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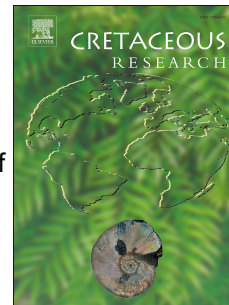
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# 1     **Implications of the ‘hemihoplitid-like’ ammonites iterative morphology in** 2             **the context of the late Tethyan Barremian (Early Cretaceous)**

3  
4                             Didier Bert<sup>a,b,c\*</sup>, Stéphane Bersac<sup>c</sup>, Léon Canut<sup>c</sup>

5  
6     \* Corresponding author: didier.paleo@gmail.com.

7     <sup>a</sup>: Réserve naturelle nationale géologique de Haute-Provence, Service Environnement, Conseil  
8     départemental des Alpes de Haute-Provence, 13 rue du Docteur Romieu, CS 70216, F-04995 Digne-  
9     Les-Bains Cedex 9, France.

10    <sup>b</sup>: Laboratoire Géosciences, UMR-CNRS 6118, Université de Rennes-1, campus Beaulieu, bâtiment  
11    15, F-35042 Rennes cedex, France.

12    <sup>c</sup>: Laboratoire du Groupe de recherche en Paléobiologie et biostratigraphie des Ammonites (GPA),  
13    Bois-Mésanges, quartier St Joseph, F-04170 La Mure-Argens, France.

## 14 15    **Highlights**

- 16       • Resemblance of *Lenicostites rusticus* with Hemihoplitidae is a case of homeomorphy.
- 17       • The numerous reported occurrences of Hemihoplitinae over the world are reviewed.
- 18       • Pareto-optimal solution explains homeomorphy of the ‘hemihoplitid-like’  
19       morphology.
- 20       • Homeomorphitinae subfam. nov. and Shasticrioceratidae fam. nov. are proposed.
- 21       • *Lenicostites* is a victim of the Gause Principle in favour of the Hemihoplitinae.

## 22 23    **Abstract**

24

25 Hemihoplitidae evolution is well documented in the north-west Tethyan margin at the lower  
26 upper Barremian. In this context, the genus *Lenicostites* gen. nov. (*L. rusticus*), with  
27 'hemihoplitid-like' morphology, is unexpected because of its age older than the earliest  
28 *Hemihoplites* and its evolutionary stasis that contrasts with the rapid changes of the  
29 Hemihoplitidae. Data show no connection between Hemihoplitidae and Lenicostitidae fam.  
30 nov. and the resemblance is homeomorphy. The numerous reported occurrences of  
31 Hemihoplitinae over the world are reviewed. Their critical revision shows that some of them  
32 are contradictory with the evolutionary history of the group. The 'hemihoplitid-like'  
33 morphology is iterative in several taxa without any phyletic links (homeomorphy). Reasons  
34 could be linked to the morphospace occupation in the zone of maximum equilibrium between  
35 different constraints (a Pareto-optimal solution), making such morphology effortless to  
36 reproduce. The Austral Homeomorphitinae subfam. nov. (with *Homeomorphites*  
37 *aguirreurretae* gen. nov. et sp. nov.) are assigned to the Neocomitidae. A phyletic link  
38 between *Shasticrioceras* and *Antarcticoceras* is suggested (Shasticrioceratidae fam. nov.).  
39 Until proven otherwise, there is no Hemihoplitinae outside the north and west margins of the  
40 Tethys (including the Essaouira Basin). Homeomorphy between Hemihoplitinae and  
41 Lenicostitidae fam. nov. is explored and convergence seems the most convincing hypothesis.  
42 The further appearance of *Camereiceras* (Hemihoplitinae) could establish favorable  
43 conditions for interspecific competition, and the disappearance of *Lenicostites* gen. nov. could  
44 be interpreted as a complete competitive replacement. In this hypothesis *Lenicostites* gen.  
45 nov. is a victim of the Gause Principle as it lost the Red Queen race.

46

47 **Key-words:** ammonites; Early Cretaceous; homeomorphy; competition; systematics; Pareto-  
48 optimal solution.

49

## 50 1. Introduction

51

52 The family Hemihoplitidae Spath, 1924a is a key element of the marine early late Barremian  
53 ammonite fauna because of its very rapid evolution and diversification, to the extent that  
54 successive representatives of this family are used in the definition of a number of stratigraphic  
55 horizons (Fig. 1). In the context of the North Tethyan margin, this family develops three  
56 major trends, materialized into three subfamilies: (1) the Gassendiceratinae Bert et al., 2006  
57 appear in the *Toxancyloceras vandenhencke* Subzone and represent the stem of the whole  
58 group (following Bert and Bersac, 2014, this subfamily actually would appear in the early  
59 Barremian in the proto-Atlantic context of the Essaouira Basin, Morocco, with *Gassendicer*  
60 *essaouirae* Bert and Bersac, 2014); (2) the Peirescinae Bert et al., 2006, which connect with  
61 the Douvilleiceratoidea Parona and Bonarelli, 1897 (spanning the *Gassendicer*  
62 *alpinum* to *Imerites giraudi* subzones); and (3) the Hemihoplitinae Spath, 1924a, which are derived from  
63 the genus *Gassendicer*  
64 *alpinum* Subzone. The older Hemihoplitinae species [*Camereiceras breistrofferi* (Sarkar,  
65 1955) and *C. marchandi* Bert et al., 2006] retain some characters from the *Gassendicer*: (1)  
66 the ontogenetic stages (the Heberti, Barremense and *Camereiceras* stages – see Bert et al.,  
67 2013 for an extensive description); (2) ornamentation with differentiated ribs; (3)  
68 trituberculate main ribs; (4) general morphology with uncoiled shell. Later, in the  
69 *Camereiceras limentinus* Subzone, the dimorphic genus *Camereiceras* Delanoy, 1990a has  
70 always its whorls in contact. It gives rise to the genera *Pachyhemihoplites* Delanoy, 1992 and  
71 *Hemihoplites* Spath, 1924a. The evolution of *Hemihoplites* shows a progressive reduction of  
72 the tubercles with, in stratigraphic order, *H. cornagoae* Bert et al., 2006, *H. astarte* (Fallot and  
73 Termier, 1923) and finally, *H. feraudianus* (d'Orbigny, 1841). The latter is morphologically

