. 10A–B) is the one with the youngest known part; it corresponds to a full whorl and to the  
563 start of the proversum. The new material includes two whorl fragments of quite large size  
564 with the departure of the proversum for the first (DBT.04133-CBL/168b.BH05 - Fig. 10C–F -  
565 and DBT.04030-TN1/163.BH04 - Fig. 9E–F), a large proversum almost complete  
566 (DBT.04173-LAC/232.BH07 - Fig. 10G–J), an intermediate-sized middle part proversum  
567 fragmented in two parts (DBT.04133-CBL/170.BH06 - Fig. 11A–B) and two smaller  
568 proversum fragment (lower part; DBT.04173-LAC/221.BI65 - Fig. 11C - and DBT.04173-  
569 LAC/230a.BH08 - Fig. 10K–L). The general morphology of the shell is tripartite, with a fairly  
570 developed spiral part that seem more or less disjointed depending on the specimens. The total  
571 length is estimated to a maximum of about 400 mm, with a corresponding spiral part variable

572 in size around  $D=120-180$  mm. Taking into account the theoretical model of variability  
573 proposed (this work), the adult size seems to vary by a factor of 1.5 if we consider the spiral  
574 part, or even much more around a factor of 3, if we consider the height of the whorl on the  
575 lower part of the proversum (particularly thin at 14.6 mm in DBT.04173-LAC/230a.BH08,  
576 and up to 45.5 mm in MNHN.R00846), which remains within the tolerance of the theoretical  
577 model (factor 4). There are currently 3 known successive ontogenetic stages during growth:

578 - (1) the Trituberculate Stage in the inner spiral (up to  $D=45-50$  mm in AN008) is a  
579 differentiated pattern ribbing with trituberculate main ribs alternately with smooth interribs  
580 (AN008). The tubercles are relatively small, located in the latero-dorsal, lateral and ventro-  
581 lateral zones, the latter being the best expressed. Some ribs are bituberculate only, lacking  
582 more and more frequently the lateral tubercle towards the next stage;

583 - (2) the Bituberculate Stage is expressed essentially over the largest known part of the  
584 spiral ( $D=100$  mm in AN008), but begins gradually with the disappearance of the lateral  
585 tubercle involved in the previous stage. This stage shows only umbilical and latero-ventral  
586 tubercles on main ribs, whereas the smooth interribs tend to adopt an increasingly similar  
587 morphology during this stage. The ventral area shows an increasingly attenuated  
588 ornamentation;

589 - (3) the Irregular monotuberculate Stage is developed on the outermost part of the  
590 spiral and most part of the proversum. The tubercles become smooth; the lateral tubercle has  
591 disappeared and the peri-umbilical tubercle also disappears rapidly at the beginning of this  
592 stage. The interribs are now similar to the main ones and the both become undistinguishable.  
593 On the proversum, the ribs show only latero-ventral reinforcements. On specimens with a low  
594 whorl height (DBT.04133-CBL/170.BH06, DBT.04173-LAC/221.BI65 and DBT.04173-  
595 LAC/230a.BH08), which are also those with the smallest spiral part (given by the curvature),  
596 the ribs tend to form the annular pattern known in earlier *Heteroceras*, with very uniform ribs

597 all around the shell, weakly clavate at the top of the flanks. On the contrary, on specimens  
598 with a higher whorl height (DBT.04173-LAC/232.BH07, MNHN.R00846), the interribs  
599 persist, including the proversum where they remain thinner than the main ribs while bearing  
600 the more often a slight peri-ventral bulge. In any case, the ornamentation is attenuated on the  
601 ventral area, until sometimes forming an almost smooth siphonal band (inner-cast).

602 The suture line is ancyloceratic with a deep trifid lateral lobe.

603 **Discussion.** When introducing *L. rouvieri*, Vermeulen et al. (2011, p. 100; Fig. 10A–B)  
604 considered that their taxon was not comparable to any other “*contemporary or sub-*  
605 *contemporary species*”. *Ancyloceras astierianum* was then not considered by these authors,  
606 probably due to the opinion of Sarkar (1955, p. 135) who considered the species *nomen*  
607 *dubium*, a proposal followed by Klein et al. (2007, p. 133). Examination of the d’Orbigny’s  
608 type leads to the conclusion that *L. rouvieri* share the same characters and is unambiguously a  
609 minor synonym of *Ancyloceras astierianum*, which is therefore placed in the genus  
610 *Lazarinicerias* of which *L. rouvieri* is the type species.

611 *L. heterostylia* sp. nov. and *L. lhaumeti* sp. nov. are described below where their affinities are  
612 discussed.

613 At first sight, *L. astierianum*, with the presence of trituberculate ribs only in the inner spiral  
614 part, seems quite different from *L. ebboi*, which has this characteristic on almost the entire  
615 spiral. However, the proversum in the both species is very similar in section and  
616 ornamentation. In particular, the modalities of the ornamentation erasure on the ventral area  
617 are the same, as well as the shape and orientation of the ribs, and the tuberculation consisting  
618 of simple flattened bulges on the peri-ventral margin. The only exception seems to be the  
619 absence of intercalary ribs on the type specimen of *L. ebboi*. However, this character is  
620 subject to variation for the both species; the specimen of *T. ebboi* figured by Bert (2017)  
621 shows a strong presence of this type of ribs at the beginning of the proversum, while in *L.*

622 *astierianum* specimens have frequent (MNHN.R00846), rarer (DBT .04173-LAC/232.BH07)  
623 or even absent intercalary ribs (DBT.04030-TN1/163.BH04; AN008). In the end, the essential  
624 difference between *L. astierianum* and *L. ebboi*, is the shift of the ornamental stages in  
625 ontogeny: they are earlier in *L. astierianum*, which leads in the latter to (1) the early  
626 disappearance of the ribs with reinforced tubercles, (2) the appearance at the end of the spiral  
627 part of the Irregular monotuberculate Stage, whereas it is later on the proversum in *L. ebboi*,  
628 (3) a more slender ornamentation on the end of the spiral part and (4) to the expression of an  
629 annular pattern of the ribs in robust specimens with low curvature. Finally, the extrapolated  
630 total adult size seems smaller in *L. astierianum* (400 mm *versus* 500 mm), but this feature is  
631 subject to substantial variation, which is difficult to estimate precisely on the basis of the  
632 fragmentary material studied and the literature.

633 The whole species belonging to the genus *Toxancyloceras* Delanoy, 2003 (including  
634 *Breskovskiceras* Vermeulen and Lazarin, 2007, considered here as its minor synonym) have  
635 trituberculate ribs on the entire proversum, with the exception of *T. bangilae* (Vermeulen et  
636 al., 2015), which has certain characteristics specific to *Lazariniceras* but only on a small  
637 portion in the middle of the proversum. *T. bangilae* is also larger as it can exceed 600 mm,  
638 making it the largest known species of *Toxancyloceras*.

639 *Moutoniceras eigenheeri* does not have the tuberculation of *L. astierianum* on the spiral part  
640 (trituberculate) and the proversum (monotuberculate). On the ventral area, the ribs show a  
641 marked inflection, but no tendency to erasure. Finally, the estimated total adult size of *M.*  
642 *eigenheeri* is larger (500–600 mm *versus* 400 mm), with a substantially wider and open spiral  
643 part.

644 Finally, there are certain affinities between *L. astierianum* and the oldest known *Jaubertites*  
645 Sarkar, 1955. These latter are probably present from the *C. limentinum* Interval Horizon  
646 (fragmentary specimen from TN1/163), while they are developing in the *G. sartousiana*

647 Acmeic Interval Horizon with (Fig. 12). These are awaiting revision but could be assigned to  
648 *Jaubertites badioticus* (Uhlig, 1887). In any case, the *Jaubertites* have a much faster growth  
649 in whorl height than *Lazarinicerias*, whether on the spiral or the proversum. Their  
650 ornamentation is less regular, with many smooth intercalary ribs (spiral part and proversum)  
651 and the development of a very strong tuberculation from the upper part of the proversum,  
652 which does not seem to be the case in any species of *Lazarinicerias* where this part of the shell  
653 is known. Finally, the tubercles in *Jaubertites* form the base of septate spines (as is also the  
654 case in *Toxancyloceras*), a feature for the moment unknown in *Lazarinicerias*, except for the  
655 very probable exception of the trituberculate stage with large tubercles on the young part of  
656 the spiral in *L. ebboi* (a '*Toxancyloceras*' feature).

657  
658 *Lazarinicerias heterostylia* sp. nov.

659 Figs. 13–14

660 **Derivation of the name.** Related to the ornamental style found in typical *Heteroceras*.

661 **Zoobank Record.** LSID

662 **Holotype.** Specimen DBT.04236-LOU2/137.BH09 collected and provided by one of us (LC;  
663 Fig. 13A–C).

664 **Type locality.** The section LOU, near Vergons (Alpes de Haute-Provence, southeastern  
665 France).

666 **Type horizon.** The bed LOU/137 of the type locality, at the very basis of the *G. provincialis*  
667 Subzone (*C. limentinum* Zone, new).

668 **Geographic distribution.** The species is currently known only in the south-east of France, on  
669 the southern margin of the Vocontian Basin.

670 **Stratigraphic distribution.** According to currently available data, the species has a restricted  
 671 distribution in the upper Barremian, at the basis of the *G. provincialis* Subzone (*G.*  
 672 *provincialis* FAD and acmeic interval horizons).

673 **Diagnosis.** Tripartite-coiled species with whorl section higher than wide. Maximum full size  
 674 estimated to be about 400 mm, the spiral part being unknown; long proversum; retroversum  
 675 tightened but wide; large size and ornamental variation. Three ornamental stages known: (1)  
 676 Annular ribbing Stage (at least on the first 1/3 of the proversum), the ribs being slightly  
 677 reinforced on the ventral part without any expressed tubercles; (2) *Heteroceras* style ribbing  
 678 Stage, with thin ribs slightly flexuous; (3) flexus and top part of the retroversum with slightly  
 679 differentiated ribs (Adult Stage), the main having elongated bulge reinforcements at their  
 680 lower part. Potentially high intraspecific variation, which correlates high whorl height with  
 681 thin ribbing and shorter Annular ribbing Stage, and conversely low whorl height with strong  
 682 ribbing and longer Annular ribbing Stage. Indented suture line with trifold, wide and deep  
 683 lateral lobe.

684 **Material studied (N=4).** The specimens are all from the southern pelagic Vocontian Basin  
 685 (southeastern France): DBT04236-LOU2/137.BH09, DBT.04007-A\*/160-2.BH10,  
 686 DBT.04236-G33/93b.BH11 and DBT.04007-G12b/331.BH12.

687

688 **Table 4. Measurements of the specimens.** All measures are in mm. Due to the fragmentary  
 689 state of the specimens, the measures are given indicatively. When present, the first  
 690 measurement corresponds to the top of the preserved part of the proversum, and the second  
 691 one to its basis.

Specimens	Lp	H	W	W/H
DBT04236-	374	69.50	49.70	0.72
LOU2/137.BH09		37.54	20.90	0.56

DBT.04007- A*/160-2.BH10	231.5	52.40	26.18	0.50
		31.32	17.62	0.56
DBT.04236- G33/93b.BH11	52.2	14.00	-	-
DBT.04007- G12b/331.BH12	26.2	-	-	-

692

693 **Description and variation of the specimens.** The 4 specimens are fragmentary, but the  
694 holotype (DBT.04236-LOU2/137.BH09 - Fig. 13A–C) is the best preserved with the  
695 complete proversum (its curvature at the base indicates the presence of a spiral part, which  
696 has not been preserved), the flexus and the very beginning of the retroversum. Specimen  
697 DBT.04007-A\*/160-2.BH10 (Fig. 14) is a large proversum portion. Finally, specimens  
698 DBT.04236-G33/93b.BH11 (Fig. 13D) and DBT.04007-G12b/331.BH12 are very partial  
699 proversum fragments (lower part). The spiral part is not known, but it is clear that the general  
700 morphology of the shell is tripartite; the total length is estimated to be a maximum of about  
701 400 mm. The first two specimens have a higher whorl height, which rises more quickly during  
702 growth than the other two latter. This character is correlated with finer (slender)  
703 ornamentation. It is not possible on the sole basis of the material studied to evaluate the  
704 variation in size, but taking into account the theoretical model of variability proposed (this  
705 work - factor of 1.7–2.5 for the total length and around a factor of 4 if we consider the height  
706 of the lower part of the proversum), the difference in size between the 2 smallest specimens  
707 and the 2 largest is not surprising (range of variation of the lower part of the proversum is  
708 here 2.2–2.7). There are at least 3 successive ontogenetic stages during growth:

709 - (1) the Annular ribbing Stage: the first part of the proversum shows ribs with a  
710 typical pattern. They are all the same, rigid, projecting slightly forward from the shell. Their  
711 strength is constant throughout their course, except at the top of the flanks and on the ventral



712 area where they are slightly reinforced (clavate) but without any tubercle. This stage seems  
713 very variable; on the both two specimens with a lower whorl height (DBT.04236-  
714 G33/93b.BH11 and DBT.04007-G12b/331.BH12) the ribs are systematically stronger and  
715 wider without interribs, with much curved interrib spaces (ornamentation more robust).  
716 Conversely, in specimens with a higher whorl height (DBT.04236-LOU2/137.BH09 and  
717 DBT.04007-A\*/160-2.BH10), the ribs are thinner without being closer together, which causes  
718 the interrib spaces to be less curved (more slender ornamentation), and the interribs are  
719 sometimes present;

720 - (2) the *Heteroceras* style ribbing Stage is only known from the two most complete  
721 specimens (those with higher whorl height); it is very close from the previous stage, but the  
722 ribs become thinner, sinuous and closer together. The peri-ventral reinforcements disappear.  
723 The ribs are much less prominent than in the previous stage with an interrib space that flattens  
724 considerably. The interribs are more frequent but less well individualized compared to the  
725 main ribs. The ornamentation is never attenuated on the venter;

726 - and (3), the flexus and the departure of the retroversum show an attenuation of the  
727 ornamentation with ribs that become less prominent than on the proversum, and which even  
728 tend to disappear on the median part of the flanks. Note the remarkable exception of two  
729 much reinforced ribs, the lower part of which has an elongated bulge. Bifurcations are  
730 frequent near the lower part of the flanks.

