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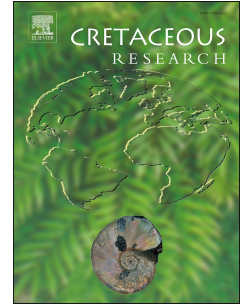
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Can the intraspecific laws of variation be used as a predictive model for understanding species with insufficient data? The example of the early Heteroceratidae in their evolutionary context (heteromorph ammonites, Tethys upper Barremian)



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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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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 *Lazariniceras 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 *Lazariniceras lhaumeti* sp. nov.; and the bed G12/331
202 delivered a fragment of *Lazariniceras 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 *Lazariniceras 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-Tallore 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 *Pseudoshastrioceras 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
Sexual dimorphism (differentiation in shell size, coiling, peristome aspect, ornamentation, or combinations)	Multipolar variation (relation between robustness of the ornamentation, thickness of the section, height of the whorl and opening of the umbilicus)
Non-sexual polymorphism (can concern a particular character such as supernumerary tubercle)	Heterochronies (variations in the rate of development, which means in ammonites the shifting of the ontogenetic stages)
Fluctuating asymmetry (linked to ecological stress)	Coiling variation (heteromorphy)
Chirality (dextrality/senestria)	Secondary erasing of ornamentation (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
Sexual dimorphism: not demonstrated	Multipolar variation: 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)
Non-sexual polymorphism: very rarely, a tubercle	Heterochronies: 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>Fluctuating asymmetry: 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>Coiling variation: 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>Chirality: 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>Secondary erasing of ornamentation: 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; α is the
 800 angle between each series of measurements.

Specimen	Dsp	H	W	Usp	h	Nt	Ni	W/H	α
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 phylogenetically) 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 *Lazariniceras*. 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 *Lazarinicer*as), 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, *Lazarinicer*as *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 *Lazarinicer*as. The
1310 discussion of the results shows that the variability observed in the *Lazarinicer*as 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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1357 **References**

1358 Arnaud, H., 2005. The South-East France Basin (SFB) and its Mesozoic evolution. *Géologie*
1359 *Alpine*, Série spéciale ‘Colloques et Excursions’, 7, p. 5–28.

1360

1361 Arthur, M.A., Dean, W.E., Schlanger, S.O., 1985. Variations in the global carbon cycle
1362 during the Cretaceous related to climate, volcanism, and changes in atmospheric CO₂. In:
1363 Sundquist, E.T., Broecker, W.E. (Eds.), *The Carbon Cycle and Atmospheric CO₂: Natural*

1364 Variations Archean to Present. *Geophysical Monograph Series*, 32, Washington DC, p. 504–
1365 529.

1366

1367 Astier, J.-E., 1851. Catalogue descriptif des *Ancyloceras* appartenant à l'étage Néocomien
1368 d'Escragnolles et des Basses-Alpes. *Annales des sciences physiques et naturelles*
1369 *d'agriculture et d'industrie*, 3 (2), 435–456.

1370

1371 Bather, F. A., 1888. Professor Blake and shell-growth in Cephalopoda. *The Annals and*
1372 *magazine of natural history*, 1 (6), 421–427.

1373

1374 Baudouin, C., Delanoy, G., Boselli, P., Bert, D., Boselli, M., 2012. Les faunes d'ammonites
1375 de la sous-zone à Sarasini (Barrémien supérieur dans les Baronnies (Drôme, France). *Revue*
1376 *de Paléobiologie*, Genève, 31 (2): 601–677.

1377

1378 Bersac, S., Bert, D., 2020. The heteromorph ammonite genus *Ancyloceras* (Ancyloceratidae)
1379 in the Paris Basin (lower Aptian, Lower Cretaceous, Northeast of France). *Annales de*
1380 *Paléontologie*, 106 (2), doi.org/10.1016/j.annpal.2019.102365.

1381

1382 Bersac, S., Bert, D., 2022. The heteromorph ammonite genus *Ammonitoceras* Dumas, 1876
1383 (Ancyloceratidae) in the lower Aptian (Lower Cretaceous) of the Les Ferres Aptian Basin
1384 (southeastern France). *Annales de Paléontologie*,
1385 <https://doi.org/10.1016/j.annpal.2022.102570>.

1386

1387 Bert, D., 2012. The Upper Barremian *pro parte* of the Angles stratotype (SE France). In:

1388 Bert, D., Bersac, S. (editors), 2012. First meeting of the Research Group for Paleobiology and

1389 biostratigraphy of the ammonites. *Boletín del Instituto de Fisiografía y Geología*, 82, 1–24.
1390 Rosario, @-@-2012. ISSN 1666-115X.

1391

1392 Bert, D., 2014a. L'influence de la variabilité intraspécifique sur la taxinomie, la
1393 biostratigraphie et l'évolution des ammonites : une approche paléobiologique. (Unpubl. PhD
1394 thesis), University of Rennes 1, 739 pp. (2 tomes), [https://tel.archives-ouvertes.fr/tel-](https://tel.archives-ouvertes.fr/tel-01138094)
1395 01138094.

1396

1397 Bert, D., 2014b. Factors of intraspecific variability in ammonites, the example of
1398 *Gassendiceras alpinum* (d'Orbigny, 1850) (Hemihoplitidae, Upper Barremian). *Annales de*
1399 *Paléontologie*, 100 (3), 217–236.

1400

1401 Bert, D., 2017. Barremian ammonite fauna from L'Estellon section (Baronnies, SE France):
1402 Additional identifications. In: Granier, B. (ed.): Some key Lower Cretaceous sites in Drôme
1403 (SE France). *Carnets de Géologie*, CG2017_B01, ISBN 978-2-916733-13-5, p. 102–109.

1404

1405 Bert, D., 2019. Les lois de la variabilité intraspécifique chez les ammonites. *Les cahiers de la*
1406 *Réserve Naturelle de Sainte-Victoire*, numéro spécial congrès APF 2019, 12.

1407

1408 Bert, D., Bersac, S., 2013. Evolutionary patterns-tested with cladistics-and processes in
1409 relation to palaeoenvironments of the upper Barremian genus *Gassendiceras* (Ammonitina,
1410 Lower Cretaceous). *Palaeontology*, 56 (3), 631–646.

1411

1412 Bert, D., Bersac, S., 2014. Origin of the Tethyan Hemihoplitidae tested with cladistics
1413 (Ancyloceratina, Ammonoidea, Early Cretaceous): an immigration event?. *Carnets de*
1414 *Géologie*, 14(13), 255–272.

1415

1416 Bert, D., Bersac, S., Delanoy, G., Canut, L., 2013. Paleontology, taxonomic revision and
1417 variability of some species of the genus *Gassendicerias* Bert et al., 2006 (Ammonitina, Upper
1418 Barremian) from southeastern France. *Acta Geologica Polonica*, 63 (3), 355–397.

1419

1420 Bert, D., Bersac, S., Juárez-Ruiz, J., nd Hughes, Z., 2018. Size reduction and ornamental
1421 oscillation within a Barremian lineage of giant heteromorphic ammonites (Early Cretaceous,
1422 northwestern Tethyan margin), *Cretaceous Research*, 88, 173–186.

1423

1424 Bert, D., Delanoy, G., 2000. Considérations nouvelles sur quelques représentants barrémiens
1425 des Pulchelliidae Douvillé, 1890 et des Hemihoplitidae Spath, 1924 (Ammonoidea). *Annales*
1426 *du Muséum d'Histoire Naturelle de Nice*, 15, 63–89.

1427

1428 Bert, D., Delanoy, G., 2009. *Pseudoshasticioceras bersaci* nov. sp. (Ammonoidea,
1429 Gassendiceratinae), and new ammonite biohorizon for the Upper Barremian of southeastern
1430 France. *Carnets de Géologie*, 2009/02 (CG2009_A02).

1431

1432 Bert, D., Delanoy, G., Bersac, S., 2006. Descriptions de représentants nouveaux ou peu
1433 connus de la famille des Hemihoplitidae Spath, 1924 (Barrémien supérieur, Sud-est de la
1434 France) : conséquences taxinomiques et phylétiques. *Annales du Muséum d'Histoire*
1435 *Naturelle de Nice*, 21, 179–253.