74 simplified with weak tubercles (two rows only) in the *H. feraudianus* Subzone, where the  
75 Hemihoplitinae disappear.

76

77 This systematic and evolutionary framework is now relatively well known and restricted to  
78 the northern Tethyan margin between the *G. alpinum* and *H. feraudianus* subzones (early late  
79 Barremian – see Bert, 2012a, 2014a, 2014b; Bert and Bersac, 2013, 2014; Bert et al., 2013).

80 In this context, the discovery of new ammonite specimens with simplified morphology very  
81 close to *Hemihoplites feraudianus* in the lower part of the upper Barremian of the Vocontian  
82 Basin (Barremian stratotype area, southeastern France), is totally unexpected. These are not  
83 only present two ammonites subzones (three if considering their appearance) before the  
84 appearance of the first *H. feraudianus*, but their appearance is also clearly anterior to the  
85 oldest known Tethyan Hemihoplitinae. These ammonites are described here in detail; they are  
86 related to the hitherto poorly known species *Hemihoplites rusticus* Vermeulen, 1996. Their  
87 study suggests that they probably do not belong to Hemihoplitidae and we propose the new  
88 genus *Lenicostites* gen. nov. and the new family Lenicostitidae nov. fam.

89

90 A review of the literature shows that this type of situation is not exceptional in the Lower  
91 Cretaceous: many occurrences of Hemihoplitinae have been reported all around the world,  
92 always with specimens of simplified morphology, while their geographical occurrence are  
93 sometimes very far between them and the Tethyan domain in disparate stages from  
94 Valanginian to Aptian. Systematics, based on relationships between morphology, ontogeny,  
95 stratigraphy and paleobiogeographical data helps reframe their taxonomy; it appears that most  
96 of them are not Hemihoplitidae. Hypothesis about phylogenetic relationships and  
97 paleoecology of these ammonites are considered and several new taxa have to be introduced:

98 the Homeomorphitinae subfam. nov., with *Homeomorphites* gen. nov. (type-species: *Ho.*  
99 *aguirreurretae* gen. nov. et sp. nov.), and Shasticrioceradidae fam. nov.

100 Finally, several hypotheses about the phyletic position of *Lenicostites* gen. nov. are discussed,  
101 which rise questions about homeomorphy and its causes (convergence, parallelism or iterative  
102 evolution), interspecific competition, competitive replacement, and Red Queen theory applied  
103 to these ammonites.

104

## 105 **2. Material**

106

107 This study focuses on the discovery of new material of the extremely rare genus *Lenicostites*  
108 gen. nov. These fossils are from four bed-by-bed sampled stratigraphic sections in the south-  
109 east of France (Alpes de Haute-Provence and Alpes-Maritimes), two of them located in the  
110 immediate vicinity of the Barremian historical stratotype of the Angles road (sections A' and  
111 A\*), and the others located in the Arc of Castellane between Rougon and Vence (sections  
112 MAN and TAI). Part of this area belongs to the protected perimeter of the Geological  
113 National Nature Reserve of Haute-Provence (RNNGHP), managed by the Departmental  
114 Council of the Alpes de Haute-Provence on behalf of the French State. All the collected  
115 material is curated by the RNNGHP.

116 The stratigraphic framework used for the North Tethyan Barremian in this work was proposed  
117 by the I.U.G.S Lower Cretaceous ammonite working group (the Kilian Group – Reboulet et  
118 al., 2018). This framework is completed by several works, which helped to reach a high  
119 stratigraphic precision level (Fig. 1): for the Barremian (Bert et al., 2008; Bert and Delanoy  
120 2009; Bert et al., 2010, 2011 and 2018), Hauterivian (Company et al., 2003; Matamales-  
121 Andreu and Company, 2019) and Aptian (Bersac and Bert 2012). For local zonations, the  
122 following works were used to make correlations: Aguirre-Urreta et al. 2007a (Chile and

123 Argentina), Aguirre-Urreta, 2002, Aguirre-Urreta et al., 2007b, Riccardi, 1988 and Riccardi  
124 and Medina, 2008 (Patagonia), Murphy, 1975 (California). The terminologies used in this  
125 paper (biostratigraphy and chronostratigraphy vs. geochronology) respect the standards of the  
126 International Commission on Stratigraphy (Salvador, 1994).