731 The suture line is ancyloceratic, indented, with trifold, wide and deep lateral lobe.

732 **Discussion.** *L. heterostylia* sp. nov. is particularly close to both *H. astierianum* and *H.*  
733 *tardieui*. The morphology and ornamentation of the shell (excluding the initial part) are  
734 almost identical, and seem to vary in the same way, with, in both cases, specimens with high  
735 whorl height and slender ornamentation (Annular ribbing Stage shorter - see e.g. Delanoy,  
736 1997, pl. 14, fig. 2) *versus* specimens with lower whorl height and more robust ornamentation

737 (longer Annular ribbing Stage - see e.g. Delanoy, 1997, pl. 11, fig. 1). However, nothing  
738 indicates the presence of a helical part in *L. heterostylia* sp. nov., while no turricone fragment  
739 has ever been reported below the *Hemihoplites feraudianus* Subzone in the literature or in our  
740 data. Apart from this, the only marked difference between *L. heterostylia* sp. nov. on the one  
741 hand, and *H. astierianum* and *H. tardieui* on the other hand, is the presence in the former of  
742 differentiated ribs with elongated bulges on the flexus. The Annular ribbing Stage is also  
743 much shorter in *H. tardieui* (base of the proversum, rarely longer).

744 The comparison of *L. heterostylia* sp. nov. with *L. astierianum* also shows a very close  
745 proximity in morphology and ornamentation, with however a number of differences: in *L.*  
746 *heterostylia* sp. nov., (1) tuberculation is totally absent on the proversum, (2) for the  
747 specimens with higher whorl height, the ribs are systematically finer, and (3) the  
748 ornamentation is never erased on the siphonal area.

749 *L. ebboi* is larger than *L. heterostylia* sp. nov. (500 mm versus 400 mm). The two species are  
750 also different in their ornamentation since *L. heterostylia* sp. nov. shows no tubercles except  
751 on the lower part of the main ribs on the flexus, and its ribs are never attenuated on the ventral  
752 area.

753 *L. heterostylia* sp. nov. is very different from all species belonging the genus *Toxancyloceras*,  
754 which have differentiated ribs with main trituberculate ribs on all (or most) of the proversum.  
755 The flexus, in some species (e.g. *T. canuti* - see Bert et al., 2018, appendix, fig. 16A), may  
756 show some similarities, in particular the weakening of the ornamentation on the ventral part  
757 and the presence (not systematic) of intercalated ribs.

758 *L. heterostylia* sp. nov. has a number of similarities with *Moutoniceras eigenheeri*: (1) the  
759 general morphology of the shell, with a rather slow growth in whorl height associated with  
760 clavate ribs morphologically close to the annular ribbing pattern, (2) the outline of the ribs, (3)  
761 the flexus with weaker ornamentation on the ventral area. However, the differences are

762 substantial with the presence of tubercles in *M. eigenheeri*, the fibula pattern on some ribs, the  
763 ventral attenuation of the ribs, their forward projection and the larger adult size of the shell  
764 (500–600 mm *versus* 400 mm).

765 Finally, *L. heterostylia* sp. nov. is contemporary with several species of *Jaubertites* with  
766 which it shares the tripartite morphology. However, in the latter, the tuberculation is  
767 systematic (sometimes very impressive), in particular on the top of the proversum and on the  
768 flexus. The ribs are differentiated there, and if the interribs are very similar to the ribs of *L.*  
769 *heterostylia* sp. nov., the strongly tuberculate main ribs are totally absent in the latter. Whorl  
770 height growth during ontogeny is also faster in *Jaubertites*, especially towards the end of the  
771 phragmocone in the upper part of the proversum (including in *J. badioticus* - Fig. 12).

772

773 *Lazarinicerias lhaumeti* sp. nov.

774 Fig. 15.

775 **Derivation of the name.** Species dedicated to the memory of Gilbert Lhaumet (1935-2022),  
776 who was specialized in the study of current and fossils Olivoideae Latreille, 1825.

777 **Zoobank Record.** LSID

778 **Holotype.** Specimen DBT.04007-G12b/310.AW51 (Fig. 15).

779 **Type locality.** The section G12, near Angles (Alpes de Haute-Provence, southeastern France).

780 **Type horizon and stratigraphic distribution.** The bed G12/310 of the type locality, just  
781 above the bed rich in *Gassendicerias alpinum* (=G12/309; *G. alpinum* Subzone, *T.*  
782 *vandenheckei* Zone).

783 **Geographic distribution.** The species is currently only known from its type locality.

784 **Diagnosis.** Tripartite heteromorph species (only the spiral part is known) with compressed  
785 section. Two ontogenetic stages are currently known: (1) inner spiral, up to D=63 mm, with  
786 the Trituberculate Stage (trituberculate main ribs regularly alternate with smooth interribs;

787 1–2 interribs per interval; wedge-shaped main ribs between the lateral and latero-ventral  
 788 tubercles); (2) outer spiral (up to D=109 mm) with the Bituberculate Stage (umbilical and  
 789 latero-ventral tubercles; 1–3 smooth interribs per interval; presence of the fibulate pattern and  
 790 some bifurcations); and (3) the Irregular monotuberculate Stage on the outermost part of the  
 791 spiral part. Tubercles are strong and well defined in stage 1, more differentiated in stage 2  
 792 with the peri-ventral tubercle stronger and flatter than the peri-umbilical tubercle, and smooth  
 793 on stage 3. On the ventral part of the shell: ribs enlarged but not erased on stages 1 and 2;  
 794 attenuated ornamentation in stage 3. Indented suture line with trifold, wide and deep lateral  
 795 lobe.

796 **Material studied (N=1).** The type specimen.

797

798 **Table 5. Measurements of the specimen.** All measures are in mm; h is the spiral hiatus; Nt  
 799 is the number of main ribs per half-whorl; Ni is the interrib number per half-whorl;  $\alpha$  is the  
 800 angle between each series of measurements.

Specimen	Dsp	H	W	Usp	h	Nt	Ni	W/H	$\alpha$
DBT.04007- G12b/310.AW51	111	39.06	21.50	47.64	6.62	19	20	0.55	
	63	20.86	8.72	29.20	2.24	18	18	0.42	200°

801

802 **Description of the specimen.** The holotype corresponds to a spiral of 111 mm in diameter.  
 803 The increasing uncoiling of the last preserved part suggests that the coiling opened up even  
 804 more and continued in a straight proversum, as is the case with tripartite species. The whorl  
 805 section is always substantially higher than wide. There are at least 3 successive ontogenetic  
 806 known stages during growth:

807 - (1) the Trituberculate Stage in the inner spiral, up to  $D=63$  mm, corresponds to a  
808 strongly differentiated rib pattern where trituberculate main ribs alternate regularly with 1–2  
809 smooth interribs per interval. The main ribs are well defined, straight and larger in their upper  
810 part between the lateral and latero-ventral tubercle, where they are wedge-shaped with an  
811 adoral projection. The interribs are thinner and they sometimes collide with the main ribs,  
812 which can result in a doubling of the latter. On the venter, the ribs are widened and smooth,  
813 but without erasure. On the dorsal part of the shell, the ribs are more numerous and thin. The  
814 peri-umbilical and lateral tubercles are conical and of equal vigor. The peri-ventral tubercles  
815 are wider and flattened in the coiling direction;

816 - (2) the Bituberculate Stage is restricted to the last half of the preserved whorl, up to  
817  $D=109$  mm. The ribs are less differentiated between them than on the previous stage, with the  
818 disappearance of the lateral tubercle, but they gain in flexibility. The peri-umbilical tubercle is  
819 reduced but remains well defined and conical. The peri-ventral tubercle is also reduced, but  
820 remains in proportion larger than the former; it retains the flattened appearance of the  
821 previous stage. The ribs widen up along the flanks and they lose their wedge-shaped  
822 appearance in the same time. The number of interribs is less regular than on the first stage,  
823 and two main ribs can follow each other, or on the contrary can be spaced out with 3 smooth  
824 interribs; in such a case, we observe a few peri-umbilical bifurcations, even a few fibulate ribs  
825 (i.e. separated in the lower part of the flank, but which meet at the peri-ventral tubercle);

826 - (3) the Irregular monotuberculate Stage is observed on the very end of the portion of  
827 the preserved spiral part. The ribs become uniform, widen, and, in parallel with the rapid  
828 disappearance of the peri-umbilical tubercle, they all bear a marked thickening in the latero-  
829 ventral area. Compared to the previous stages, the ornamentation tends to erase on the venter.  
830 The suture line is ancyloceratic, indented, with trifold, wide and deep lateral lobe.

831 **Discussion.** *L. lhaumeti* sp. nov. is particularly close to *L. ebboi*, with which it shares both the  
832 same ontogenetic stages and ornamentation. However, in *L. lhaumeti* sp. nov. the stages are  
833 always much earlier: the trituberculate stage (1) ends at D=63 mm *versus* D=135 mm in *L.*  
834 *ebboi* (i.e. almost the entire spiral part); likewise the bituberculate stage (2) measures D=109  
835 mm in *L. lhaumeti* sp. nov. *versus* D=160 mm in *L. ebboi*. Finally, the reinforced tubercle  
836 ornamentation present in the inner whorls of *L. ebboi* is absent in *L. lhaumeti* sp. nov.

837 *L. lhaumeti* sp. nov. is also very close to *L. astierianum*, with which it shares the first two  
838 ornamental stages on the spiral part. However, these stages are earlier in the latter: the  
839 Trituberculate Stage reaches D=63 mm in *L. lhaumeti* sp. nov. *versus* D=45–50 mm in *L.*  
840 *astierianum*; the same with the Bituberculate Stage respectively of D=109 mm and 100 mm.  
841 In *L. lhaumeti* sp. nov., the annular ornamentation does not seem to be present, and the  
842 ornamentation is erased only on the Irregular monotuberculate Stage at the end of the spiral  
843 part.

844 If the trituberculate stage of *L. lhaumeti* sp. nov. is very comparable to the homologous stages  
845 in the different species of *Toxancyloceras*, the latter do not present the bituberculate and  
846 monotuberculate stages.

847 Compared to the more recent genus *Jaubertites*, the tubercles are never so large and the whorl  
848 section is much more compressed in *L. lhaumeti* sp. nov.

849 Finally, *Moutoniceras eigenheeri* is never trituberculate and the marked inflection of the ribs  
850 on the ventral area is absent from *L. lhaumeti* sp. nov. whose spiral part is much tighter.

851

## 852 **7. Taxonomic remarks**

853

### 854 **7.1. Nomenclatural notes about some *Heteroceras-Martelites***

855

856 While modeling the intraspecific variation in *Lazarinicerias*, it is necessary to consolidate the  
857 systematics of the taxa used. The genera *Heteroceras* and *Martelites* Conte, 1989 were both  
858 revised in 1997 by Delanoy who shed new and remarkably comprehensive light on this whole  
859 group. On this occasion, a number of taxonomic opinions were formulated, which were  
860 largely taken up by Klein et al. (2007 - note 131, p. 174; note 132, p. 175; note 135, p. 178).  
861 Some of those have important consequences for the understanding of the Heteroceratidae and  
862 needed to be discussed.