1436

- 1437 Bert, D., Delanoy, G., Bersac, S., 2008. Propositions pour un nouveau découpage bio-zonal
1438 ammonitique, et nouveaux bio-horizons pour le Barrémien supérieur. *Carnets de Géologie*,
1439 2008/03 (CG2008_A03).
- 1440
- 1441 Bert, D., Delanoy, G., Canut, L., 2009. L'origine des *Imerites* Rouchadze, 1933 : résultat
1442 d'une innovation chez les Gassendiceratinae Bert, Delanoy et Bersac, 2006 (Ammonoidea,
1443 Ancyloceratina). *Annales de Paléontologie*, 95, 21–35.
- 1444
- 1445 Bert, D., Busnardo, R., Delanoy, G., Bersac, S., 2010. Problems in the identity of '*Crioceras*'
1446 *barremense* Kilian, 1895, (Ancyloceratida, Upper Barremian), and their proposed resolution.
1447 *Carnets de Géologie*, 2010/01 (CG2010_A01).
- 1448
- 1449 Bert, D., Delanoy, G., Bersac, S., 2011. The Dichotomus Horizon: a new biochronologic unit
1450 of the Giraudi Zone of the Upper Barremian of southeastern France, and considerations
1451 regarding the genus *Imerites* Rouchadze (Ammonoidea, Gassendiceratinae). *Carnets de*
1452 *Géologie*, 2011/01 (CG2011_A01).
- 1453
- 1454 Bert, D., Reboulet, S., Vernet, B., Bersac, S., Canut, L., 2021. Early *Crioceratites*
1455 (heteromorphic ammonites) from the lower Hauterivian of south-eastern France: systematics,
1456 intraspecific variation and biostratigraphic implications. *Cretaceous Research*, 126,
1457 <https://doi.org/10.1016/j.cretres.2021.104903>.
- 1458
- 1459 Bert, D., Bousquet, V., Guiomar, M., Bariani, F., Hippolyte, J.-C., Bromblet, Ph. Garciaz, J.-
1460 L., Fleury, J., Mathieu, P., Pagès, J.-S., Tardieu, P., Dupuis-Caillet, M., Leong, K., Faure, E.,
1461 2022. The Geotouristic Project 'the Geological Adventure' to the Rescue of an Iconic World

1462 Heritage Geosite, the Ammonites Slab of Digne-les-Bains (National Geological Nature
1463 Reserve of Haute-Provence and Unesco Global Geopark, France). *Geoheritage*, 14, 101, 24
1464 p., <https://doi.org/10.1007/s12371-022-00739-z>.

1465
1466 Bodin, S., Godet, A., Adatte, Th., Föllmi, K.B., 2005. Paleoceanographic and paleoclimatic
1467 changes of the northern tethyan realm during the Hauterivian-Barremian: New insight from
1468 the Angles section (SE France). *Géologie Alpine*, série ‘Colloques et excursions’, 7, 138–146.

1469
1470 Bodin, S., Fiet, N., Godet, A., Matera, V., Westermann, S., Clément, A., Janssen, N., Stille,
1471 P., Föllmi, K. B., 2009. Early Cretaceous (late Berriasian to early Aptian)
1472 palaeoceanographic change along the northwestern Tethyan margin (Vocontian Trough,
1473 southeastern France): $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and Sr-isotope belemnite and whole-rock records.
1474 *Cretaceous Research*, 30, 1247–1262.

1475
1476 Busnardo, R., 1970. Les *Pseudothurmannia* (Ammonoidea) de l’Hauterivien supérieur de la
1477 Montagne de Lure. *Document du Laboratoire de Géologie de Lyon*, 37, 133–145.

1478
1479 Cecca, F., Marini, A., Pallini, G., Baudin, F., Begouën, V., 1994. A guide-level of the
1480 Uppermost Hauterivian (Lower Cretaceous) in the pelagic succession of Umbria–Marche
1481 Apennines (Central Italy): the Faraoni Level. *Rivista Italiana di Paleontologia Stratigrafia*,
1482 99, 551–568.

1483
1484 Company, M., Sandoval, J., Tavera, J. M., 2004. El Barremiense de Foncalent y l’Alcoraia
1485 (Alicante). *Geo-Temas*, 7, 217–221.

1486

- 1487 Conte, G., 1989. Fossiles du plateau d'Albion. *Les Alpes de Lumière*, 99, 73 pp.
- 1488
- 1489 Cotillon, P., Banvillet, M., Gaillard, Ch., Grosheny, D., Olivero D., 2000. Les surfaces à
1490 *Rhizocorallium* de l'Aptien inférieur sur la bordure méridionale du bassin vocontien (France,
1491 Sud-Est), marqueurs de dynamiques locales ; leur relation avec un événement anoxique
1492 global. *Bulletin de la Société géologique de France*, 171 (2), 223–238.
- 1493
- 1494 Cottreau, J., 1937. Types du prodrome de paléontologie stratigraphique universelle de
1495 d'Orbigny. B. Néocomien Supérieur ou Urgonien. *Annales de Paléontologie*, 26, 17–48.
- 1496
- 1497 Courville, Ph., 2011. Caractères ornementaux, disparité et diversité chez les Ammonitina :
1498 exemples des Kosmoceratinae (Stephanoceratoidea), Callovien moyen et supérieur
1499 (Jurassique moyen, Bassin de Paris). *Comptes Rendu Paleovol*, 10, 155–170.
- 1500
- 1501 Courville, P., Crônier, C., 2005. Les hétérochronies du développement : on outil pour l'étude
1502 de la variabilité et des relations phylétiques ? Exemple de *Nigericeras*, Ammonitina du
1503 Crétacé supérieur africain. *Comptes Rendu Paleovol*, 2, 535–546.
- 1504
- 1505 Courville, P., Crônier, C., 2005. Diversity or disparity in the Jurassic (Upper Callovian) genus
1506 *Kosmoceras* (Ammonitina): a morphometric approach. *Journal of Paleontology*, 79, 5, 944–
1507 953.
- 1508
- 1509 Cuvier, G., 1795. Second Mémoire sur l'organisation et les rapports des animaux à sang blanc,
1510 dans lequel on traite de la structure des Mollusques et de leur division en ordre, lu à la société

- 1511 d'Histoire Naturelle de Paris, le 11 prairial an troisième [30 May 1795]. *Magazine*
1512 *Encyclopédique, ou Journal des Sciences, des Lettres et des Arts*, 2, 433–449
1513
- 1514 Danchin, E., 2022. La Synthèse inclusive de l'évolution, l'hérédité au-delà du Gène égoïste.
1515 *Actes Sud*, Paris, 374 pp.
1516
- 1517 Darlu, P., d'Haese, C., Tassy P., Zaragüeta i Bagils, R., 2019 La reconstruction
1518 phylogénétique. Concepts et méthodes. *Editions Matériologiques*, 432 p.
1519
- 1520 De Baets, K., Klug, Ch., Monet, C., 2013 Intraspecific variability through ontogeny in early
1521 ammonoids. *Palaeobiology*, 39, 75–94.
1522
- 1523 De Baets, K., Bert, D., Hoffmann, R., Monnet, C., Yacobucci, M., Klug, Ch., 2015.
1524 Ammonoid intraspecific variability. In: Klug, Ch. et al. (eds), *Ammonoid Paleobiology: from*
1525 *anatomy to ecology. Topics in Geobiology*, 43, 359–426, doi:10.1007/978-94-017-9630-9_9.
1526
- 1527 Delanoy, G., 1990a. *Camericeras* nov. gen. (Ammonoidea, Ancyloceratina) du Barrémien
1528 supérieur du Sud-Est de la France. *Géobios*, 23 (1), 71–93.
1529
- 1530 Delanoy, G., 1990b. Précisions nouvelles sur '*Emericeras*' *collignoni* Thomel
1531 (Ammonoidea) et proposition d'un nouveau schéma zonal dans le Barrémien supérieur du
1532 Sud-Est de la France. *Comptes Rendus de l'Académie des Sciences*, Paris, 311 (II), 259–264.
1533

- 1534 Delanoy, G., 1994. Les zones à Feraudianus, Giraudi et Sarasini du Barrémien supérieur de la
1535 région stratotypique d'Angles – Barrême – Castellane (Sud-Est de la France). *Géologie*
1536 *Alpine*, mémoire Hors série n°20, 279–319.
- 1537
- 1538 Delanoy, G., 1997. Biostratigraphie des faunes d'Ammonites à la limite Barrémien-Aptien
1539 dans la région d'Angles-Barrême-Castellane. Etude particulière de la Famille des
1540 Heteroceratidae (Ancyloceratina, Ammonoidea). *Annales Muséum Histoire Naturelle de*
1541 *Nice*, 12, 1–270.
- 1542
- 1543 Delanoy, G., 1998. Pseudoshastrioceras gen. nov. : un nouveau genre d'ammonites
1544 hétéromorphes du Barrémien supérieur du Sud-Est de la France. *Annales du Muséum*
1545 *d'Histoire Naturelle de Nice*, 13, 432–439.
- 1546
- 1547 Delanoy, G., 2003. *Toxancyloceras* gen. nov. (Ammonoidea, Ancyloceratina) un nouveau
1548 genre du Barrémien supérieur. *Annales du Muséum d'Histoire Naturelle de Nice*, 18, 1–19.
- 1549
- 1550 Delsol, M., 1977. Embryogenesis, Morphogenesis, Genetics and Evolution. In: Hecht, M. K.,
1551 Goody, P. C., Hecht, B. M. (eds). *Advanced Study Institutes Series*, 14, 120–138.
- 1552
- 1553 Dimitrova, N., 1967. Les fossiles de Bulgarie. 4. Crétacé inférieur. Cephalopoda (Nautiloidea
1554 et Ammonoidea). *Académie Bulgare des Sciences*, 424.
- 1555
- 1556 Fallot, P., Termier, H., 1923. Ammonites nouvelles des Îles Baléares. *Trabajos del Museo*
1557 *Nacional de Ciencias Naturales*, 32, 97 pp.
- 1558