127

### 128 **3. Geological setting and sections studied**

129

130 During the Mesozoic Era, the Vocontian Basin (south-east of France) was a large subsident  
131 intracratonic area opened towards the Alpine ocean. The sedimentary basin is now bordered  
132 by the Mediterranean Sea (south), the Jura (north), the Massif Central (west) and the Alps  
133 (east). The Barremian, in the stratotype area (Angles, department of the Alpes de Haute-  
134 Provence), is characterized by pelagic sedimentation with an alternation of 0.10–1m thick  
135 marlstones and limestones. The outcrops are usually of good quality with continuous  
136 sedimentation and abundant fossils, with dominance of the ammonites. However, the lower  
137 upper Barremian in this area, and especially the *Toxancyloceras vandenheckei* Zone and the  
138 most part of the *Gassendiceras alpinum* Subzone, contain very few macrofossils and the beds  
139 require long time sampling.

140

#### 141 *3.1. Pelagic sections A\* and A'*

142

143 The section A\* was described and figured by Bert (2012b) and Bert et al. (2018). It  
144 corresponds to the complementary section to the Barremian historical stratotype of the Angles  
145 road (section A). In section A, the lower part of the upper Barremian (*T. vandenheckei* and  
146 *Gerhardtia sartousiana* zones) is poorly exposed because of growth faults that disrupt the bed  
147 successions (see more explanations in Bert, 2012b, p. 4). Given these difficulties the new



148 reference section A\*, in the immediate lateral continuity of the stratotype, allows to make  
149 good study of these beds. Section A' is another complementary section in the adjacent hill to  
150 the Barremian stratotype. For the *T. vandenheckei* Subzone, the bed succession is the same in  
151 the both sections A' and A\*.

152

### 153 *3.2. Neritic sections MAN and TAI*

154

155 Section MAN was reported by Cotillon (1971). It is close to the section SO in the Rougon  
156 area, which was described previously (Bert et al., 2013, p. 359–361, text-fig. 8). Section TAI  
157 was described and figured in a previous work (Bert et al., 2013, p. 361–362, text-fig. 9). This  
158 area is part of the neritic domain in the southern Vocontian platform border, which is rich in  
159 glauconite, benthic faunas and cephalopods. Sedimentation rates are usually low and  
160 discontinuous with some episodes of condensation and sedimentary gaps (sedimentation in a  
161 system of tilted blocks); despite of this, the beds benefit from a good stratigraphic attribution  
162 given their abundant ammonite content.

163

## 164 **4. Descriptive palaeontology**

165

166 Class: Cephalopoda Cuvier, 1798

167 Order: Ammonoidea Agassiz, 1846

168 Suborder: Ancyloceratina Gill, 1871

169 Superfamily: Ancyloceratoidea Gill, 1871

170 Family: Lenicostitidae fam. nov.

171 *Type genus.* This family is currently monotypic, with *Lenicostites* gen. nov.

172 *Discussion.* It is undeniable that *Lenicostitidae* fam. nov. are morphologically very close to  
173 *Hemihoplitinae*, and especially to *Hemihoplites feraudianus* (d'Orbigny, 1841) and the adult  
174 microconchs of *Camereiceras marchandi* and *C. limentinus* with smooth simple ribbed  
175 ontogenetic stage on body chamber. However, the total absence of the ontogenetic stages  
176 common to all *Hemihoplitidae*, which are lacking here (see description below), but also the  
177 stratigraphic position of the oldest representatives of the genus *Lenicostites* gen. nov. is  
178 problematic. *Lenicostites* gen. nov. appears long before the cladogenesis between the first  
179 *Camereiceras* (the direct ancestor of *Hemihoplites*) and the genus *Gassendiceras*, which  
180 occurs in the late part of the *Gassendiceras alpinum* Subzone (Fig. 1). *Lenicostites rusticus*  
181 (Vermeulen, 1996) gen. nov. appears in southeastern France from the middle part of the *T.*  
182 *vandenheckei* Subzone, at the same time as the first *Gassendiceras* of the *G. cf. essaouirae*  
183 Bert and Bersac, 2014 group that migrate to the northwestern Tethyan margin from Moroccan  
184 representatives (see Bert and Bersac, 2014; Company et al., 2008). There is no argument to  
185 indicate a link between *Gassendiceras* and *Lenicostites* gen. nov., which have a very different  
186 morphology, and above all a very different ontogeny (see the discussion of the genus  
187 *Lenicostites* gen. nov.). In this context, it is not possible to include the genus *Lenicostites* gen.  
188 nov. into the family *Hemihoplitidae*, which would make this family polyphyletic; family  
189 *Lenicostitidae* fam. nov. is thus proposed. Pending new data, this family is currently classified  
190 into the *Ancyloceratoidea* superfamily, a position reinforced by the presence of a widely  
191 perforated umbilicus (Vermeulen, 1996, pl. 3, fig. 5).

192

193 Genus *Lenicostites* gen. nov.

194 *Denomination.* From latin *lenis*, which means smooth (here smooth ribs).

195 *Type-species.* *Lenicostites rusticus* (Vermeulen, 1996) gen. nov.

196 *Specific content.* *Lenicostites* gen. nov. is currently monospecific.