863

## 864 **7.2. Rehabilitation of *Heteroceras astierianum* as a major synonym of *H. coulleti***

865

866 The implicit abandonment of *H. astierianum* was proposed by Delanoy (1997, p. 42–43)  
867 because of a ‘possible doubt’ about the identity of the type specimen MNHN.F.R00874 (ex.  
868 n°5441B of the d’Orbigny’s collection), which would be not, according to him, the one  
869 having served d’Orbigny as a reference for the original figuration. Delanoy indeed noted a  
870 discrepancy between the current size of the specimen kept in collection and that announced by  
871 d’Orbigny (1851; 200 mm *versus* 260 mm). Delanoy also pointed out a problem in the  
872 locality of origin between the handwritten label of the specimen (Angles) compared to the  
873 original description (Barrême). Finally, Delanoy listed certain differences between the  
874 original drawing and the specimen currently preserved in the d’Orbigny’s collection (helical  
875 part slightly disjointed although it is contiguous in the drawing; break in the end of the  
876 proversum looking different; curvature more pronounced near the terminal part in the  
877 drawing). Delanoy’s long demonstration and his insistence on the recent handwritten label,  
878 clearly suggest that, to his opinion, the original specimen, the trace of which would have  
879 disappeared, has been substituted by the one currently kept in the collection (“*form with a*

880 *delicate interpretation whose type does not seem to have been preserved*”, translated from p.  
881 43).

882 Based on this hypothetical disappearance and on the differences noted with the original  
883 drawing, Delanoy thus refused the type status to specimen MNHN.F.R00874 and implicitly  
884 proposed to consider *H. astierianum* as *specia dubia* (restriction of synonymy to the only  
885 original figuration, p. 42; obligation to “*remain cautious about the interpretation of this*  
886 *taxon*”, translated from p. 43). At the same time, Delanoy proposed in replacement the use of  
887 *H. couletti*, including for specimen MNHN.F.R00874 itself.

888

889 However, this opinion was not followed by all the authors, and Vermeulen proposed as early  
890 as 2005 (p. 162) the synonymy of *H. couletti* with *H. astierianum*. Some of the points raised  
891 by Delanoy deserve to be discussed:

892 - the original location of specimen MNHN.F.R00874 is provided on the website of the  
893 National Museum of Natural History  
894 (<https://science.mnhn.fr/institution/mnhn/collection/f/item/r00874>, consulted on October 24,  
895 2022), and it clearly specifies Barrême as well as the name of the collector: Astier. If there  
896 was a moment of confusion with Angles on the specimen label, it now appears to be  
897 corrected;

898 - the difference between the size announced by d’Orbigny, the shape of the terminal  
899 break and the difference in curvature precisely in this part, could be explained by the fact that  
900 in nearly 150 years this fragile specimen has suffered damage and is broken at several points.  
901 The various collages bear witness to this. Examination of the specimen also shows that the  
902 fossilization did not stop at the current break and one of the adhesive points concerns  
903 precisely this part;



904 - the difference in the helical part, with the whorls in contact on the drawing while it is  
905 slightly disjointed on the specimen, can also be easily explained. On the one hand, although  
906 looking complete on the drawing, the helical part is not complete on the specimen  
907 MNHN.F.R00874 as it has been broken and glued back at several points. On the other hand, a  
908 helical part as shown in the original figure, with the first whorl embracing the rest of the helix  
909 in the same plane with an almost perpendicular axis and very little growth in whorl height, is  
910 not a feature usually seen in *Heteroceras*. To our opinion, this shows that the drawer has over  
911 interpreted this part of the shell. We observe exactly the same over interpretation on the  
912 original figure of *Heteroceras bifurcatum* d'Orbigny, 1851 without being there any possible  
913 doubt about the identity between the specimen itself and its status of type (see Delanoy, 1997,  
914 pl. 39, figs 3–4). This divergence is not an isolated example in the d'Orbigny's work: the  
915 drawings are very often idealized, and in some cases rise to the category of synthetogram  
916 (Gauthier et al., 2006);

917 - here, the possibility that the original drawing represents a synthetogram (hypothesis  
918 considered by Delanoy, 1997, p. 43), whereas there is indeed a surprisingly similar specimen  
919 in the d'Orbigny's collection, does not hold. It goes hand in hand with the idea according to  
920 which there would have been substitution of the original specimen by an identical specimen  
921 which would 'pull out of the hat'. Such an extrapolation is not supported by any facts and is  
922 not credible;

923 - while introducing *H. couletti* (Delanoy, 1994, p. 298), the comparison with *H.*  
924 *astierianum* was omitted; this comparison would probably have highlighted the identity of the  
925 both forms. This is probably indirectly why there was a subsequent preference for *H. couletti*  
926 in the taxonomic choices of the authors, and the position of casting doubt on the interpretation  
927 of *H. astierianum* despite the fact that this species was rather well received by ancient authors  
928 (e.g. Roman, 1938; see Delanoy, 1997, p. 52).

929

930 In conclusion, it appears that the specimen MNHN.F.R00874 is perfectly interpretable and  
931 that there is no factual evidence implying that it would not be the one that was used for the  
932 original figuration of *H. astierianum* by d'Orbigny. To our opinion, this latter taxon is *de*  
933 *facto* a major synonym of *H. coulleti*. This is the position adopted in the rest of the present  
934 work.

935

### 936 **7.3. The status of *Heteroceras emericianum***

937

938 Delanoy (1997, p. 52, then again in Gauthier et al., 2006, p. 168), discussed at length the  
939 validity of *Heteroceras emericianum* and its status of type species for the genus *Heteroceras*  
940 by subsequent designation by Meek (1876). He proposed the specimen from the Sismonda's  
941 collection figured by d'Orbigny in 1851 (pl. 3, fig. 1) to be retained as a neotype, in place of  
942 the indeterminable fragments of the type-series, which come from a condensed level of the  
943 Escragnolles surroundings (SE France - d'Orbigny, 1842). For this, he proposed the  
944 application of article 75.5 of the ICZN under the plenary power of the International  
945 Commission on Zoological Nomenclature.

946

947 However, it turns out that this proposal is not, in our opinion, the most suitable for several  
948 reasons:

949 - since 1997, the Commission has, to our knowledge, never been seized to rule,  
950 without any problems in the meantime for the understanding of the genus *Heteroceras*;

951 - d'Orbigny introduced the species *Turrilites emericianus* in 1842 (in the  
952 Paléontologie Française) based on a series of fragmentary syntypes whose state is

953 unanimously recognized as uninterpretable by recent authors, which de facto making this  
954 taxon *specia dubia* (e.g. Delanoy, 1997, p. 52; Vermeulen et al., 2016, p. 21);

955 - the genus *Heteroceras* was introduced by d'Orbigny almost simultaneously in two  
956 different works. (1) The Cours élémentaire de paleontologie et de geologie stratigraphiques  
957 (1850a, vol. 1, p. 291), in which d'Orbigny described *Heteroceras* without naming the two  
958 species he claimed to recognize. Despite the absence of citation of nominal species, this  
959 nomenclatural act is valid (ICZN, Art. 67.2.2). And (2) the Prodrome de paléontologie  
960 stratigraphique universelle des animaux mollusques et rayonnés (1850b, vol. 2, p. 102), where  
961 d'Orbigny reported a single and unique species “\*653. *Emericianus d'Orb.* 1847. Turrilites  
962 *emerici d'Orb., 1842*”. This nomenclatural act is also valid and is the first subsequent citation  
963 mentioning at least one nominal species within the meaning of the ICZN (Art. 12.2.5). In the  
964 present case, the Prodrome refers only one nominal species, *H. emericianum*, which is  
965 therefore the type species by monotypy in application of the ICZN (Art. 68.3). Consequently,  
966 contrary to the opinion of the authors, the designation of Meek (1876) is not a nomenclatural  
967 act, but simply an opinion;

968 - the status *specia dubia* for *H. emericianum* poses no problem concerning the validity  
969 of the genus *Heteroceras*, since the name of the type species remains in this case available in  
970 application of the ICZN (Art. 67.1.2). More broadly, there is consensus of use for the  
971 definition of the genus *Heteroceras* and the Commission's request for the designation of a  
972 possible neotype apart from the syntypes for *H. emericianum* is therefore not necessary. On  
973 the other hand, the choice of the specimen from the Sismonda's collection would be  
974 problematic since it has disappeared (only one cast is known), and neither its locality of origin  
975 nor its exact age are known (Gauthier et al., 2006, p. 168).

976

977 *Heteroceras emericianum* being uninterpretable, the use of *H. tardieui*, the oldest taxon  
978 usually considered as its synonym by the authors (Delanoy, 1997, p. 51), should be  
979 encouraged. Its use has several advantages: (1) its type specimen, preserved in the collections  
980 of the University of Grenoble (France), comes from a well-known place and stratigraphic  
981 level (Morteiron, see Delanoy, 1997); (2) this specimen is a very characteristic complete  
982 adult; and (3) this specimen represents a median morphology within the range of intraspecific  
983 variation recognized in the species (Delanoy, 1997, p. 55).

984

#### 985 **7.4. Rehabilitation of *Heteroceras bifurcatum* as a *Martelites***

986

987 In the same way as for *H. astierianum*, Delanoy (1997, p. 43–44) proposed to no longer use  
988 the taxon *H. bifurcatum*, and even to consider it as a *nomen nudum*. However, as this taxon  
989 respects the criteria of articles 11 and 12 of the ICZN, the *nomen nudum* cannot therefore be  
990 applied to it. We can thus consider that Delanoy rather wished to propose the *nomen dubium*,  
991 which is a matter of taxonomic opinion. This opinion is supported by the aspect of the type  
992 specimen considered too incomplete (MNHN.F.R00875, formerly 5441C) and would leave  
993 too much to interpretation.

994

995 A reexamination of the type specimen of *H. bifurcatum* allows us to consider that it does not  
996 belong to the genus *Heteroceras*, but to the genus *Martelites*, and in this context this taxon is  
997 to our opinion actually perfectly interpretable. This position is confirmed by the rapid growth  
998 in whorl height of the shell and the particularly tight coiling, the curvature of which clearly  
999 suggests a contact between the whorls beyond the helical part. The popularization of  
1000 *Martelites sarasini* Rouchadze, 1933 since 1990, through its proposal as an upper Barremian

1001 zonal index (see Delanoy, 1990b; Hoedemaeker and Company, 1993; Delanoy, 1994),  
1002 certainly played a role in the ‘evacuation’ of *M. bifurcatus*.

1003 Just like Delanoy (1997, p. 129), then Baudouin et al. (2012, p. 644), we consider that the  
1004 species belonging to *Martelites* present a very large intraspecific variation, which can  
1005 concern, among other, the whorl height, the strength and the orientation of the ribs, their  
1006 erasure on the flanks, the number of bifurcations and coiling aspect related to the orientation  
1007 and size of the helical part. Within the sample studied by Baudouin et al. (2012), which they  
1008 attribute to *M. sarasini*, some of the specimen they figured (pl. 13, fig. 3, pl. 14, fig. 2, pl. 15,  
1009 fig. 1–2) are particularly demonstrative in this respect. It can thus be seen that the type  
1010 specimen of *Martelites bifurcatus* falls within the same range of variation (median variant) of  
1011 this sample, which is clearly visible on the morphological space modeled in Figure 16. For  
1012 comparison, the type specimen of *M. ellipticus*, which is usually considered as a distinct  
1013 species because of its particular elliptical whorls in the juvenile stage (see Delanoy, 1997, p.  
1014 149; Baudouin et al, 2012, p. 645), is clearly an outsider in this morphospace.

1015 Consequently, we consider that *M. bifurcatus* is indeed a valid taxon and that the specimens  
1016 usually identified in the literature under *M. sarasini* in southeastern France must be attached  
1017 to the former species due to the principle of priority. Synonymy between the two species  
1018 could also be considered.