- 1559 Gauthier, H., with collaboration of Busnardo, R., Combémoré, R., Delanoy, G., Fischer, J.-
1560 C., Guérin-Franiatte, F., Joly, B., Kennedy, W.J., Sornay, J., Tintant, H., 2006. Révision
1561 critique de la Paléontologie Française d'Alcide d'Orbigny, Vol. IV, Céphalopodes Crétacés,
1562 sous la direction de J.C. Fischer. *Backhuys Publisher*, 292 pp.
- 1563
- 1564 Giebel, Ch. G. A., 1852. Fauna der Vorwelt mit steter Berücksichtigung der lebenden Thiere.
1565 Dritter Band: Mollusken. *Erste Abteilung Cephalopoden*, 856 pp.
- 1566
- 1567 Gill, Th. N., 1871. Arrangement of the families of Mollusks. *Smithsonian Miscellaneous*
1568 *Collection*, 227, 49 pp.
- 1569
- 1570 Goloboff, P., Catalano, S., 2016. TNT, version 1.5, with a full implementation of
1571 phylogenetic morphometrics Cladistics. doi:10.1111/cla.12160.
- 1572
- 1573 Haeckel, E., 1866. Generelle morphologie der organismen. Allgemeine grundzüge der
1574 organischen formen-wissenschaft, mechanisch begründet durch die von Charles Darwin
1575 reformirte descendenztheorie. *Georg Reimer*, Berlin, 574 pp.
- 1576
- 1577 Haug, E., 1889. Beitrag zur Kenntniss der oberneocomen Ammonitenfauna der Puezalpe bei
1578 Corvara (Südtirol). *Beiträge zur Palaeontologie Oesterreich-Ungarns und des Orients*, 7,
1579 193–230.
- 1580
- 1581 Hoedemaeker, Ph.J. and Company, M. (reporters) and 16 co-authors 1993. Ammonite
1582 zonation for the Lower Cretaceous of the Mediterranean region; basis for the stratigraphic
1583 correlations within IGCP-Project 262. *Revista España de Paleontologia*, 8, 1, 117–120.

- 1584
- 1585 Hörandl, E. , d Stuessy, T.F., 2010. Paraphyletic groups as natural units of biological
1586 classification. *Taxon*, 59 (6), 1641–1653.
- 1587
- 1588 Hyatt, A., 1903. *Pseudoceratites* of the Cretaceous. Monographs of the United States
1589 Geological Survey, 44, 348 pp.
- 1590
- 1591 I.C.Z.N. (International Commission on Zoological Nomenclature) 1999. International Code of
1592 Zoological Nomenclature, 4th ed. *International Trust for Zoological Nomenclature*, 29, 306
1593 pp.
- 1594
- 1595 Kakabadze, M.V., 1967. Questions on the systematic position and classification of the
1596 Colchiditids. *Soobshcheniya Akademii Nauk GSSR*, 48 (2), 437–442 (in Russian).
- 1597
- 1598 Kakabadze, M.V., 1970. Un nouveau genre *Kutatissites* gen. nov. des sediments du Crétacé
1599 inférieur de Géorgie occidentale. *Soobshcheniya Akademii Nauk GSSR*, 58, 3, 733–736 [in
1600 Russian].
- 1601
- 1602 Kazansky, P.A., 1914. Description d'une collection des Céphalopodes des terrains Crétacés
1603 du Daghestan. Tomsk, 127 pp. [in Russian].
- 1604
- 1605 Kennedy, W.J., Cobban, W.A., 1976. Aspects of ammonite biology, biogeography, and
1606 biostratigraphy. *Special Papers in Palaeontology*, 17, 94 pp.
- 1607

1608 Kilian, W., 1888. Description géologique de la Montagne de Lure. *Bibliothèque de l'école des*
1609 *Hautes Etudes, section des sciences naturelles*, 34 (2), 236 pp.

1610

1611 Klein, J., Busnardo, R., Company, M., Delanoy, G., Kakabadze, M.V., Reboulet, S., Ropolo,
1612 P., Vašíček, Z., Vermeulen, J., 2007. Lower Cretaceous Ammonites III. Bochianitoidea,
1613 Protancyloceratoidea, Ancyloceratoidea, Ptychoceratoidea. *Fossilium Catalogus I : Animalia*,
1614 vol. 144. *Backhuys Publishers*, 381 pp.

1615

1616 Latreille, P.A., 1825. Familles naturelles du règne animal, exposées succinctement et dans un
1617 ordre analytique, avec l'indication de leurs genres. *Baillière*, Paris, 570 pp.

1618

1619 Laurent, O., Stephan, J.-F., Popoff, M., 2000. Modalités de la structuration miocène de la
1620 branche sud de l'arc de Castellane (chaînes subalpines méridionales). *Géologie de la France*,
1621 3, 33–65.

1622

1623 Léveillé, Ch., 1837. Description de quelques nouvelles coquilles fossiles du Département des
1624 Basses-Alpes. *Mémoires de la Société géologique de France*, 10 (2), 313–315.

1625

1626 Marchand, D., Dommergues, J.-L., 2008. L'approche paléontologique des concepts
1627 biologiques de l'espèce : défi pour l'étude de la paléobiodiversité. L'exemple des ammonites
1628 jurassiques. In: Prat D., Raynal-Roques, A., Roguenant, A. (eds) *Peut-on classer le vivant ?*
1629 *Linné et la systématique aujourd'hui*. *Belin*, Paris, 203–214.

1630

- 1631 Meek, F.B., 1876. A report on the invertebrate Cretaceous and Tertiary fossils of the Upper
1632 Missouri Country. F. V. Hayden, *Report of the United States Geological and Geographical*
1633 *Surveys of the Territories*, 9, 629 pp.
- 1634
- 1635 Orbigny, A. d', 1840-1842. Paléontologie française - Terrains crétacés - Tome 1,
1636 Céphalopodes (liv. 16). *Masson*, Paris, 121–430.
- 1637
- 1638 Orbigny, A. d', 1850a. Cours élémentaire de paléontologie et de géologie stratigraphique.
1639 *Masson*, Paris. (1849), volume 1, 300 pp.
- 1640
- 1641 Orbigny, A. d', 1850b. Prodrome de paléontologie stratigraphique universelle des animaux
1642 mollusques et rayonnés, faisant suite au cours élémentaire de paléontologie et de géologie
1643 stratigraphique. *Masson*, Paris, volume 2, 427 pp.
- 1644
- 1645 Orbigny, A. d', 1851. Notice sur le genre *Heteroceras* de la classe des Céphalopodes. *Journal*
1646 *de Conchyliologie*, 2, 217–222.
- 1647
- 1648 Paquier, V. L., 1900. Recherches géologiques dans le Diois et les Barronies orientales.
1649 *Bulletin de la Société de Statistique des Sciences Naturelles et des Arts industriels du*
1650 *Département de l'Isère*, 5, 77–476.
- 1651
- 1652 Pictet, F., Campiche, G., 1861. Description des fossiles du terrain Crétacé des environs de
1653 Sainte-Croix, part 2. *Matériaux pour la Paléontologie Suisse*, 3, 1–144.
- 1654

- 1655 Reboulet, S., Szives, O., Aguirre-Urreta, B., Barragán, R., Company, M., Frau, C.,
1656 Kakabadze, M.V., Klein, J., Moreno-Bedmar, J.A., Lukeneder, A., Pictet, A., Ploch, I.,
1657 Raisossadat, S.N., Vašíček, Z., Baraboshkin, E.J., Mitta, V.V., 2018. Report on the 6th
1658 International Meeting of the IUGS Lower Cretaceous Ammonite Working Group, the Kilian
1659 Group (Vienna, Austria, 20th August 2017). *Cretaceous Research*, 91 (4), 100–110.
1660
- 1661 Reeside, J. B., Cobban, W. A., 1960. Studies of the Mowry Shale (Cretaceous) and
1662 Contemporary Formations in the United States and Canada. *Geological survey professional*
1663 *paper*, 355, 234 pp.
1664
- 1665 Roman, F., 1938. Les ammonites Jurassiques et crétacées: essai de genera. *Masson and Cie*,
1666 Paris.
1667
- 1668 Rouchadze, I., 1933. Les ammonites Aptiennes de la Géorgie occidentale. *Bulletin de*
1669 *l'Institut géologique de Géorgie* (1932), 165–273.
1670
- 1671 Sarkar, S.S., 1955. Révision des ammonites déroulées du Crétacé inférieur du Sud-Est de la
1672 France. *Mémoires de la Société Géologique de France*, 34 (72), 1–176.
1673
- 1674 Salfeld, H., 1921. Kiel- und Furchenbildung auf der Schalenaussenseite der Ammonoideen in
1675 ihrer Bedeutung für die Systematik und Festlegung von Biozonen. *Zentralblatt für*
1676 *Mineralogie, Geologie und Paläontologie*, 343–347.
1677
- 1678 Spath, L.F., 1922. On Cretaceous Ammonoidea from Angola, collected by Professor J.W.
1679 Gregory, D.Sc., F.R.S. *Transactions of the Royal Society of Edinburgh*, 53, 91–160.