197 *Geographic occurrence.* *Lenicostites* gen. nov. is known in southeastern France, both in  
198 basinal and platform area.

199 *Stratigraphic occurrence.* *Lenicostites* gen. nov. is currently known to be present in several  
200 occurrences in the lower upper Barremian (Fig 1): (1) in the middle part of the *T.*  
201 *vandenheckei* Subzone in association with *Toxancyloceras ebboi* Delanoy, 2003 (see Bert et  
202 al., 2018, fig. 5 for the stratigraphical occurrence of this species) and *Gassendiceras* cf.  
203 *essaouirae*; (2) in the upper part (non-terminal) of the *G. alpinum* Subzone associated with  
204 numerous Barremitidae [the ‘bed with little *Barremites*’ of Cotillon, 1971, Vermeulen, 1996  
205 and Bert, 2009; these Barremitidae have a morphology close to *Nikolovites charrieri*  
206 (d’Orbigny, 1841)]. And (3) in the *Camereiceras limentinus* Horizon.

207 Note that *L. rusticus* gen. nov. was used by Vermeulen (1998a, 1998b) to define an ammonite  
208 horizon in the upper part of the *Toxancyloceras vandenheckei* Zone. Although this horizon  
209 was no longer used later (see Vermeulen, 2003), the discovery of *L. rusticus* gen. nov. in a  
210 very wide range renders its use impossible in high resolution biostratigraphy.

211 *Diagnosis.* Medium sized genus (up to D=140 mm) with slightly overlapping planispiral  
212 whorls. Umbilicus wide and shallow, perforated in the innermost whorls. Subcircular whorl  
213 section, quite thick, which tends to heighten with growth. Convex flanks, periventral margin  
214 very rounded that gradually passes to the rounded venter. Abrupt peri-umbilical wall.  
215 Ornamentation consisting of ribs most often simple, undifferentiated, thick, radial to slightly  
216 retroverse, sometimes a little sinuous but without forming an inflection on the venter. Thinner  
217 intercalary ribs, which do not always reach the base of the flanks; they are only present on the  
218 robust morphology of the species. In the inner whorls, the ribs are uniformly wide from the  
219 base to the top of the flanks and on the ventral area, while on the outermost whorls they widen  
220 from the upper quarter of the flanks and on the venter. Reinforcements of the ribs are visible

221 at the base and at the top of the flanks; they are inconspicuous without ever forming a tubercle  
222 and they are more developed in the periventral zone of the body chamber.

223 *Discussion.* By their morphological and ornamental characteristics, the representatives of  
224 *Lenicostites* gen. nov. have been reported in the subfamily Hemihoplitinae (Hemihoplitidae)  
225 in the literature (= *Hemihoplites rusticus*, in Vermeulen, 1996; Klein et al., 2007).  
226 Morphologically, this genus undeniably recalls *H. feraudianus* (d'Orbigny, 1841), which is  
227 the least tuberculate species of *Hemihoplites* (compare Fig. 2, 3 with Fig. 4). However, in  
228 *Lenicostites* gen. nov., the whorl section is rounded, whereas in *H. feraudianus* the flanks are  
229 systematically flatter with a well-defined ventral area. On terms of ornamentation,  
230 bifurcations are very common at the base of the flanks in *H. feraudianus*, whereas they are  
231 almost absent in *L. rusticus* gen. nov. The intercalated ribs are likewise very much rarer in  
232 *Lenicostites* gen. nov. But above all, in the latter, the ribs are radial with a slightly retroverted  
233 tendency, whereas in *H. feraudianus* the tendency is for the projection towards the front of the  
234 shell. Finally, in the inner and middle whorls of *H. feraudianus*, the ribs bear true small  
235 punctiform tubercles at the base and at the top of the flanks, contrary to *L. rusticus* gen. nov.  
236 (see below the chapter description and ontogenesis of *L. rusticus* gen. nov.). Note that the first  
237 representatives of *L. rusticus* gen. nov. and the first *H. feraudianus* are separated by more  
238 than three ammonite subzones (Fig. 1).

239 All the other species belonging to the different genera of Hemihoplitinae (*Hemihoplites*,  
240 *Camereiceras*, *Pachyhemihoplites*) and Peirescinae (*Spinocrioceras* Kemper, 1973,  
241 *Peirescites* Bert et al., 2006) systematically have a differentiated ornamentation with  
242 trituberculate main ribs, which is never the case for *Lenicostites* gen. nov. However in this  
243 context, *Lenicostites* gen. nov. recalls the adult morphology (stage with smooth ribs, only  
244 present on body chamber) of the *Pachyhemihoplites* and *Camereiceras* microconchs [see for  
245 example the microconch morphology *janus* Thieuloy, 1979 of *Pachyhemihoplites gherti*

246 (Sarkar, 1955), *Camereciceras marchandi*, or *C. limentinus* Thieuloy, 1979 – Fig. 5B-C]. In  
247 all cases, the ribs tendency is to retroversion in *Lenicostites* gen. nov., and in contrast to the  
248 forward projection in Hemihoplitinae.