1019

## 1020 **8. Discussion on the *Heteroceras* model for variation applied to *Lazarinicerias***

1021

1022 Discontinuous variability has not yet been demonstrated in *Lazarinicerias*. On the other hand,  
1023 on the basis of the results obtained, it appears that the variability of *Lazarinicerias* takes up  
1024 most of the continuous factors of the theoretical *Heteroceras* model, of which several seem to  
1025 be correlated with each other. The taking into account, by extrapolation, of this theoretical

1026 variation within the framework of the general ‘laws’ of intraspecific variability in ammonites,  
1027 leads to consider within the same species of *Lazarinicerias* specimens sometimes  
1028 morphologically distant from each other, or which would not be currently linked by  
1029 intermediaries due to high sampling bias (very rare and most often very incomplete  
1030 specimens). With all due caution, this is indeed the application of a predictive model. More  
1031 precisely, in the case of application for the two species *L. astierianum* and *L. heterostylia* sp.  
1032 nov.:

1033 - (1) the variation in size observed is substantial, especially if we consider the whorl  
1034 height at the base of the proversum, which serves as a proxy for incomplete specimens:  
1035 between 2.2 (in *L. heterostylia* sp. nov.) to 3 (in *L. astierianum*). This value is however lower  
1036 than that obtained in the *Heteroceras* model (factor 4), but this is possibly the result of a  
1037 sampling bias;

1038 - (2) the variation in the size of the spiral part can lead to the expression of large or  
1039 reduced coiling (based on the curvature of the shell when the spiral is incompletely known). It  
1040 is uncertain whether this factor can be correlated with the variation known in *Heteroceras*  
1041 between specimens with small turricones and large spiral and vice versa. This is, on the one  
1042 hand, due to the lack of evidence of any helical part in *Lazarinicerias*, and on the other hand  
1043 because the adult size is also a factor likely to influence the size of the spiral part in  
1044 heteromorph ammonites (see Bersac and Bert, 2020, 2022);

1045 - (3) the multipolar variation seems here organized around two poles and correlates  
1046 ornamentation and whorl height: high whorl height and slender ornamentation *versus* lower  
1047 whorl height and more robust ornamentation;

1048 - (4) the heterochronic variation is quite marked with the shift of the ontogenetic  
1049 stages with annular/wedge shaped ribs, depending on the specimens.

1050

1051 It seems that at least the factors of points 3 and 4 are correlated with each other, since we  
1052 observe specimens with a high whorl height and a rather slender and peramorphic  
1053 ornamentation *versus* specimens with a lower whorl height and more robust and neotenic  
1054 ornamentation.

1055 The ‘laws’ of intraspecific variability impose a number of constraints on the morphology of  
1056 ammonite shells. The possibility of using them predictively is a powerful tool provided that a  
1057 group sufficiently close (morphologically and phyletically) to the one to be tested, and whose  
1058 variation is well known, can serve as a comparative theoretical model. In this case, we start  
1059 from the postulate that in a given phyletic lineage and under relatively stable environmental  
1060 conditions (taking into account the possibility of a certain tolerance), the general ‘laws’ are  
1061 preferentially oriented in the same direction, failing to present the same range of variation  
1062 (e.g. Reeside and Cobban, 1960; Kennedy and Coban, 1976). The application to the  
1063 *Lazariniceras*, with the confrontation between the *Heteroceras* theoretical model and the data  
1064 of descriptive palaeontology, seems to agree with this proposal.

1065

## 1066 **9. Phyletic reconstruction and evolution**

1067

### 1068 **9.1. Cladistic analysis**

1069

#### 1070 **9.1.1. Method**

1071

1072 A cladistic analysis was performed in order to test the morphological relationships between  
1073 Ancyloceratidae and Heteroceratidae, and to better understand the systematic position of  
1074 *Lazariniceras* (the method used was described in detail previously by Bert and Bersac, 2013,

1075 2014). In a second step, the results of the analysis are crossed with the stratigraphic data, in  
1076 order to propose a robust and reproducible phyletic reconstruction.

1077

### 1078 **9.1.2. Taxa and characters analyzed**

1079

1080 We built a taxon-character matrix (Table 6) with 14 taxa and 12 characters. For the analysis,  
1081 we retained the 5 known species of the genus *Toxancyloceras* (including its minor synonym  
1082 *Breskowskiceras*) and the 4 species of *Lazarinicerias*. We also added the most ancient species,  
1083 in the current state of knowledge, belonging to the genus *Jaubertites* (= *J. badioticus*), which  
1084 is very probably at the origination of the other more recent Ancyloceratidae str. s.  
1085 (*Audouliceras* Thomel, 1965, *Ancyloceras* d'Orbigny, 1842...). Additionally, we considered  
1086 the 2 best known and oldest species belonging to the genus *Heteroceras*: *H. astierianum* and  
1087 *H. tardieui*. Finally, we added one species of the genus *Martelites* (= *M. bifurcatus*), which is  
1088 considered as the direct descendant of *Heteroceras* (Delanoy, 1997). We choose two outgroup  
1089 taxa to resolve polarization of the cladogram: *Moutoniceras eigenheeri* and *Toxancyloceras*  
1090 *canuti*. The former is known to be at the origination of the genus *Toxancyloceras*, and the  
1091 latter to be the older representative of this genus in a well known evolutionary context (Bert et  
1092 al., 2018). As such, they are deemed to have more 'primitive' states of the characters  
1093 compared to the ingroup.

1094

1095 For the characters, we have taken into account the morpho-dimensional parameters of the  
1096 shell (characters 0–1 and 8), and the ornamentation linked to ontogeny (2–7 and 9–11). When  
1097 the state of a character is unknown it has been coded by '?'. Some characters were subject to  
1098 variation; they were coded with their different states. As only 5 data are concerned with such  
1099 polymorphic states, we considered that the potential homoplasy they would introduce (soft





<i>Toxancyloceras bailense</i>	0	2	1	1	0	0	0	0	0	0	0	0
<i>Toxancyloceras bangilae</i>	0	0	1	1	0	1	0	0	0	0	0	0
<i>Toxancyloceras canuti</i>	0	1	1	1	0	0	0	0	0	1	1	1
<i>Toxancyloceras vandenheckei</i>	0	2	1	1	0	0	0	0	0	0	0	0

1117

1118

1119 **9.1.3. Results**

1120

1121 The analysis was performed with the TNT software, version 1.5 for Windows (Goloboff and  
 1122 Catalano, 2016) using the implicit enumeration method (exact solution) that allows finding for  
 1123 sure the most parsimonious trees (Darlu et al., 2019). One tree of 22 steps (Fig. 17) was  
 1124 found, which reveals very few homoplasy (all reversions) supported by only 4 characters (1,  
 1125 2, 5 and 6 - Consistency Index=0.909; Retention Index=0.941; Adjusted Homoplasy=0.5).  
 1126 Some nodes (16, 24, 26) received a high bootstrap value (80–95 - 1000 replications) and  
 1127 average Bremer support values (2–3), which increase the confidence in their robustness and  
 1128 some aspects of the tree topology.

1129

1130 The tree shows two major clades. The first one is well supported by node 16 (bootstrap value  
 1131 of 80 and Bremer of 2) with the synapomorphies carried by characters 1 (large size), 2 (the  
 1132 Trituberculate Stage with large tubercles on the spiral part), 10 and 11 (respectively the aspect  
 1133 of the flexus and the retroversum with strong tubercles). This clade groups, in a pectinate  
 1134 structure, the whole *Toxancyloceras* species and *Jaubertites badioticus* with the respective  
 1135 appearance up passing the tree of *T. vandenheckei*, *T. bangilae*, *Toxancyloceras bailense*  
 1136 (Vermeulen, 1996), *Toxancyloceras anglesensis* (Vermeulen and Lazarin, 2007) and  
 1137 *Jaubertites badioticus*.

1138 The second clade is moderately supported by node 23 (bootstrap value of 67 and Bremer of 1)

1139 and mainly by the synapomorphy carried by character 3 (loss of the Irregular trituberculate

1140 Stage on the proversum). This clade is itself separated into two clades: the first one grouping  
1141 the *Lazarinicerias* species except *L. heterostylia* sp. nov. (mainly supported by the  
1142 synapomorphies carried by character 2 with the Trituberculate Stage on the spiral part with  
1143 small tubercles, and character 5 with the Irregular monotuberculate Stage on the whole  
1144 proversum). The second one (supported by the synapomorphies carried by character 6 with  
1145 the appearance of the Annular ribbing Stage and character 7 with the *Heteroceras* style  
1146 ribbing Stage) groups as sister taxa both *L. heterostylia* sp. nov. and a clade formed by the  
1147 *Heteroceras* and *Martelites* species (synapomorphies are: the loss of the Trituberculate Stage  
1148 on the spiral part - character 2 -, the early helical coiling - character 8 -, and the Adult Stage  
1149 without any tubercles - characters 10–11). The both a latter clades are the most robust of the  
1150 tree (node 24, bootstrap 84 and Bremer of 3; node 26, bootstrap value of 95 and Bremer of 2).

1151

#### 1152 **9.1.4. Tree time calibration and discussion**

1153

1154 From the tree obtained by the cladistic analysis, a calibration over time by cross-checking the  
1155 stratigraphic data is necessary in order to determine the minimum age of the taxa, to highlight  
1156 the hypothetical ancestors and to highlight the minimum implied gaps (MIGs, in other words  
1157 the ghost phyletic lineages - Wills, 1999). The tree calibrated over time is given in Figure 18.

1158

1159 The analysis of the cladogram and the tree calibrated over time calls for several remarks:

- 1160 - (1) the two main clades mark very clearly the delimitation between strict  
1161 Ancyloceratidae and Heteroceratidae. The position of this demarcation unambiguously  
1162 includes the placement of *Lazarinicerias* within the Heteroceratidae;
- 1163 - (2) at least 4 MIGs are highlighted (dot lines in Fig. 18). They concern the branching  
1164 of the *Martelites* and the *Lazarinicerias*;

- 1165 - (3) associated with the previous point, the weakness of nodes 17 and 18 leaves open  
1166 the possibility of different branching for the *Lazarinicerias* (see below the Phyletic  
1167 reconstruction in chapter 6.2);
- 1168 - (4) *L. heterostylia* sp. nov. is grouped with the clade formed by  
1169 *Heteroceras/Martelites*, with a high confidence (bootstrap of 84 and Bremer of 3 on  
1170 node 24), despite the fact that the descriptive palaeontology allowed to class this taxon  
1171 in the *Lazarinicerias* genus. Future data on the juvenile part of the shell, currently  
1172 unknown in *L. heterostylia* sp. nov., could bring new lights. For example the presence  
1173 of a helical early coiling will result in the reclassification of this species within the  
1174 *Heteroceras*; conversely if such coiling is absent (see discussion in the descriptive  
1175 palaeontology chapter) while the Trituberculate Stage is present, the assignation of  
1176 this species to *Lazarinicerias* would be reinforced.

1177

## 1178 9.2. Phyletic reconstruction

1179

1180 The MIGs were removed in order to respect the order of stratigraphic appearance of the taxa  
1181 observed from the data, by making the most direct connections possible from the result  
1182 obtained by the cladistic analysis. In particular, concerning the *Martelites*, palaeontological  
1183 data (Delanoy, 1997) suggest a phyletic proximity with *Heteroceras tardieui*. On the other  
1184 hand, the confrontation with palaeontological, developmental and stratigraphic data (this  
1185 work) suggests a close phyletic connection between *T. bangilae* and *L. ebboi*. By its  
1186 morphological characters and its ontogenetic sequence, it appears that *L. ebboi* could be at the  
1187 origin of the phyletic lineage formed by the *Lazarinicerias* while the *Toxancyloceras* continue  
1188 their evolution towards the *Jaubertites*. This does not question the placement of *Lazarinicerias*  
1189 among the Heteroceratidae, but would *de facto* imply the paraphylia of the Ancyloceratidae.

1190 However, this last point should be qualified, since even with a different Heteroceratidae  
1191 branching, the Ancyloceratidae (which include the *Moutoniceras* - see Bert et al., 2018) are  
1192 already paraphyletic anyway, which is a frequent case in palaeontology (Hörandl and Stüssy,  
1193 2010).

1194 The new topology obtained is presented in Figure 19, it is the one used for the study of  
1195 evolutionary patterns and processes.

1196

### 1197 **9.3. Evolutionary patterns and processes**

1198

1199 A number of ornamental patterns are remarkably similar between the different species of  
1200 *Lazarinicerias*, and more broadly when compared with *Toxancyloceras* or *Heteroceras*. These  
1201 stages are considered to be homologous and make it possible, by crossing with the  
1202 stratigraphic data, to consider the evolutionary patterns between the species considered over  
1203 time (Figure 20). In all, eight ontogenetic stages can potentially be expressed (see descriptive  
1204 palaeontology chapters for an extensive description):

- 1205 - the Trituberculate Stage on the spiral part;
- 1206 - the Bituberculate Stage on the spiral part or the beginning of the proversum;
- 1207 - the Irregular trituberculate Stage on the proversum;
- 1208 - the Irregular monotuberculate Stage on the proversum;
- 1209 - the Annular ribbing Stage;
- 1210 - the *Heteroceras* style ribbing Stage;
- 1211 - the helical coiling in early part of the shell;
- 1212 - the Adult stage with strong ribs (flexus and retroversum): this stage is considered as an  
1213 'adult variation' (see Delsol, 1977), and it can vary between species with the more or  
1214 less marked presence, or absence, of tuberculation. An interesting character is the

1215 absence of tubercles on the ventral and peri-ventral part of the flexus in *Lazarinicer*  
1216 and *Toxancyloceras*, unlike the Hemihoplitidae (tripartite *Gassendicer* Bert,  
1217 Delanoy and Bersac, 2006) or other Ancyloceratidae (*Jaubertites*, *Ancyloceras*,  
1218 *Pseudocrioceras* Spath, 1924, *Kutatissites* Kakabadze, 1970, etc.).