- 1680
- 1681 Spath, L.F., 1924. On the ammonites of the Speeton Clay and the subdivisions of the
1682 Neocomian. *Geological Magazine*, 61, 73–89.
- 1683
- 1684 Thieuloy, J.-P., 1966. Leptocères berriasiens du massif de la Grande Chartreuse. *Géologie*
1685 *Alpine, Travaux du Laboratoire de Géologie de la Faculté des Sciences de Grenoble*, 42,
1686 281–295.
- 1687
- 1688 Thieuloy, J.-P., 1979. *Matheronites limentinus* n. sp. (Ammonoidea) espèce-type d'un
1689 horizon-repère barrémien supérieur du Vercors méridional (Massif subalpin français).
1690 *Géobios*, Mémoire spécial 3, 305–317.
- 1691
- 1692 Thomel, G., 1965. Contribution à la connaissance des céphalopodes créacés du sud-est de la
1693 France. Note sur les ammonites déroulées du Crétacé inférieur vocontien. *Mémoires de la*
1694 *Société géologique de France*, nouvelle série 43 (2), 101, 80 pp.
- 1695
- 1696 Toula, F., 1890. Geologische Untersuchungen im östlichen Balkan und in den angrenzenden
1697 Gebieten. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, mathematisch-*
1698 *physikalisch Classe*, 57, 323–400.
- 1699
- 1700 Uhlig, V., 1887. Über neocom Fossilien vom Gardenzazza in Südtirol nebst einem Anhang
1701 über das Neocom von Ischl. *Jahrbuch der Kaiserlich-Königlichen Geologischen*
1702 *Reichsanstalt*, 37, 69–108.
- 1703

- 1704 Vašíček, Z., Wiedmann, J., 1994. The Leptoceratoidinae: small heteromorph ammonites from
1705 the Barremian. *Palaeontology*, 37 (1), 203–239.
- 1706
- 1707 Vermeulen, J., 1996. Le Barrémien de Saint-Martin, Escragnolles (Alpes-Maritimes, France).
1708 *Riviera Scientifique*, 53–76.
- 1709
- 1710 Vermeulen, J., 1997. Biohorizons ammonitiques dans le Barrémien du Sud-Est de la France
1711 (de la zone à Hugii à la zone à Sartousiana). *Géologie Alpine*, 73, 99–117.
- 1712
- 1713 Vermeulen, J., 1998. Nouvelle biostratigraphie ammonitique du Barrémien (pro parte) du
1714 Sud-Est de la France. *Comptes Rendus de l'Académie des Sciences*, Paris, 327, 619–624.
- 1715
- 1716 Vermeulen, J., 2002. Etude stratigraphique et paléontologique de la famille des Pulchellidae
1717 (Ammonoidea, Ammonitina, Endemoceratidae. *Géologie Alpine* HS 42, 332 pp.
- 1718
- 1719 Vermeulen, J., 2003. Ammonites nouvelles ou peu connues du Barrémien méditerranéen.
1720 *Annales du Muséum d'Histoire Naturelle de Nice*, 18, 57–109.
- 1721
- 1722 Vermeulen, J., 2005. Boundaries, ammonite fauna and main subdivisions of the stratotype of
1723 the Barremian. *Géologie Alpine*, série 'colloques et excursions' 7, 147–173.
- 1724
- 1725 Vermeulen, J., 2006. Nouvelle classification à fondement phylogénétique des ammonites
1726 hétéromorphes du Crétacé inférieur. *Annales du Muséum d'Histoire Naturelle de Nice*, 21,
1727 137–178.
- 1728

1729 Vermeulen, J., Damais, L., Lepinay, P., 2015. Nouvelles données sur le genre
1730 *Breskovskiceras* Vermeulen and Lazarin, 2007 et sur son espèce-type. *Annales du Muséum*
1731 *d'Histoire Naturelle de Nice*, 30, 13–28.

1732

1733 Vermeulen, J., Lazarin, P., 2007. Nouvelles données sur les Ancyloceratoides Gill, 1871
1734 (Ancyloceratina Wiedmann, 1966 emend. Vermeulen, 2005) du Barrémien supérieur et de
1735 l'Aptien inférieur. *Annales du Muséum d'Histoire Naturelle de Nice*, 22, 27–86.

1736

1737 Vermeulen, J., Lepinay, P., Mascarelli, E., 2011. *Lazariniceras rouvieri* sp. nov. et
1738 *Berthouceras leroyi* sp. nov., deux ammonites particulières du Barrémien supérieur du sud-est
1739 de la France. *Annales du Muséum d'Histoire Naturelle de Nice*, 26, 95–106.

1740

1741 Vermeulen, J., Lazarin, P., Lepinay, P., Leroy, L., Mascarelli, E., 2016. Silesitidae du
1742 Barrémien du Sud-Est de la France (Ammonitina, Silesitoidea). *Strata*, 53, 97 pp.

1743

1744 Wiedmann, J., 1966. Stammesgeschichte und System der posttriadischen Ammonoideen, ein
1745 Überblick (2. Teil). *Neues Jahrbuch für Geologie und Palaeontologie*, 127, 13–81.

1746

1747 Wills, M.A., 1999. Congruence Between Phylogeny and Stratigraphy: Randomization Tests
1748 and the Gap Excess Ratio. *Systematic Biology*, 48, 3, 1 July 1999, 559–580,
1749 <https://doi.org/10.1080/106351599260148>.

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.

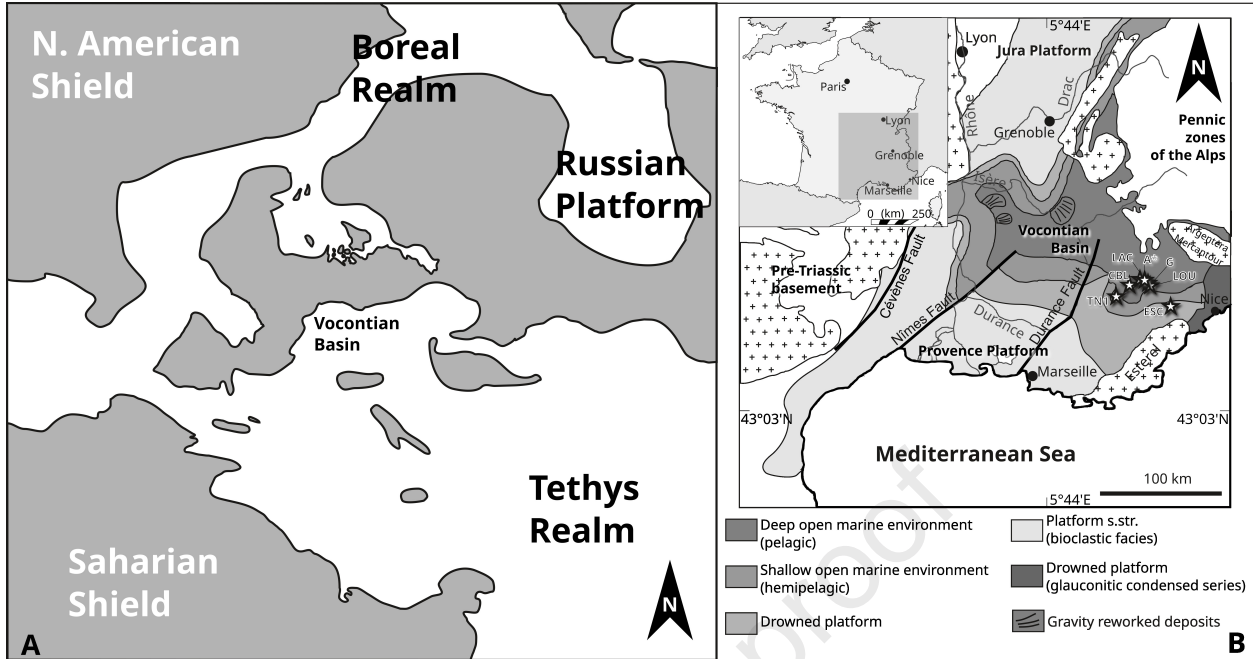
1831 See text for explanations.