249 Compared with *Lenicostites* gen. nov., the Gassendiceratinae *Gassendiceras* and  
250 *Pseudoshasticioceras* Delanoy, 1998 are large sized heteromorphs with widely-differentiated  
251 ribs. Generally, one does not recognize in *Lenicostites* gen. nov. the ontogenetic stages, or  
252 their derivatives, common in all Hemihoplitidae (the Heberti, Barremense, etc., stages; see  
253 Bert et al., 2006, 2010 and 2013). Conversely to *Lenicostites* gen. nov., trituberculate ribs  
254 (prolonged by spines) are strongly present in the Gassendiceratinae.

255 Apart from Hemihoplitidae, some robust *Martelites* Conte, 1989 have a morphology close to  
256 *Lenicostites* gen. nov. In addition to a much more recent age (*Martelites sarasini* Subzone),  
257 the genus *Martelites* Conte, 1989 (Heteroceratidae Spath, 1922) shows young helical whorls,  
258 which is never the case in *Lenicostites* gen. nov., and a relationship between these two genera  
259 is therefore totally excluded.

260 Patagonian ammonites classified as *Hemihoplites* (*H. ploszkiewiczzi* Riccardi and Aguirre-  
261 Urreta, 1989, *H. varicostatus* Riccardi and Aguirre-Urreta, 1989 and *H. feraudianus* Aguirre-  
262 Urreta, 2002 non d'Orbigny, 1841 – here *Homeomorphites* gen. nov., see below chapter 5.8)  
263 by Riccardi and Aguirre-Urreta (1989) and Aguirre-Urreta (2002), are morphologically close  
264 to *Lenicostites rusticus* gen. nov. because of the lack of tubercles and their general appearance  
265 (coiling). However, their ornamentation is different because of the numerous bifurcations of  
266 the ribs, their flexuous appearance from the inner whorls of the shell, the higher presence of  
267 intercalary ribs, and what looks like to rare reinforced ribs, low constrictions, or even 'zigzag'  
268 stages on the ventral area (perisphinctoid characters). The whorl section in *Homeomorphites*  
269 gen. nov. is also different with more angulous peri-umbilical and peri-ventral margins. The  
270 adult size is larger in the upper Barremian species *Homeomorphites aguirreurretae* gen. nov.

271 et sp. nov., which have a different ontogenetic development with the presence of a smooth  
272 adult stage, absent in *Lenicostites rusticus* gen. nov. Finally, in the oldest species of this  
273 group, *Homeomorphites ploszkiewiczii* gen. nov., the ornamentation is much denser than in *L.*  
274 *rusticus* gen. nov.

275

276 *Lenicostites rusticus* (Vermeulen, 1996) gen. nov.

277 Figs. 2, 3

278 v 1996 *Hemihoplites rusticus* sp. nov.; Vermeulen: p. 67–68; pl. 3, figs. 2–5.

279 v 1998a *Hemihoplites rusticus* Vermeulen, 1996; Vermeulen: pl. 4, figs. 7–8.

280 *Holotype*. Specimen No. 4141351 of the J. Vermeulen's collection (see Vermeulen, 1996, pl.  
281 3, fig. 2–5, refigured here in Fig. 2A).

282 *Type locality*. The Saint-Martin ravine, near Escragnolles (crop-section VM – Alpes-  
283 Maritimes, southeastern France).

284 *Type horizon*. Bed VM/20 of the type section, which also delivers many small *Barremites*.  
285 The bed 19 delivered *Toxancyloceras vandenheckei* (Astier, 1851) and *T. bailense*  
286 (Vermeulen, 1996). In the same area, an equivalent bed also delivered *Gassendiceras*  
287 *multicostatum* (Sarkar, 1955) and *G. alpinum* (d'Orbigny, 1850) (Bert et al., 2013, 2018).

288 These faunas indicate the lower half of the *T. vandenheckei* Zone (*T. vandenheckei* Subzone  
289 and *G. alpinum* Horizon at the base of the *G. alpinum* Subzone). The bed 21a delivered some  
290 *Gassendiceras quelquejeui* Bert et al. 2006 (unpublished data) of the top of the *G. alpinum*  
291 Subzone. Thus, the bed 20 is constrained in the non-terminal upper part of the *G. alpinum*  
292 Subzone. This bed corresponds to the level 108 of the Majastre crop-section described by Bert  
293 (2009).

294 *Geographic occurrence*. The same as the genus.

295 *Stratigraphic occurrence*. The same as the genus.

296 *Material studied* ( $N=8$ ). Four specimens are from the Barremian stratotype area in the  
 297 Vocontian Basin (Alpes de Haute-Provence, southeastern France), from bed A\*/149-3 (No.  
 298 RNNGHP.DBT.04007-A\*/149-3.AX95 and RNNGHP.DBT.04007-A\*/149-3.BA54 – Fig.  
 299 2E) and A’/149-4 (No. RNNGHP.DBT.04007-A’/149-4.AJ49 – Fig. 2B – and  
 300 RNNGHP.DBT.04007-A’/149-4.BA53).

301 Three specimens are from the platform borders in the Arc de Castellane (Alpes de Haute-  
 302 Provence and Alpes-Maritimes, southeastern France): from the ‘*Camereiceras limentinus*  
 303 beds’ of section MAN near Rougon (No. RNNGHP.DBT.04171-MAN.BB34 – Fig. 2C), and  
 304 from bed 99 of the section TAI near Vence (No. RNNGHP.SBC.06050-TAI/99.TAI153 –  
 305 Fig. 3 – and RNNGHP.SBC.06050-TAI/99.TAI155 – Fig. 2D). In addition, the holotype (No.  
 306 4141351 of the J. Vermeulen’s collection) was also examined; it is here refigured (Fig. 2A).