1219  
1220 According to the above phyletic reconstruction, the following successive species are here  
1221 considered into an evolutionary context: *Toxancyloceras vandenheckei* -> *Toxancyloceras*  
1222 *bangilae* -> *Lazarinicer* *ebboi* -> *Lazarinicer* *lhaumeti* sp. nov. -> *Lazarinicer*  
1223 *astierianum* -> *Lazarinicer* *heterostylia* sp. nov. -> *Heteroceras astierianum*. The evolution  
1224 of older species from *Moutoniceras nodosum* (d'Orbigny, 1850) to *Toxancyloceras*  
1225 *vandenheckei* (including both *M. eigenheeri* and *T. canuti*) has already been the subject of  
1226 previous work (Bert et al., 2018).

1227  
1228 From the size reduction initiated in *Moutoniceras*, and which is maximal in *T. vandenheckei*  
1229 (425 mm; Bert et al., 2018), we observe a rebound in this parameter with a very clear increase  
1230 in *T. bangilae*, which can exceed 600 mm in total height (pers. obs. and Vermeulen et al.,  
1231 2015). In the more recent species, the data are few and to be taken with caution in view of the  
1232 substantial possible variation, but the size seems to decrease again in *L. ebboi* (500 mm), then  
1233 probably also in the rest of the lineage (estimates of 400 mm for *L. astierianum* and *L.*  
1234 *heterostylia* sp. nov.), before stabilizing with a very wide range of variation in *H. astierianum*  
1235 (330–800 mm) and *H. tardieui* (285–500; Delanoy, 1997) at the same time the helical coiling  
1236 appears.

1237 Concerning ontogeny, we note that between *T. vandenheckei* and *T. bangilae*, the increase in  
1238 size is accompanied by an increase in the duration of the ontogenetic stages up to a form of  
1239 gigantism. The only marked difference in the stages themselves is, in the middle of the

1240 proversum of *T. bangilae*, a tendency to the disappearance of the trituberculate pattern with  
1241 the new Irregular monotuberculate Stage very briefly expressed.

1242 The transition to *L. ebboi* occurs according to two main parameters: size and trituberculate  
1243 reduction. The trituberculate reduction occurs, on the one hand, by the extension to almost the  
1244 entire proversum of the Irregular monotuberculate Stage, adjoining the Bituberculate Stage at  
1245 the very end of the spiral part and the beginning of the proversum; this stage acts like a buffer  
1246 between the very distinct trituberculate pattern of the spiral and the weakly tuberculate stage  
1247 of the proversum. And on the other hand, by the heterochronic acceleration of ontogenesis  
1248 with the reduction of the Trituberculate Stage on the spiral part, which previously occupied  
1249 the entire spiral part. Also note the attenuation of the tubercles on the retroversum.

1250 This evolutionary channeling initiated with *L. ebboi* continues very clearly with *L. lhaumeti*  
1251 sp. nov. and *L. astierianum*, which show a smaller estimated size, an ever shorter  
1252 Trituberculate Stage on the spiral in the young whorl, and an ever earlier appearance of the  
1253 Bituberculate Stage and Irregular monotuberculate Stage. In *L. astierianum*, there is even an  
1254 innovation in the modification of the design of the ribs, in the lower part of the proversum, to  
1255 give the Annular ribbing Stage present only in morphologies with lower whorl height.

1256 We can consider that the latter morphologies must have been advantageously selected by  
1257 conditions that were favorable to them, since the well-marked Annular ribbing Stage is more  
1258 expressed in *L. heterostylia* sp. nov., and more so in *H. astierianum*. In parallel, any form of  
1259 tuberculation disappears, the last known expressed tubercles being on the lower part of the  
1260 flexus in the form of stretched bulges in *L. heterostylia* sp. nov. The disappearance of the  
1261 tubercles in *Heteroceras* is then almost total (only extremely rare specimens show relict of  
1262 tubercles, see Vermeulen, 1996; Delanoy, 1997, p. 37-38, pl. 40, fig. 3). Finally, the young  
1263 whorls of the shell are modified in *H. astierianum*, with the appearance of a helical part,  
1264 which forms the major innovation of the genus *Heteroceras*.

1265 In the current state of knowledge, it is interesting to note that this helical part seems to appear  
1266 more or less at the same time around the limit between the *C. limentinum* (new) and *I. giraudi*  
1267 interval zones in several different groups (somehow, a ‘turruculate event’ in Hemihoplitidae  
1268 and Heteroceratidae at least, where the lost of symmetry could be interpreted as an extreme  
1269 case of fluctuating asymmetry induced by environmental stress - Figure 19). The boundary  
1270 between these two zones represents a substantial change in lithology and probably to some  
1271 extent in local environmental conditions (Arnaud, 2005; Bodin et al., 2005, 2009; Bert et al.,  
1272 2008, 2009).

1273  
1274 To summarize (Figure 20), the evolution of the early Heteroceratidae is done from the  
1275 *Toxancyloceras* and is expressed by (1) changes in adult size (reduction from *T. bangilae*,  
1276 which is a giant *Toxancyloceras*); (2) a peramorphic process with heterochronic modifications  
1277 resulting in the regression, then the disappearance, of tuberculate patterns (heterochronic  
1278 acceleration of the different ontogenetic stages); in parallel with (3) innovations, which result  
1279 in a simplification of the ornamentation; finally associated with (4) the appearance of a helical  
1280 part in the young whorls of the shell. The oscillation with the disappearance then the  
1281 reappearance of tubercles already highlighted in *Moutoniceras* and *Toxancyloceras* (Bert et  
1282 al., 2018), seems to continue in *Lazarinicerias* until their definitive disappearance in  
1283 *Heteroceras*.

1284

## 1285 **10. Concluding remarks**

1286

1287 The generalized ‘laws’ of intraspecific variability in ammonites used as a predictive model  
1288 appear to be a powerful tool if we start from the postulate that in a given phyletic lineage, and  
1289 under relatively stable environmental conditions (in order to limit aspects related to extrinsic



1290 factors in the reasoning, but taking into account the possibility of a certain tolerance), the  
1291 variation is preferentially oriented in the same direction. Such a model can be used to define  
1292 the limits of a given species with insufficient data (here the *Lazarinicerases*), if at least one  
1293 species of the same phylogenetic group, with a similar occupation of the morphological space,  
1294 is well known with the extent of its variation (here the *Heteroceras*). The example of the early  
1295 Heteroceratidae developed in this work seems to agree with this proposal. Used in this way,  
1296 these ‘laws’ could make it possible to remove part of the sampling bias, with all due caution,  
1297 this being the result of the application of a theoretical predictive model.

1298  
1299 To remove all possible ambiguities due to stratigraphic imprecision, we propose the  
1300 replacement of the *G. sartousiana* Zone by the *C. limentinum* Zone (new). Moreover, the  
1301 taxonomic discussion led us to discuss and finally to reject the use of *Heteroceras couletti*  
1302 (minor synonym), *H. emerici* (*specia dubia*) and *Martelites sarasini* (misidentification or  
1303 probable minor synonym) for the benefit of the rehabilitation respectively of *H. astierianum*,  
1304 *H. tardieui* and *M. bifurcatus*. Additionally, *Lazarinicerases astierianum* is revised, *L.*  
1305 *heterostylia* sp. nov. and *L. lhaumeti* sp. nov. are introduced.

1306  
1307 The proposed methodology allowed the construction of the *Heteroceras* theoretical model of  
1308 variation through the prism of the 8 known factors of the ‘laws’ of intraspecific variability in  
1309 ammonites. This model was then confronted and extended to the *Lazarinicerases*. The  
1310 discussion of the results shows that the variability observed in the *Lazarinicerases* species takes  
1311 up most of the continuous factors of the theoretical *Heteroceras* model.

1312  
1313 The results obtained thanks to this theoretical model then contributed to define the states of  
1314 characters in the matrix used for the cladistic analysis. This analysis, crossed with the

1315 stratigraphic data, made it possible to test the relationships between Ancyloceratidae and  
1316 Heteroceratidae and to propose a phylogenetic reconstruction, which allows a better  
1317 understanding of the systematic position of the *Lazarinicerases*. *Lazarinicerases* is  
1318 unambiguously a Heteroceratidae despite the absence of the early helical coiling (in the  
1319 current state of knowledge). The results also show that the Ancyloceratidae is a paraphyletic  
1320 taxon, which is not a surprise since this family continues to exist after the appearance of  
1321 Heteroceratidae. In this respect, it seems that the first species of *Lazarinicerases* (*L. ebboi*)  
1322 originated within the genus *Toxancyloceras*. According to the available palaeontological data,  
1323 it is possible to consider a close phyletic connection between *T. bangilae* and *L. ebboi*.

1324 The evolution of the early Heteroceratidae from *Toxancyloceras* is expressed by: (1) changes  
1325 in adult size (reduction from *T. bangilae*, which is a giant *Toxancyloceras*); (2) a peramorphic  
1326 process with heterochronic modifications resulting in the regression, then the disappearance,  
1327 of tuberculate patterns (heterochronic acceleration of the different ontogenetic stages); in  
1328 parallel with (3) innovations, which result in a simplification of the ornamentation; finally  
1329 associated with (4) the appearance of a helical part in the young whorls of the shell. The  
1330 oscillation with the disappearance then the reappearance of tubercles already highlighted in  
1331 *Moutoniceras* and *Toxancyloceras* (Bert et al., 2018), seems to continue in *Lazarinicerases* until  
1332 their definitive disappearance in *Heteroceras*.

1333  
1334 The question of the relative importance of intrinsic and extrinsic factors in the expression and  
1335 direction of intraspecific variation is posed. It would be interesting in the future to check  
1336 whether the use of the generalized ‘laws’ of intraspecific variability as a predictive model also  
1337 works in cases where extrinsic effects (environmental changes for example) are less stable  
1338 and have a greater influence due to the natural selection and epigenetic expression (in the  
1339 sense of Danchin, 2022) they impose on organisms. In a certain way, it is perhaps finally

1340 some of that between *Heteroceras* and *Lazarinicerias*, since the morphological change which  
1341 justifies the distinction between these two genera (young helical coiling) occurs  
1342 concomitantly with a change of lithology and a renewal faunal associations. The appearance  
1343 of the helical morphology in the young is materialized independently more or less at the same  
1344 time also in other phylogenetically unrelated groups (Hemihoplitidae).

1345

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1352

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1356

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1750

### 1751 **Captions of the figures**

1752 **Figure 1.** A. Palaeogeography of the Western Tethys Realm for the Barremian times  
1753 (modified after Bert and Bersac, 2014); B. Palaeogeographic map of the Vocontian Basin for

1754 the Barremian (southeastern France, modified after Arnaud, 2005). The stars point out the  
 1755 sections mentioned in the text: TN1 (near Blieux); CBL (near Moriez); LAC (near Saint-  
 1756 André-les-Alpes); A\* and G (including G5, G12 and G33 near Angles and Vergons); LOU  
 1757 (near Vergons); ESC (Ravin Saint-Martin, near Escragnoles).

1758

1759 **Figure 2.** Alternation of limestones and marlstones of the section G33 (pars) near Vergons  
 1760 with the position of the *Lazarinicer*s and some characteristic ammonites. The chert bed of  
 1761 the *Hemihoplites astarte* Interval Horizon is G33/100; layers in black are dark laminites. Gsa  
 1762 = *Gerhardtia sartousiana* Acmeic Interval Horizon; GP = *Gerhardtia provincialis* FAD  
 1763 Interval Horizon; GPa = *G. provincialis* Acmeic Interval Horizon; HA = *Hemihoplites astarte*  
 1764 Interval Horizon; HF = *Hemihoplites feraudianus* Interval Horizon; PB =  
 1765 *Pseudoshastrioceras bersaci* Interval Horizon; PM = *Pseudoshastrioceras magnini*  
 1766 Interval Horizon; PA = *Pseudoshastrioceras autrani* Interval Horizon.

1767

1768 **Figure 3.** Log of the section LOU near Vergons with the position of the *Lazarinicer*s and  
 1769 some characteristic ammonites. Same legend as in Fig. 2; CM = *Camereiceras marchandi*  
 1770 Interval Horizon; CL = *C. limentinum* Interval Horizon.

1771

1772 **Figure 4.** Log of the section CBL near Moriez with the position of the *Lazarinicer*s and  
 1773 some characteristic ammonites. Same legend as in Fig. 2.