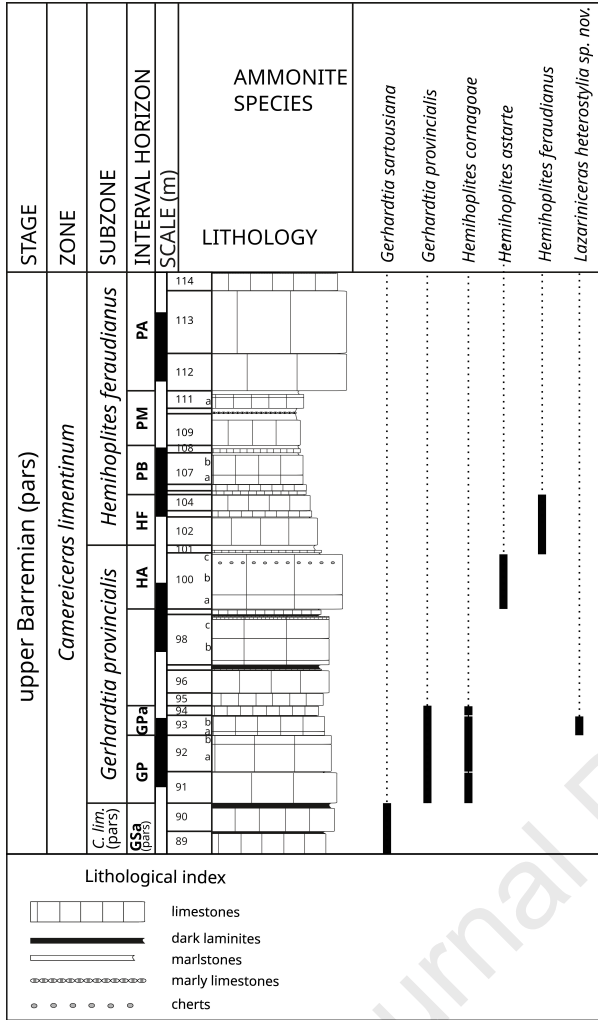
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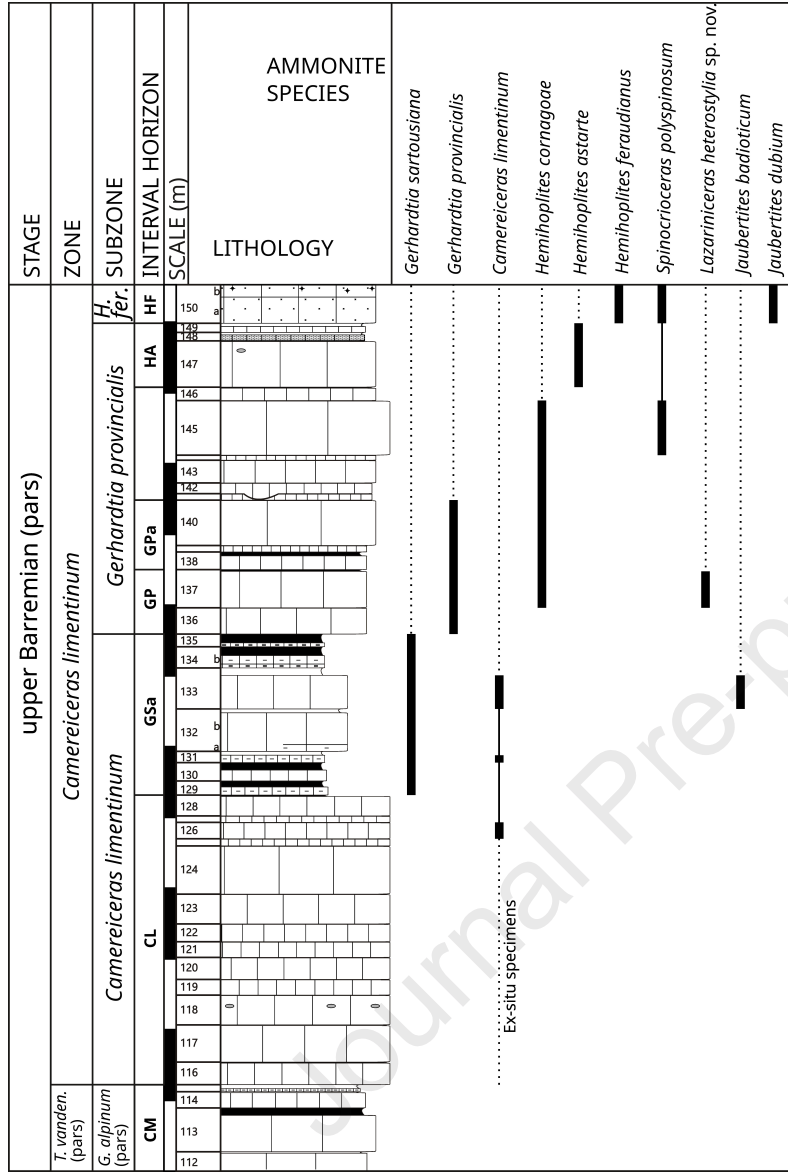
1833 **Figure 19.** Phyletic reconstruction proposed for the early Heteroceratidae from the
1834 Ancyloceratidae. The gray area points out the onset level almost at the same time of the
1835 turriculate morphology in the Heteroceratidae and Hemihoplitidae ('turriculate event').

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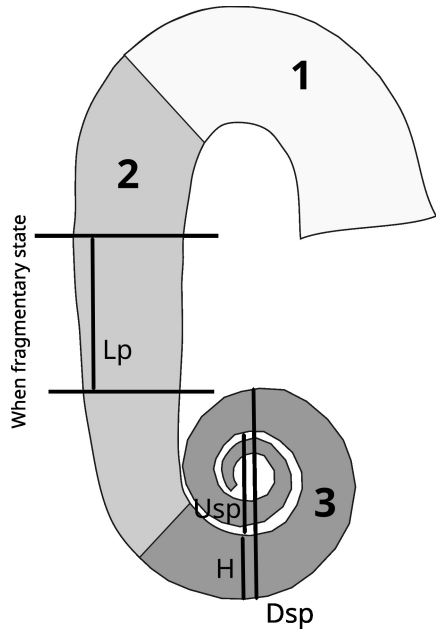
1837 **Figure 20.** Ontogeny and heterochronies within the
1838 *Toxancyloceras/Lazarinicerias/Heteroceras* lineage. See text for explanations. Note that
1839 compared to Bert et al. (2018), the cartouches have been corrected to take into account the
1840 presence of the peri-dorsal and lateral tubercles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