307 *Measurements*. Only one specimen is complete enough to be measured (mm). It is compared  
 308 with the holotype (see Vermeulen, 1996). D is the maximum measured diameter, Dph is the  
 309 diameter of the phragmocone, H, W and U are respectively the height and width of the whorl  
 310 and the diameter of the umbilicus.

311

312 **Table 1.** Measurements of the two most complete specimens.

N° specimens	D	Dph	H	W	U	H/D	W/D	U/D	W/H
RNNGHP.SBC.06050- TAI/99.TAI153 Fig. 3	140.00	118	53.72	47.76	56.48	0.38	0.34	0.40	0.89
4141351 (holotype – Fig. 2A)	52.40	?	19.00	18.90	19.60	0.36	0.36	0.37	1.00

313

314 *Description and ontogenesis*. The collected specimens are few, but they give a good  
 315 representation of the species. Specimen No. RNNGHP.SBC.06050-TAI/99.TAI153 (Fig. 3) is  
 316 interpreted as robust morphology; it is the most complete, probably an adult, with a quarter

317 whorl of the body chamber preserved. Specimens No. RNNGHP.DBT.04007-A\*/149-  
318 3.AX95, RNNGHP.DBT.04007-A\*/149-3.BA54 (slender morphology – Fig. 2E),  
319 RNNGHP.DBT.04007-A'/149-4.BA53, RNNGHP.SBC.06050-TAI/99.TAI155 (Fig. 2D) and  
320 RNNGHP.DBT.04171-MAN.BB34 (robust morphology – Fig. 2C) are fragments of inner  
321 whorls. Finally, specimen No. RNNGHP.DBT.04007-A'/149-4.AJ49 (Fig. 2B) is a two-part  
322 fragmented half-whorl of an adult body chamber at a maximal extrapolated diameter of  
323  $D=120$  mm. The shell is plan-spiraled with slightly covering whorls. The whorl section is in  
324 all cases rounded and changes during growth, which makes it possible to distinguish two  
325 ontogenetic stages:

326 - (1) The inner and middle whorls, up to a diameter of about  $D=80$  mm. At this point,  
327 the whorl section is thick, sub-circular with very convex flanks. The umbilical wall is very  
328 abrupt and connects to the flanks by an angular margin, blunted towards the end of the stage.  
329 On the other hand, the periventral margin is very rounded and the flanks progressively move  
330 towards the rounded venter. The ornamentation consists of ribs, mostly simple, with the  
331 presence of thinner intercalated ribs on robust morphology (No. RNNGHP.SBC.06050-  
332 TAI/99.TAI153, Fig. 3, and RNNGHP.DBT.04171-MAN.BB34 – Fig. 2C), while they are  
333 almost absent otherwise. The ribs are thick, almost uniformly but slightly wide on the flanks,  
334 with a relatively radial to slightly retroverted pattern, without forming any inflection on the  
335 ventral area, where they are a little wider. However, they present inconspicuous enlargements  
336 at the base and the top of the flanks, but which cannot be described as bulges or never form a  
337 tubercle. There are no constrictions. At the end of this stage, the ornamentation becomes  
338 barely sinuous on the flanks and the ribs widen strongly from their upper third.

339 - (2) The outer whorl, known from the diameter of  $D=100$  mm, corresponds to the end  
340 of the phragmocone and the body chamber. On this part of the shell, the whorl section is  
341 modified by increasing the height of the flanks (reduction of the value  $W/H$ ), to become



342 subquadratic rounded. The periventral margin remains very rounded and progressive while  
343 the flanks flatten. The ribs are enlarged from the upper third of the flanks and on the ventral  
344 area while they are weakened on the rest of the shell. The intercalated ribs are very rare from  
345 the mid-flank, even in the robust form, and do not seem to connect to the main ribs. Any  
346 evidence of reinforcement on the ribs has disappeared, with the exception of an increasingly  
347 pronounced shoulder during growth on the periventral margin (better visible on the robust  
348 morphology).

349 The number of specimens is too low to quantify validly the intraspecific variation under a  
350 statistical approach. However, the variation observed between robust and gracile  
351 morphologies seems here to concern only the strength of the ornamentation and the presence  
352 of intercalated ribs. Considering the general laws of intraspecific variation in ammonites (see  
353 Bert, 2013, 2014), this isolated character is not taken here to be the result of a species  
354 differentiation.

355 The suture lines could not be studied.

356 *Discussion.* The same as the genus.

357

## 358 **5. Critical review of the taxa classified as Hemihoplitinae**

359

360 In the literature, many occurrences of Hemihoplitinae have been reported all over the world in  
361 a large stratigraphic range (Fig. 6 – Valanginian to Aptian, see references in Klein et al.,  
362 2007), some of them being contradictory with the evolutionary history of the group. Thus, a  
363 critical review is essential to understand the geographic and stratigraphic distribution of the  
364 group, which appears in all probability in the late Tethyan Barremian (Bert and Bersac, 2014).