1774

1775 **Figure 5.** Log of the section TN1 near Blieux with the position of the *Lazarinicer*s and some  
 1776 characteristic ammonites. Same legend as in Fig. 2; ID = *Imerites dichotomus* Interval Horizon.

1777

1778 **Figure 6.** The measurements made on the specimens studied, fragmentary most of the time.

1779 1=retroversum; 2=proversum; 3=spiral part; Lp=length of the preserved proversum;

1780 Dsp=diameter of the preserved spiral part; H=whorl height at Dsp or Lp; Usp=umbilicus

1781 diameter at Dsp;

1782

1783 **Figure 7.** *Gerhardtia sartousiana* (d'Orbigny, 1841), robust specimen DBT.04007-A\*/156-

1784 15.BC72 from the Angles area, in the *Camereiceras marchandi* Interval Horizon, top of the

1785 *Toxancyloceras vandenheckei* Zone.

1786

1787 **Figure 8.** Exemplification of variation in fragmentary specimens of *Heteroceras astierianum*

1788 d'Orbigny, 1851. A–B: specimen with high height proversum DBT.04236-G28/202.BI66; C–

1789 D: specimen with slender proversum DBT.04236-G33/112.BI67, both from the Vergons area,

1790 *Pseudoshastrioceras autrani* Interval Horizon.

1791

1792 **Figure 09.** *Lazarinicerias astierianum* (d'Orbigny, 1850); A–D: the type specimen

1793 MNHN.R00846 from the Escragnoles area with the whole fragments in connection (D is the

1794 ventral view of the spiral part); E–F: specimen DBT.04030-TN1/163.BH04 from the Blieux

1795 area (*C. limentinum* Interval Horizon).

1796

1797 **Figure 10.** *Lazarinicerias astierianum* (d'Orbigny, 1850); A–B: the original figuration (form

1798 Vermeulen et al., 2011) of the type specimen of *L. rouvieri* AN008 from the Comps-sur-

1799 Artuby area (SE France); C–F: specimen DBT.04133-CBL/168b.BH05 from the Moriez area

1800 (*C. limentinum* Interval Horizon); G–J: specimen DBT.04173-LAC/232.BH07; K–L:

1801 specimen DBT.04173-LAC/230a.BH08 with thin whorl height. G–J and K–L are from the *C.*

1802 *limentinum* Interval Horizon of the St André-les-Alpes area.

1803

1804 **Figure 11.** *Lazarinicerias astierianum* (d'Orbigny, 1850); A–B: specimen DBT.04133-  
1805 CBL/170.BH06 with medium whorl height, fossilized in two parts, from the Moriez area (*C.*  
1806 *limentinum* Interval Horizon); C: specimen DBT.04173-LAC/221.BI65 with thin whorl height  
1807 of the St André-les-Alpes area (*C. breistrofferi* Interval Horizon).

1808

1809 **Figure 12.** *Jaubertites badioticus* (Uhlig, 1887), specimen LCT.04236-LOU/133.LD-1 from  
1810 the Vergons area, *Gerhardtia sartousiana* Acmeic Interval Horizon.

1811

1812 **Figure 13.** *Lazarinicerias heterostylia* sp. nov.; A–C: the holotype DBT.04236-  
1813 LOU2/137.BH09, *Gerhardtia provincialis* FAD Interval Horizon; D: specimen DBT.04236-  
1814 G33/93b.BH11 with thin whorl height, *Gerhardtia provincialis* acmeic Interval Horizon. Both  
1815 are from the Vergons area.

1816

1817 **Figure 14.** *Lazarinicerias heterostylia* sp. nov., specimen DBT.04007-A\*/160-2.BH10 from  
1818 the Angles area, *Gerhardtia provincialis* FAD Interval Horizon.

1819

1820 **Figure 15.** *Lazarinicerias lhaumeti* sp. nov., type specimen DBT.04007-G12b/310.AW51  
1821 from the Vergons area, just above the *Gassendicerias alpinum* Interval Horizon.

1822

1823 **Figure 16.** Modeling of the morphological space of *Martelites bifurcatus* based on log-  
1824 transformed data from Baudouin et al., 2012 (= *M. sarasini*). The methodology used was  
1825 described in detail in Bersac & Bert (2012). Type specimens of different species have been  
1826 added; here, only the type specimen of *M. ellipticus* departs significantly from the sample.

1827

1828 **Figure 17.** The cladogram resulting from the cladistic analysis.

1829

1830 **Figure 18.** The tree calibrated over time. The dot lines are MIGs. Same nodes as in Fig. 16.

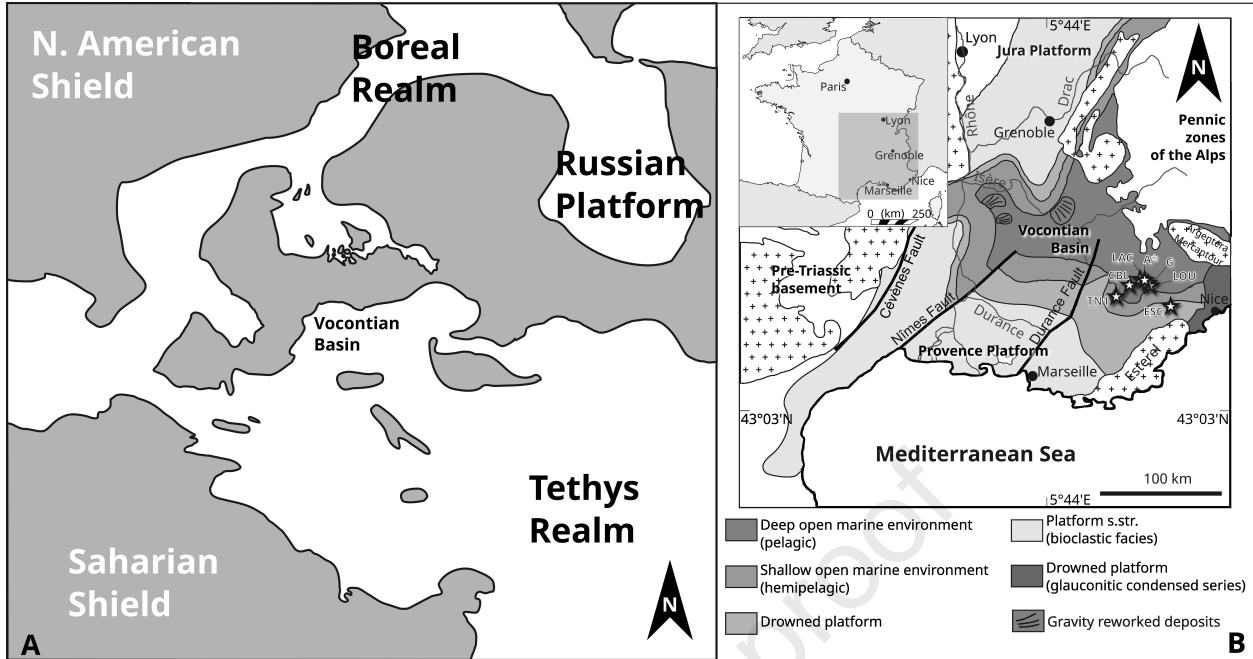
1831 See text for explanations.

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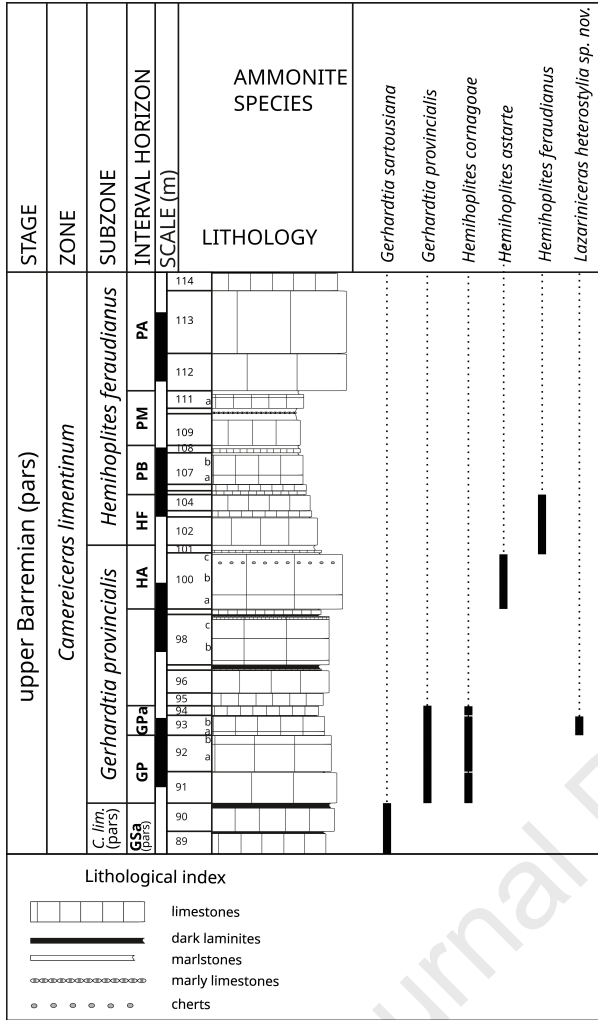
1833 **Figure 19.** Phyletic reconstruction proposed for the early Heteroceratidae from the  
1834 Ancyloceratidae. The gray area points out the onset level almost at the same time of the  
1835 turriculate morphology in the Heteroceratidae and Hemihoplitidae ('turriculate event').

1836

1837 **Figure 20.** Ontogeny and heterochronies within the  
1838 *Toxancyloceras/Lazarinicerias/Heteroceras* lineage. See text for explanations. Note that  
1839 compared to Bert et al. (2018), the cartouches have been corrected to take into account the  
1840 presence of the peri-dorsal and lateral tubercles in the flexus in *T. canuti* and *T. vandenheckei*.



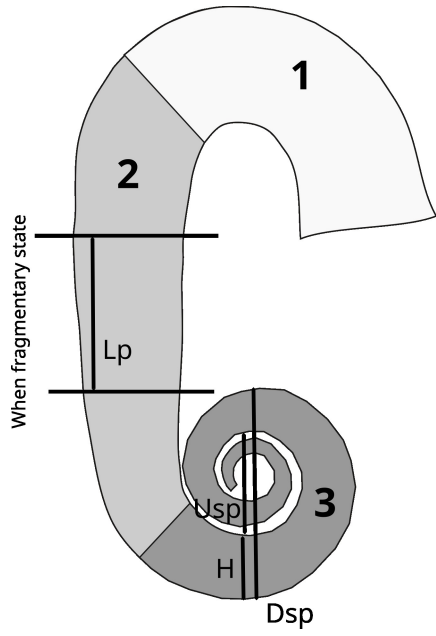




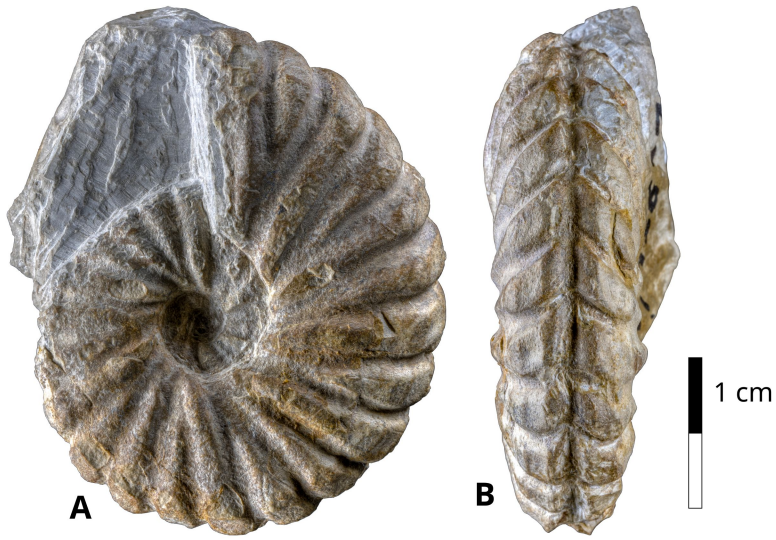


upper Barremian (pars)	STAGE
<i>Camereiceras limentinum</i>	ZONE
<i>Camereiceras limentinum</i>	SUBZONE
CL	INTERVAL HORIZON
Gsa	SCALE (m)
Gp	LITHOLOGY
GPa	AMMONITE SPECIES
HA	
168 a	
169 b	
170	
173	
174	
175	
178	
180	
181	
182	
183	
	<p><i>Gerhardtia sartousiana</i></p> <p><i>Gerhardtia provincialis</i></p> <p><i>Camereiceras limentinum</i></p> <p><i>Hemihoplites cornagoae</i></p> <p><i>Hemihoplites astarte</i></p> <p><i>Lazarineras astierianum</i></p>