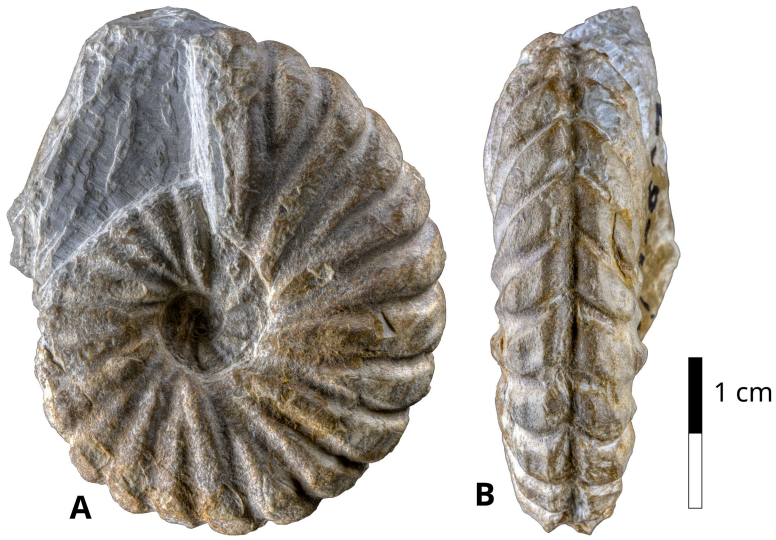




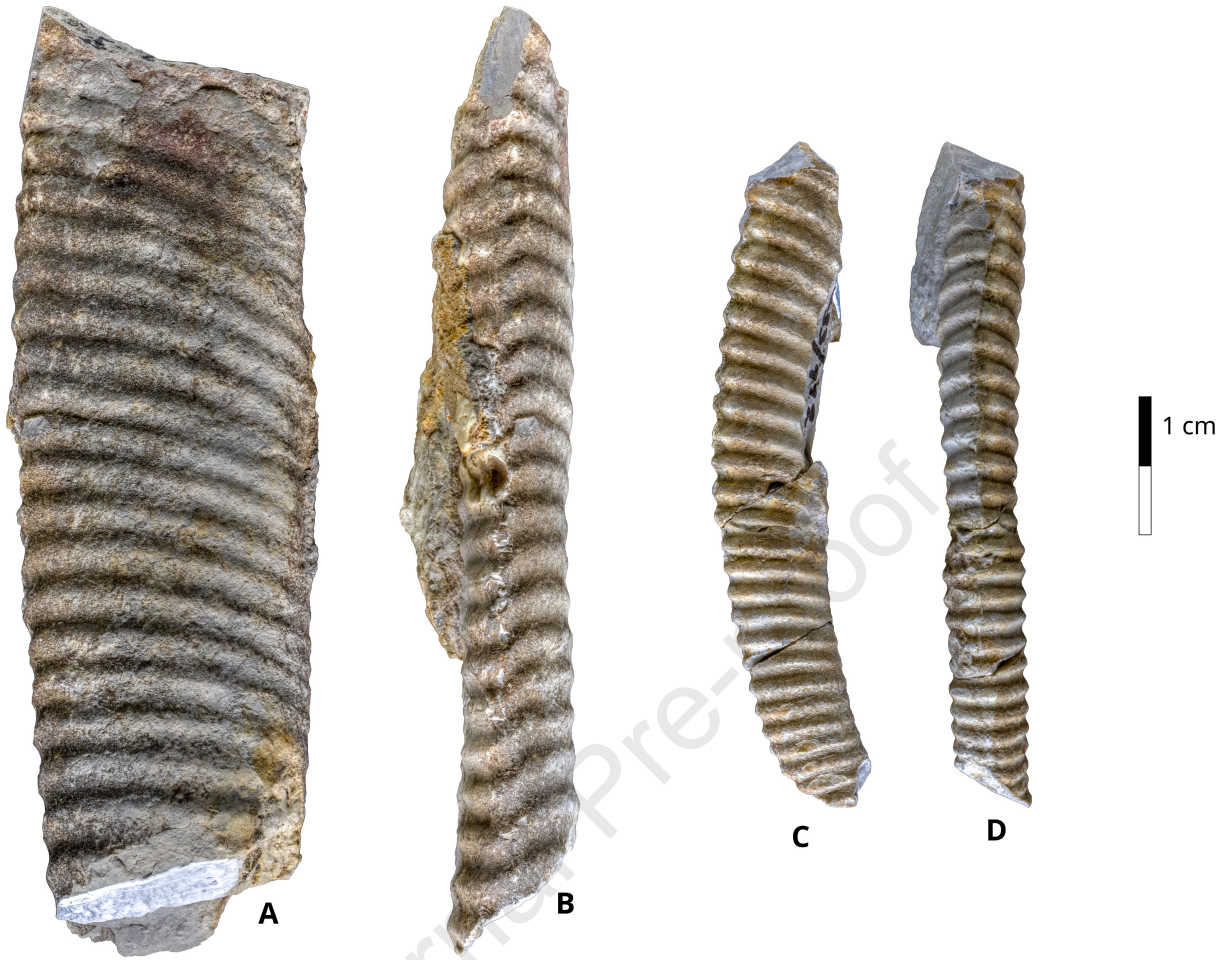
upper Barremian (pars)	STAGE
<i>Camereiceras limentinum</i>	ZONE
<i>Camereiceras limentinum</i>	SUBZONE
CL	INTERVAL HORIZON
Gsa	SCALE (m)
Gp	LITHOLOGY
GPa	AMMONITE SPECIES
HA	
168 a	
169 b	
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183	
	<p><i>Gerhardtia sartousiana</i></p> <p><i>Gerhardtia 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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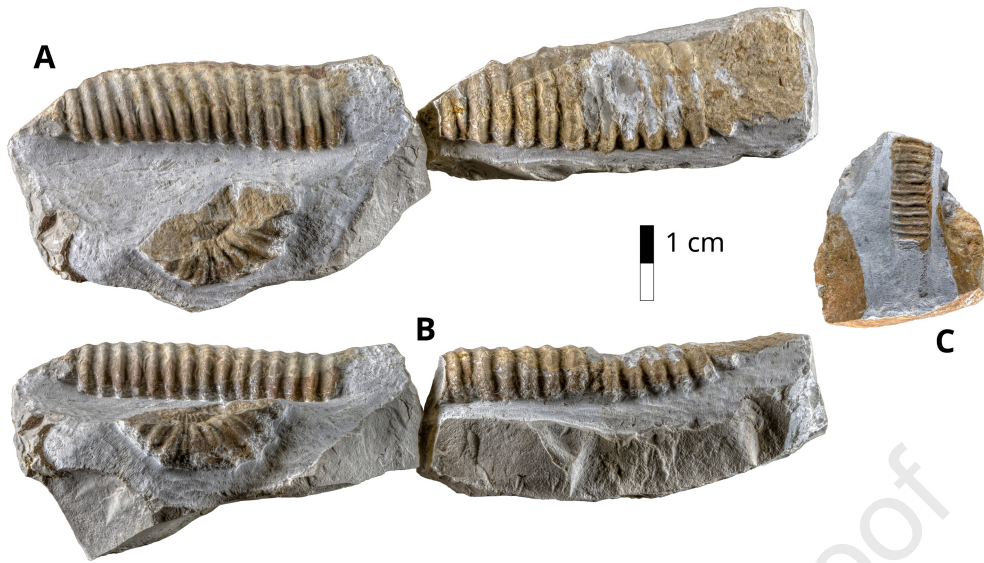


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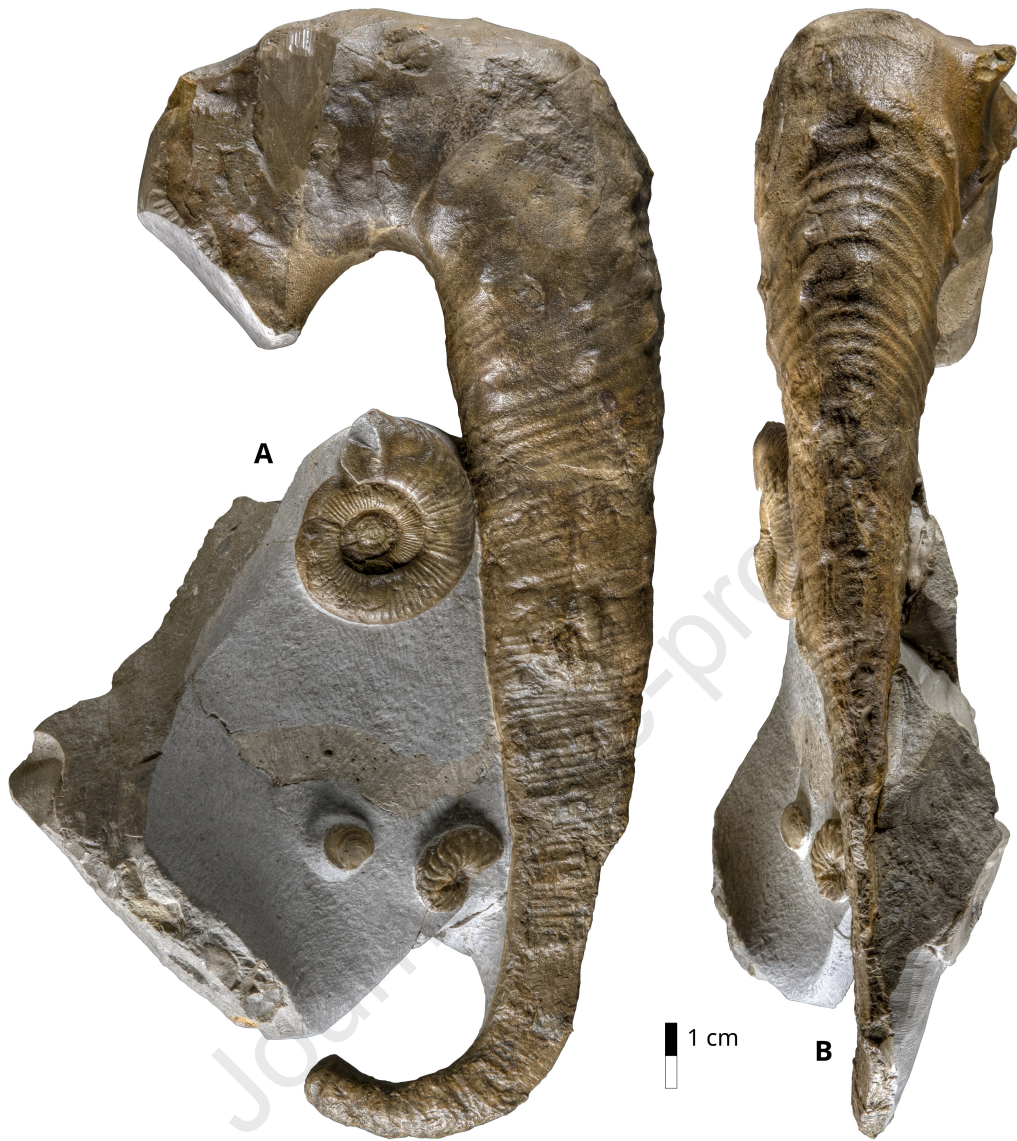