365

366 5.1. The 'Hemihoplitinae' of Eastern Europe (Bulgaria) and Central Asia (Caucasus and  
367 Turkmenistan)

368

369 *Matheronites khwamliensis* Rouchadzé, 1933 is reported from the locality of Lakhépa  
370 (Georgia) together with upper Barremian faunas. It is highly probable that this taxon belongs  
371 to the genus *Hemihoplites* (of which *Matheronites* Renngarten, 1926 is a junior synonym, see  
372 Klein et al., 2007) that seems to confirm the depiction of Kotetishvili (1970) and the  
373 stratigraphic distributions given by Kotetishvili et al. (2005, p. 417). In this case, its  
374 morphology with two peri-umbilical and periventral tubercles brings it closer to *H.*  
375 *feraudianus* with which the synonymy is proposed here.

376

377 *Matheronites ukensis* Dimitrova, 1967 from the upper Barremian of Bulgaria was classified in  
378 the genus *Camereiceras* by Delanoy (1990a), followed by Klein et al. (2007). In our view,  
379 this taxon, based on an incomplete type-specimen without the preserved inner whorls, is to be  
380 attached to the genus *Martelites* (Heteroceratidae), of which it represents a robust  
381 morphotype. This view is supported by the shape of the ribs and the high presence of  
382 bifurcations at the top of the flanks at the pre-adult stage, but also by the change of  
383 ornamentation at the adult stage with the acquisition of a majority of simple ribs progressively  
384 more spaced (compare Delanoy, 1997, pl. 51, fig. 1).

385

386 The type specimen of *Acanthoceras ridzewskyi* Karakasch, 1897 is quite small and  
387 morphologically resembles the Heberti stage known in most Hemihoplitidae (see Bert et al.,  
388 2013), with ribs all identical bearing ventro-lateral and lateral tubercles. However, and  
389 contrariwise to what is known in Hemihoplitidae, the umbilical tubercles are lacking here and  
390 the lateral tubercles are high on the flanks. When introduced, *A. ridzewskyi* Karakasch, 1897

391 was quoted with aptian faunas such as *Hoplites deshayesi* d'Orbigny, 1841, *Acanthoceras*  
392 *martini* d'Orbigny, 1841, *Acanthoceras cornuelianum* d'Orbigny, 1841, *Aspidoceras*  
393 *royerianum* d'Orbigny, 1841 and *Costidiscus recticostatus* d'Orbigny, 1841 in the sandy  
394 glauconitic marlstones near the village of Detich (Caucasus). More recently *A. ridzewskyi* was  
395 most precisely assigned to the *Turkmeniceras turkmenicum* Zone in the uppermost Barremian  
396 (Bogdanova and Prozorovski, 1999), and was considered to be a probable Hemihoplitidae  
397 (see Klein et al., 2007, p. 215–216). The lack of umbilical tubercles and the top Barremian  
398 stratigraphical assignation lead us to exclude *A. ridzewskyi* from Hemihoplitidae. In our  
399 opinion, the only comparable other taxon known in the uppermost Barremian with such  
400 morphology in the innermost whorls is *Pseudocrioceras* Spath, 1924a (both taxa are assumed  
401 to be contemporaneous by Kakabadze and Kotetishvili, 1995, p. 108). Description or  
402 figuration of innermost whorls of *Pseudocrioceras* are quite rare in the literature: the coiling  
403 could be crioconic or with contiguous whorls, the lateral tubercles are high on the flanks and  
404 the umbilical tubercles could be very attenuated or absent (Kakabadze and Thieuloy, 1991, p.  
405 90), just as in *A. ridzewskyi*. More exploration of this hypothesis is prevented by the very  
406 small size of the type specimen of *A. ridzewskyi*; thus, we tentatively propose this taxon in  
407 open nomenclature in the vicinity of the genus *Pseudocrioceras* (= *P. ? ridzewskyi*).

408  
409 *Matheronites brevicostatus* Bogdanova, 1971 was assigned to the genus *Hemihoplites* by  
410 Riccardi and Aguirre-Urreta (1989, p. 451), followed by Klein et al. (2007, p. 214). Despite of  
411 comparable suture line of ELUI type (compare Bogdanova, 1971, fig. 2 and Wiedmann, 1966,  
412 fig. 35), its stratigraphic assignation to the *Turkmeniceras turkmenicum* Zone (uppermost  
413 Barremian – Bogdanova and Prozorovski, 1999) and its morphology with innermost rounded  
414 whorls, ornamentation with very flexuous ribs (especially in inner whorls) bearing a single  
415 row of marginal tubercles, intercalatory ribs present since the innermost whorls and most

416 often only present on the venter (there are no intercalatory ribs in the trituberculate  
417 Hemihoplitidae's Heberti stage), discard *M. brevicostatus* from the Hemihoplitidae.

418

419 *Matheronites turkmenicus* Luppov, 1936, figured only once by Luppov (1936, p. 122, pl. 1,  
420 fig. 1–3), was likened as well to *Hemihoplites feraudianus* by Riccardi and Aguirre-Urreta  
421 (1989, p. 451, 456), and later accepted in the genus *Hemihoplites* by Bogdanova and  
422 Prozorovsky (1999, p. 50) and Klein et al. (2007, p. 217). Its morphology seems very close to  
423 *M. brevicostatus*, and for the same reason we discard *M. turkmenicus* from the  
424 Hemihoplitidae. Pending more data about these two taxa, we left them in open nomenclature.