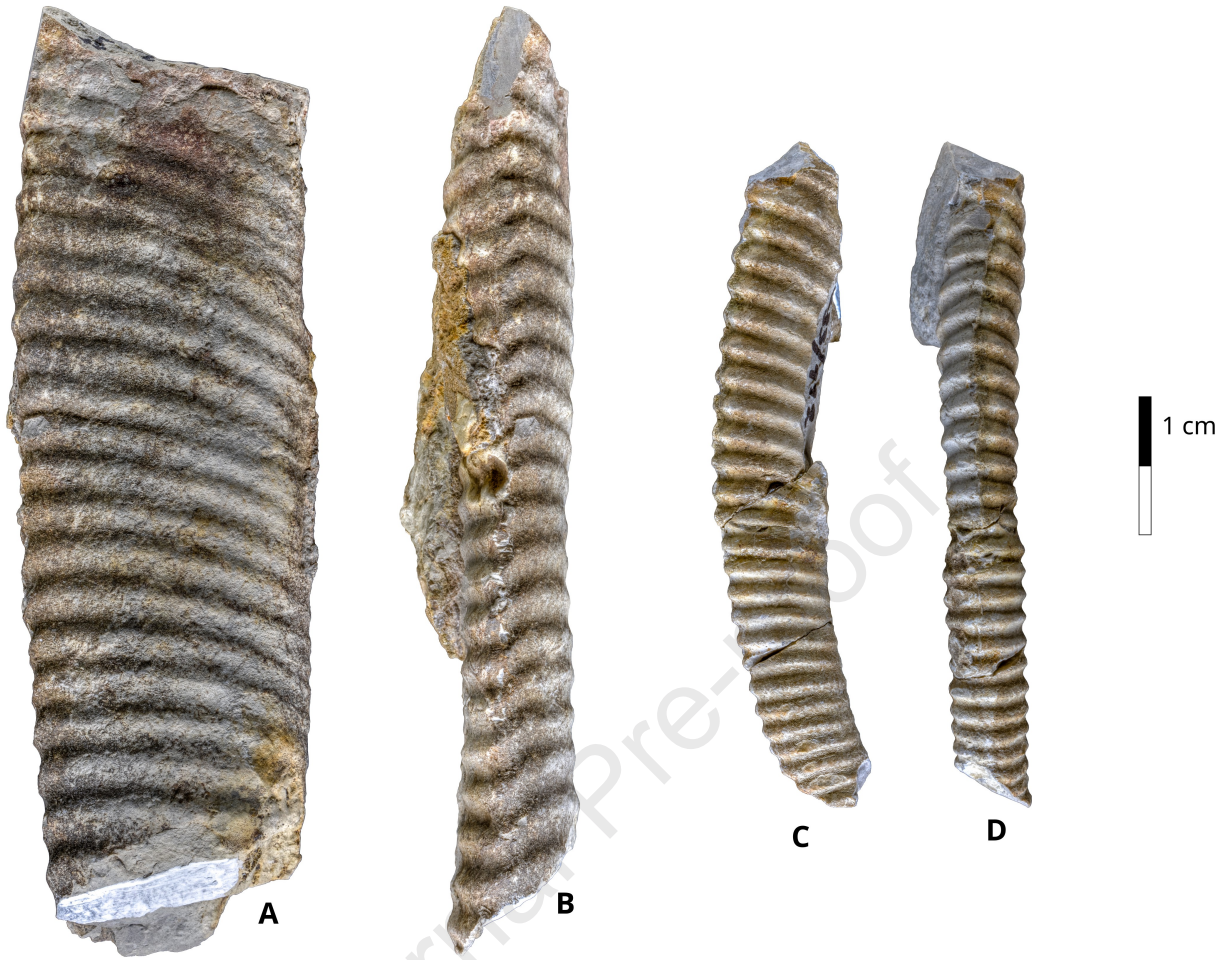




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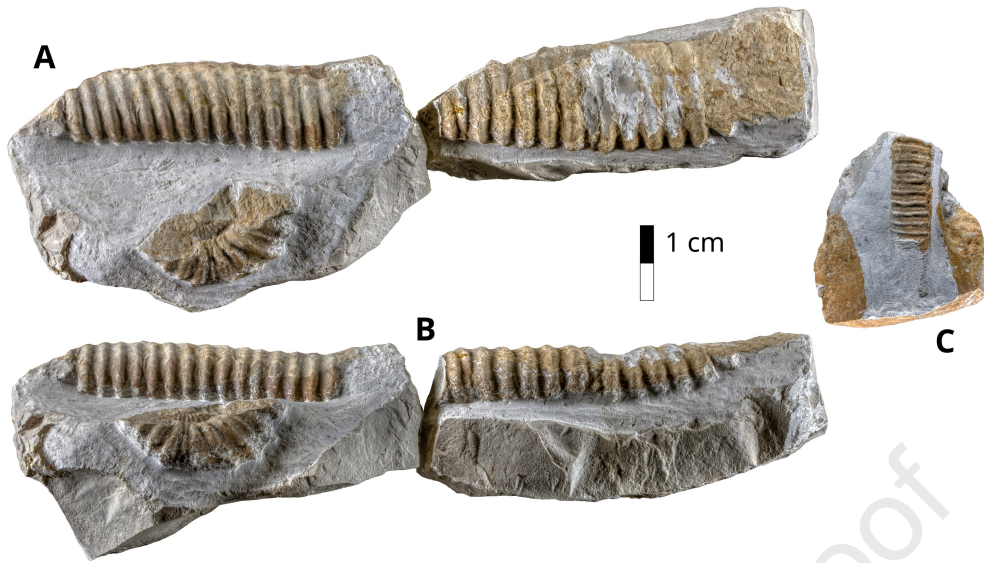












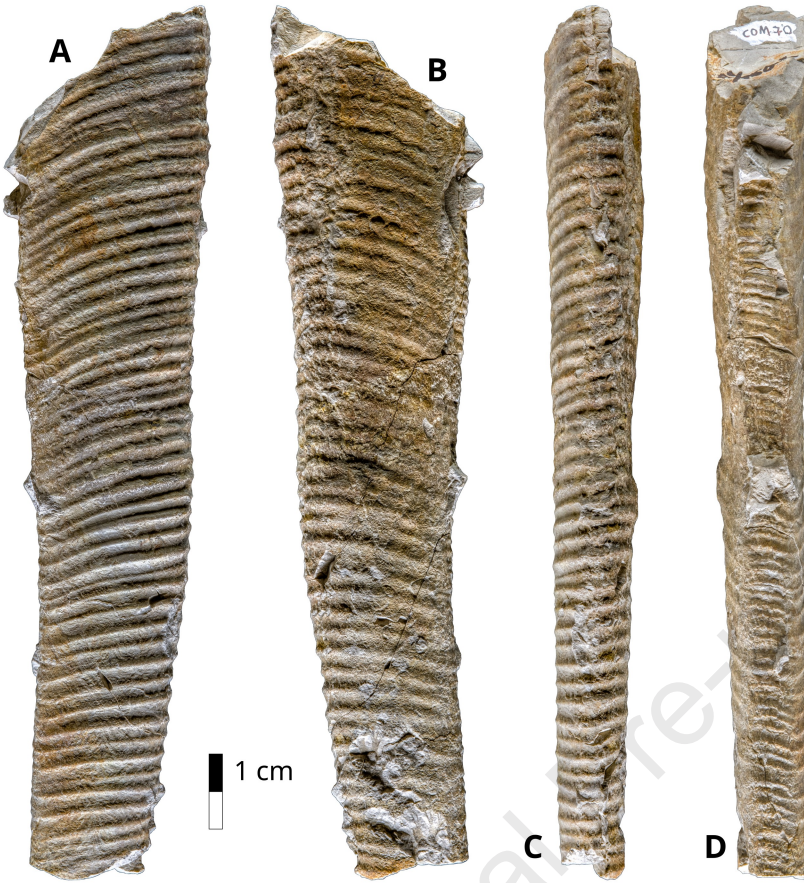
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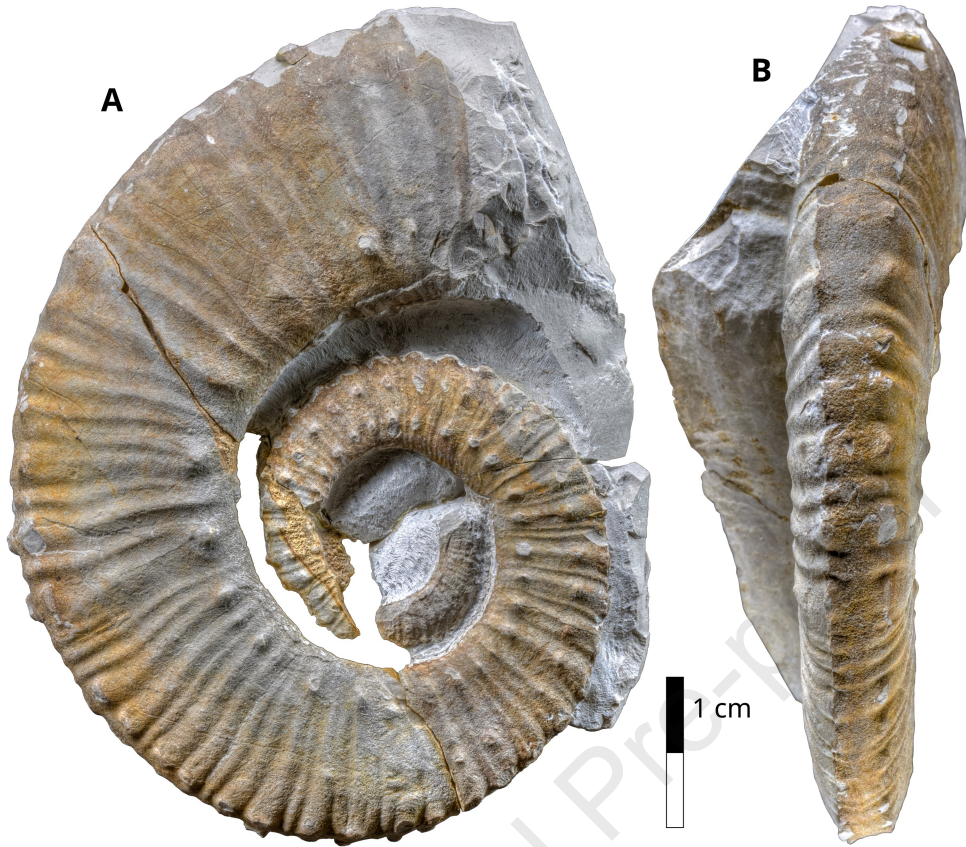