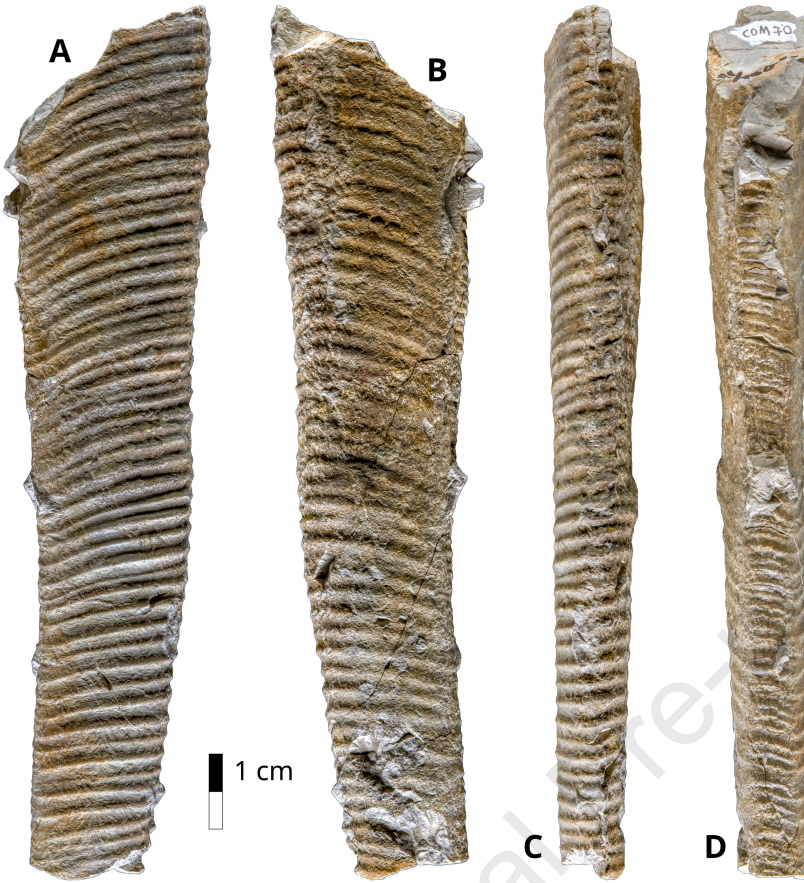


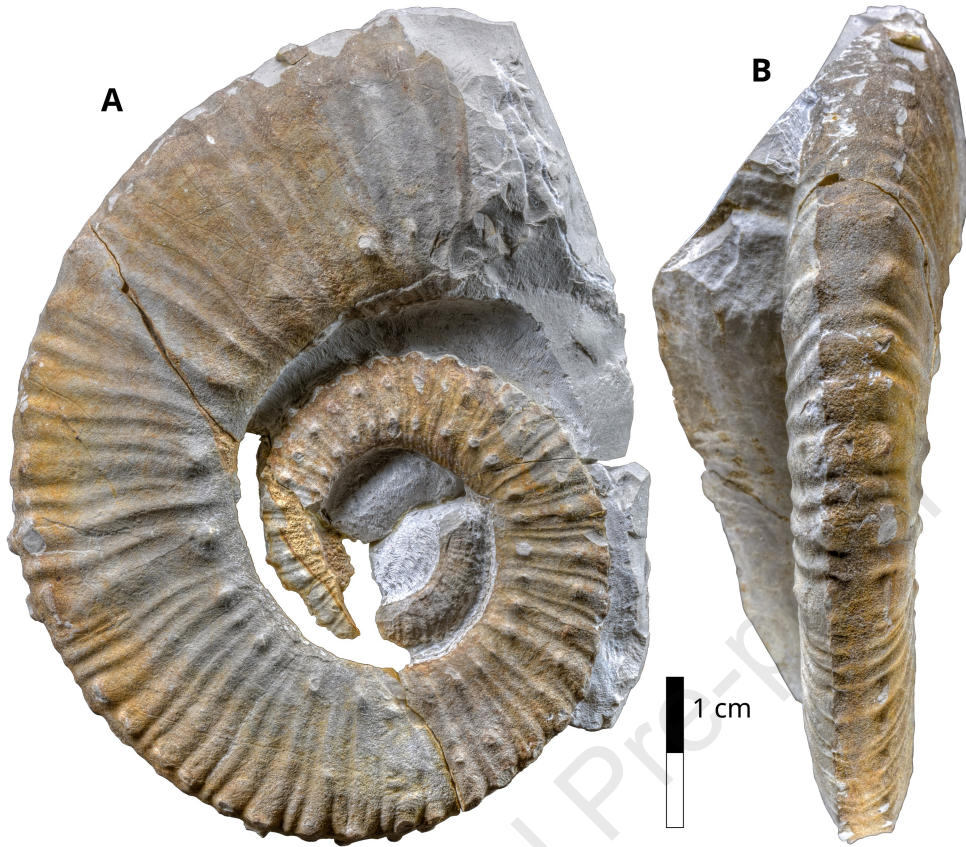


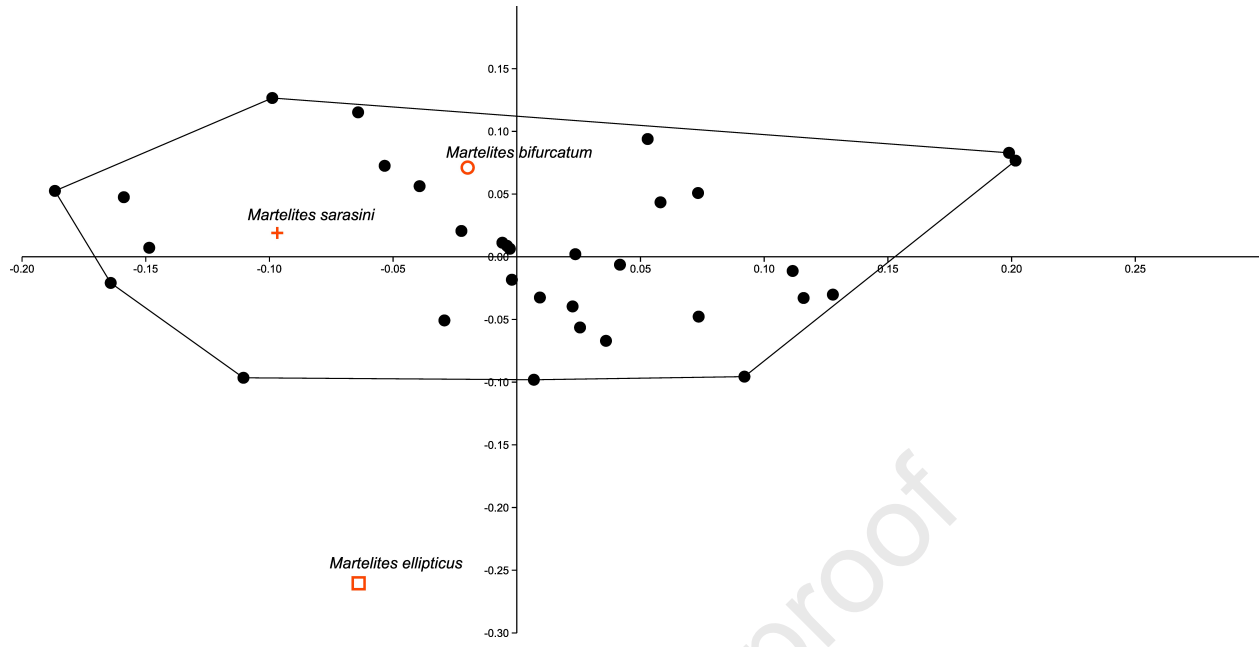
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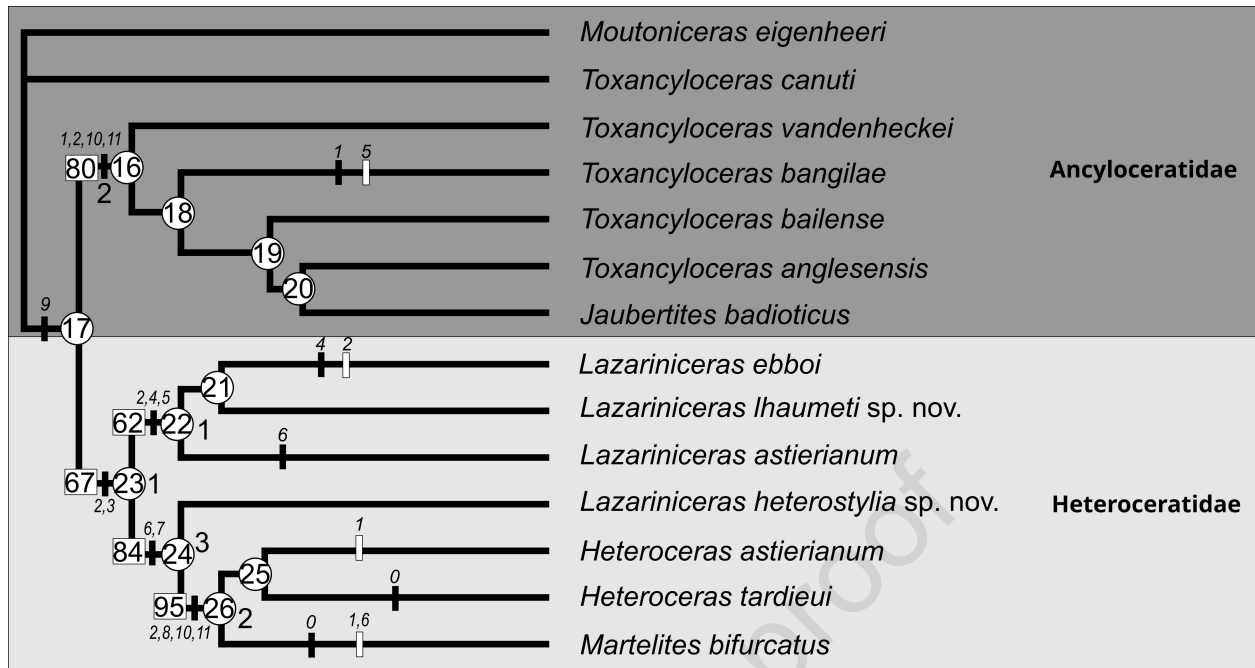












① Nodes

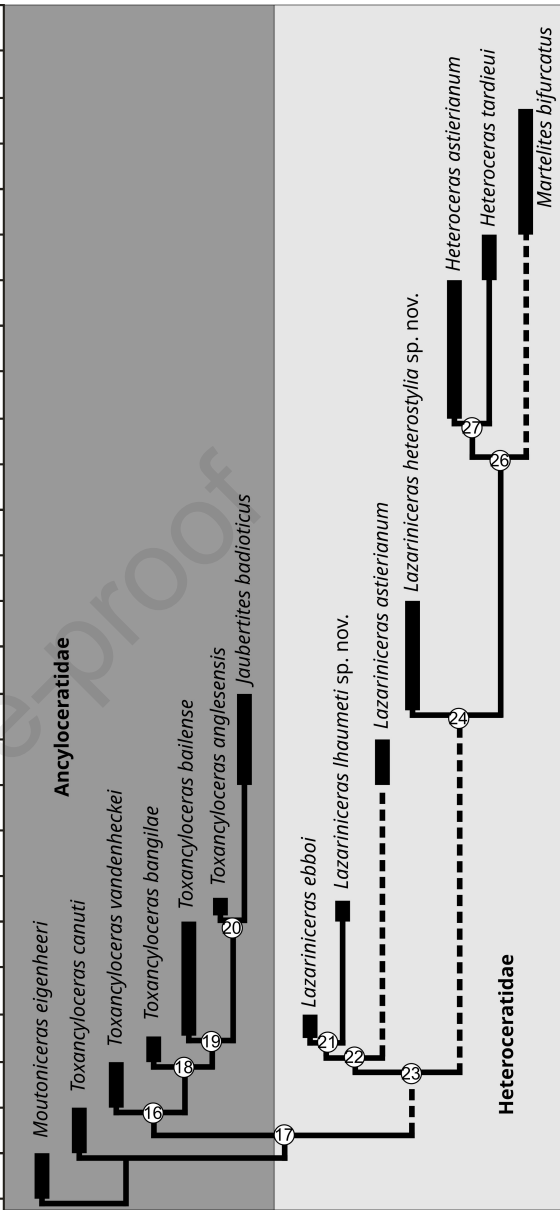
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▮ Homoplasies with changed characters

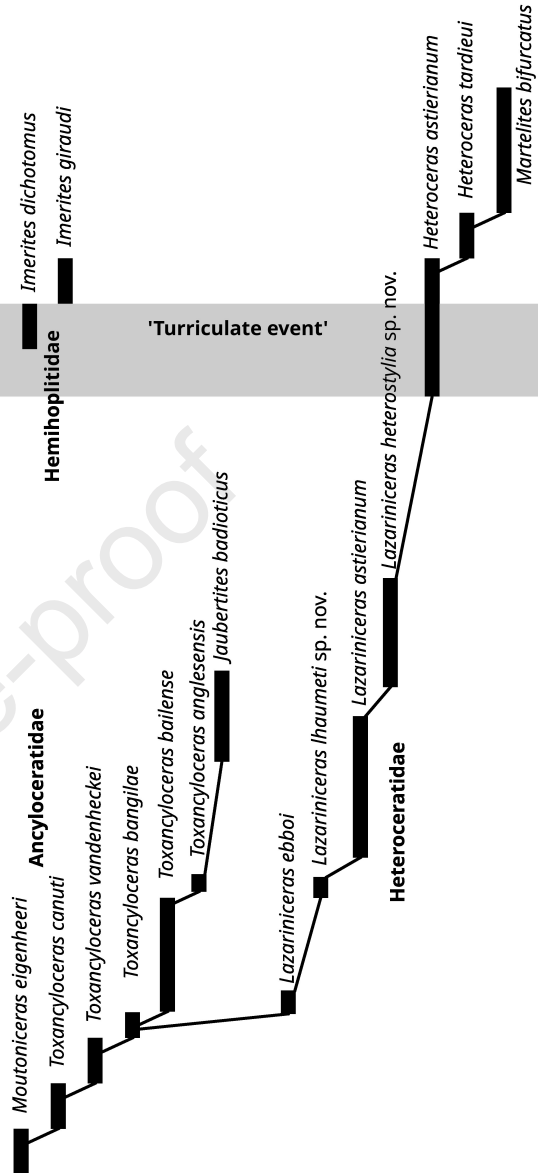
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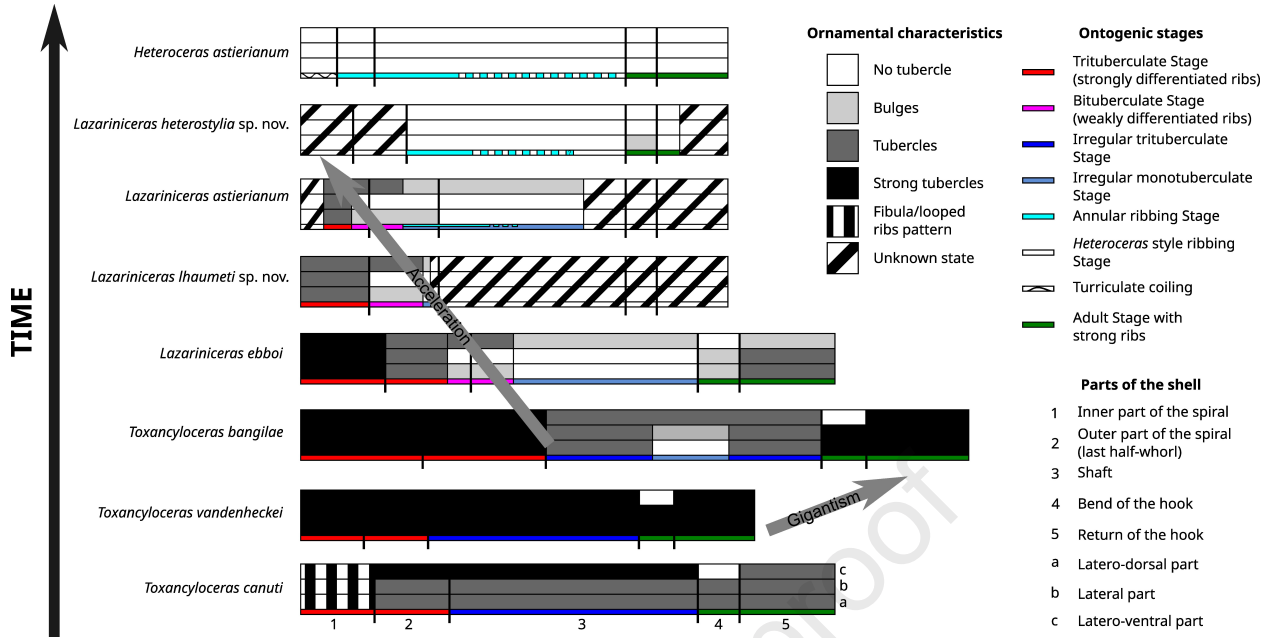
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STAGES	ZONES	SUBZONES	INTERVAL HORIZONS	
BARREMIAN	UPPER	<i>Imerites giraudi</i>	<i>Pseudocrioceras waagenioides</i>	
			<i>Martelites sarasini</i>	<i>Anglesites puzosianum</i>
			<i>Imerites giraudi</i>	<i>Heteroceras tardieui</i>
				<i>Imerites giraudi</i>
				<i>Imerites dichotomus</i>
		<i>Camereiceras limentinum</i>	<i>Hemihoplites feraudianus</i>	<i>Pseudoshasticrioc. austrani</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>Gassendiceras alpinum</i>	
		<i>Toxancyloceras vandenheckei</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>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>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>		
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		<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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