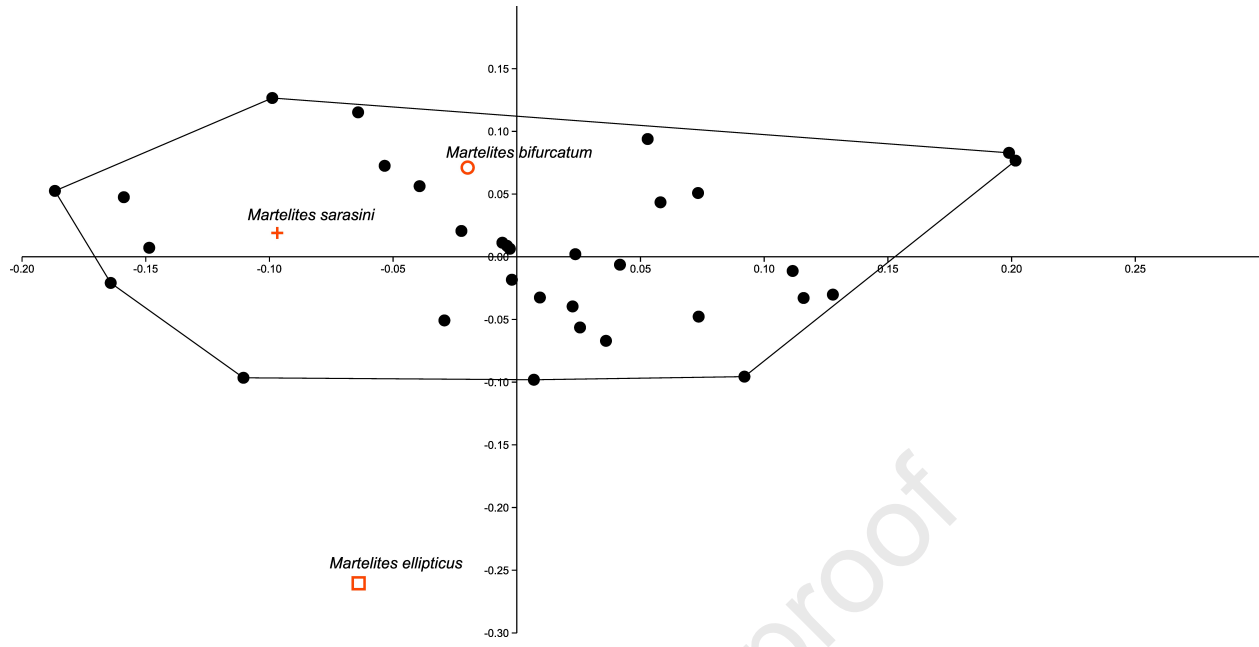




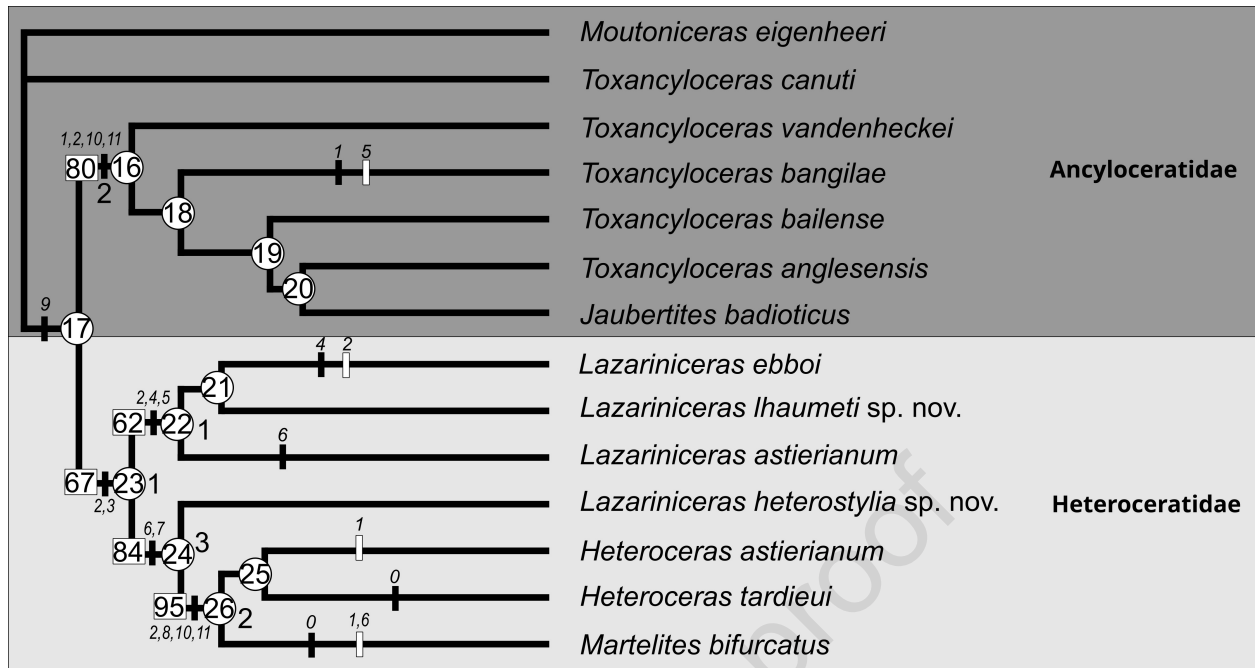








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① Nodes

■ Apomorphies with changed characters

▨ Homoplasies with changed characters

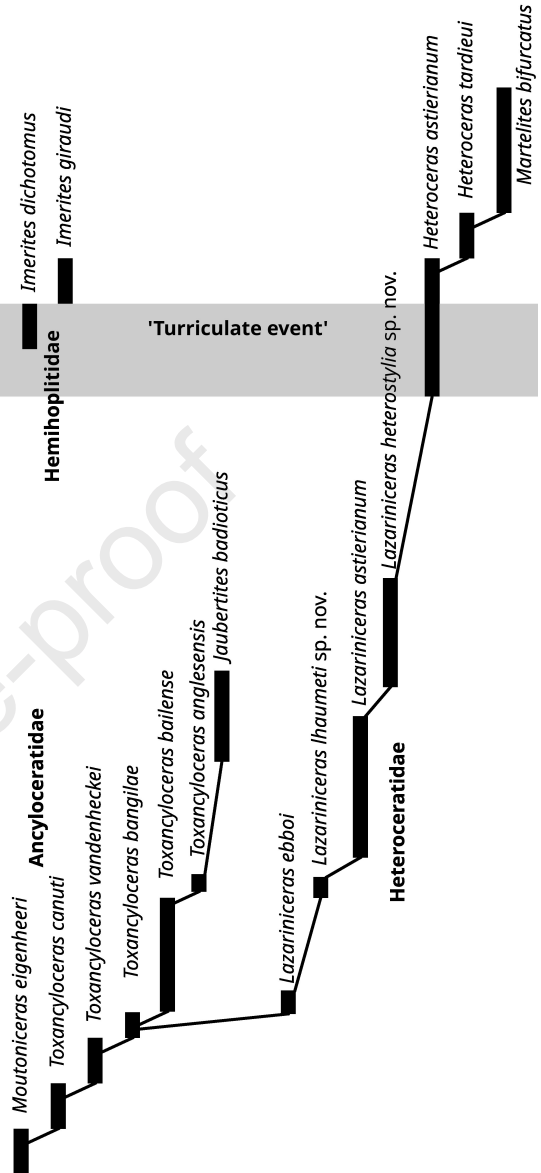
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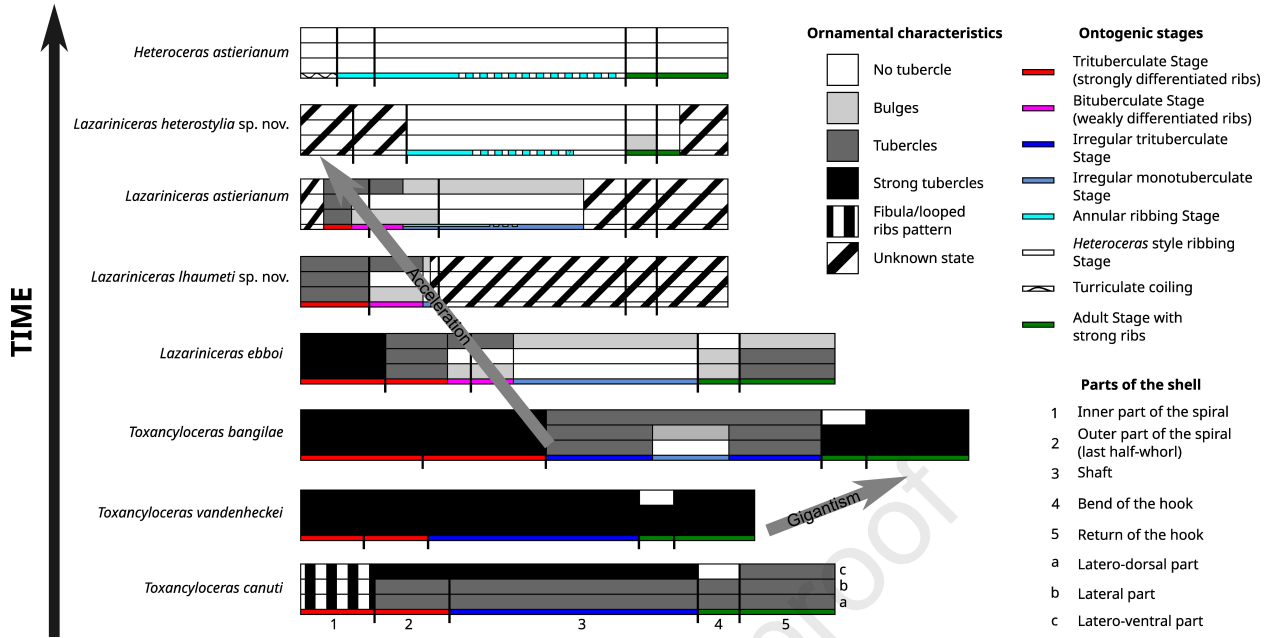
84 Bootstrap value



STAGES	ZONES	SUBZONES	INTERVAL HORIZONS	
BARREMIAN	UPPER	<i>Pseudocrioceras waagenioides</i>		
		<i>Imerites giraudi</i>	<i>Martelites sarasini</i>	<i>Anglesites puzosianum</i>
			<i>Imerites giraudi</i>	<i>Heteroceras tardieui</i>
				<i>Imerites giraudi</i>
		<i>Camereiceras limentinum</i>	<i>Hemihoplites feraudianus</i>	<i>Pseudoshasticrioc. autrani</i>
				<i>Pseudoshasticrioc. magnini</i>
				<i>Pseudoshasticrioc. bersaci</i>
				<i>Hemihoplites feraudianus</i>
			<i>Gerhardtia provincialis</i>	<i>Hemihoplites astarte</i>
				<i>Gerhardtia provincialis acme</i>
				<i>Gerhardtia provincialis</i>
		<i>Camereiceras limentinum</i>	<i>Gerhardtia sartousiana acme</i>	
			<i>Camereiceras limentinum</i>	
	<i>Toxancyloceras vandenheckei</i>	<i>Gassendiceras alpinum</i>	<i>Camereiceras marchandi</i>	
			<i>Camereiceras breistrofferi</i>	
		<i>Toxancyloceras vandenheckei</i>	<i>Gassendiceras alpinum</i>	
			<i>Gassendiceras multicoatum</i>	
			<i>Toxancyloceras bangilae</i>	
			<i>Toxancyloceras vandenheckei</i>	
			<i>Toxancyloceras canuti</i>	
	LOWER	<i>Moutoniceras moutonianum</i>	<i>Moutoniceras eigenheeri</i>	
			<i>Heinzia caicedi</i>	
<i>Coronites darsi</i>				
<i>Kotetishvilia compressissima</i>		<i>Holcodiscus caillaudianus</i>		
		<i>Holcodiscus fallax</i>		
<i>Nicklesia pulchella</i>			<i>Leptohamulina lukenederi</i>	
<i>Kotetishvilia nicklesi</i>				
<i>Taveraidiscus hugii</i>		<i>Psilotissotia colombiana</i>		
		<i>Taveraidiscus hugii</i>		

STAGES	ZONES	SUBZONES	INTERVAL HORIZONS		
BARREMIAN	UPPER	<i>Imerites giraudi</i>	<i>Pseudocrioceras waagenioides</i>		
			<i>Martelites sarasini</i>	<i>Anglesites puzosianum</i>	
		<i>Imerites giraudi</i>	<i>Imerites giraudi</i>	<i>Heteroceras tardieui</i>	
				<i>Imerites giraudi</i>	
				<i>Imerites dichotomus</i>	
		<i>Camereiceras limentinum</i>	<i>Hemihoplites feraudianus</i>	<i>Pseudoshasticrioc. autrani</i>	
				<i>Pseudoshasticrioc. magnini</i>	
				<i>Pseudoshasticrioc. bersaci</i>	
				<i>Hemihoplites feraudianus</i>	
			<i>Gerhardtia provincialis</i>	<i>Hemihoplites astarte</i>	<i>Gerhardtia provincialis acme</i>
					<i>Gerhardtia provincialis</i>
		<i>Camereiceras limentinum</i>	<i>Gerhardtia sartousiana acme</i>	<i>Camereiceras limentinum</i>	
				<i>Camereiceras marchandi</i>	
				<i>Camereiceras breistrofferi</i>	
	<i>Toxancyloceras vandenheckei</i>	<i>Gassendiceras alpinum</i>	<i>Camereiceras marchandi</i>		
			<i>Camereiceras breistrofferi</i>		
			<i>Gassendiceras alpinum</i>		
			<i>Gassendiceras multicostatum</i>		
			<i>Toxancyloceras bangilae</i>		
		<i>Toxancyloceras vandenheckei</i>	<i>Toxancyloceras vandenheckei</i>		
			<i>Toxancyloceras canuti</i>		
			<i>Moutoniceras eigenheeri</i>		
			<i>Heinzia caicedi</i>		
			<i>Coronites darsi</i>		
	LOWER	<i>Moutoniceras moutonianum</i>			
		<i>Kotetishvilia compressissima</i>	<i>Holcodiscus caillaudianus</i>		
			<i>Holcodiscus fallax</i>		
<i>Nicklesia pulchella</i>			<i>Leptohamulina lukenederi</i>		
<i>Kotetishvilia nicklesi</i>					
<i>Taveraidiscus hugii</i>		<i>Psilotissotia colombiana</i>			
	<i>Taveraidiscus hugii</i>				





**Declaration of interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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