425

### 426 5.2. The boreal 'Hemihoplitinae'

427

428 *Ancyloceras brevispina* Von Koenen, 1902 and *Ancyloceras trispinosum* (Von Koenen, 1902  
429 non Kakabadze, 1981) were assigned to the genus *Hemihoplites* by Kakabadze (1981),  
430 followed with doubt by Klein et al. (2007). In our view, these taxa are close to the  
431 *Parancyloceras* of the *P. aegoceras* (Von Koenen, 1902) and *P. bidentatum* (Von Koenen,  
432 1902) group from the *P. bidentatum* Zone (Boreal uppermost Barremian) because of their  
433 very particular morphology (paucituberculate in *P. brevispina* and with weaker tubercles in *P.*  
434 *trispinosum*). Consequently, they are assigned here to the boreal genus *Parancyloceras*  
435 (*Paracrioceratidae* Bert and Bersac, 2014).

436

### 437 5.3. The case of the Patagonian 'Hemihoplites'

438

439 The morphology of the Argentinian 'Hemihoplites' (here *Homeomorphites* gen. nov., see  
440 below chapter 5.8), very close to *H. feraudianus*, as well as the report of this last taxon in a

441 convincing local evolutionary context [*H. ploszkiewicz* → *H. varicostatus* → *H. feraudianus*  
442 (here *Ho. aguirreurretae* gen. nov et sp. nov.)], led Aguirre-Urreta (2002) to consider an  
443 evolutionary and migratory history of the Hemihoplitidae from South America to Europe  
444 (Aguirre-Urreta, 2002), while a certain endemism for the Austral Basin was usually assumed  
445 (see for example Leanza and Wiedmann, 1980). However, Delanoy had proposed (1990b) an  
446 origin of the Tethyan *Hemihoplites feraudianus* from older tuberculate European forms, but  
447 without further details. More recently, an origin of *Hemihoplites* among *Camereiceras* has  
448 been considered with an older rooting among *Gassendiceras* (Vermeulen, 2003; Bert et al.,  
449 2006; Bert, 2012a). Finally, Bert and Bersac (2014) proposed an origin of the Hemihoplitidae  
450 (*Gassendiceratinae*), supported by a cladistic analysis, among the boreal Paracrioceratidae  
451 considering a migration via the Moroccan platform where intermediates are present (*G.*  
452 *essaouirae* Bert and Bersac, 2014). New data collected in southeastern France (work in  
453 progress) assert that the direct ancestor of *H. feraudianus* is the trituberculate species *H.*  
454 *astarte* (previously reported as *H. casanovai* in Bert et al., 2008, p. 3), present in the  
455 immediately older levels in the Barremian stratotype area (*H. astarte* Horizon). This species is  
456 derived from *Camereiceras limentinus* via *H. cornagoae*.

457 All these elements do not support the migratory hypothesis of *H. feraudianus* from  
458 populations of the Austral Basin, formulated by Aguirre-Urreta (2002), and the  
459 Homeomorphitinae subfam. nov. are here classified into the Neocomitidae (Perisphinctoidea  
460 – see below chapter 5.8. the discussions related to Homeomorphitinae subfam. nov. and  
461 *Homeomorphites* gen. nov.).

462

463 5.4. The other Austral, American and south African 'Hemihoplites'

464

465 In 1992, Klinger and Kennedy depicted two lower upper Barremian specimens from  
466 Zululand, which they compared to *Hemihoplites varicostatus* and *H. ploszkiewiczzi* (here  
467 *Homeomorphites* gen. nov., see below chapter 5.8) because of their morphological similarity  
468 to the Argentinean faunas published by Riccardi and Aguirre-Urreta (1989). Following  
469 Kakabaze and Hoedemaeker (2004), it is clear today that these forms are not Hemihoplitidae.  
470 Their very different coiling (involute) with a high and compressed section, as well as their  
471 particular ornamentation with mid-flanks bifurcations, an almost smooth siphonal band and  
472 inflated ribs on the venter, also distances them from *Homeomorphites* gen. nov. These  
473 specimens can rather be compared with the genus *Hatchericeras*, and especially with *H.*  
474 *argentinense* Stanton, 1901 (compare Riccardi, 1988, pl. 10, fig. 1–2 and Leanza, 1970, pl.  
475 39), which have very thin ribbing, similar to the specimens from Zululand; the suture line  
476 shows also a great resemblance (compare Stanton, 1901, pl. 9 with Klinger and Kennedy,  
477 1992, fig. 37).

478  
479 Due to its very particular morphology with a very narrow umbilicus, *Hemihoplites?*  
480 *mexicanus*, Imlay 1940, from upper Valanginian (Fig. 6 – upper member of the Taraises  
481 Formation, see Barragán and González-Arreola, 2009 and references), superficially recalls the  
482 faunas of south Africa figured by Klinger and Kennedy (1992) under *Hemihoplites* sp. cf.  
483 *ploszkiewiczzi* and *H.* sp. cf. *varicostatus* (here *Hatchericeras argentinense*). Pending more  
484 data, *H.? mexicanus* is left in open nomenclature.

485  
486 In his PhD thesis, Cantú Chapa (1963) reported the presence of *Hemihoplites* cf. *feraudianus*  
487 (pl. 3, fig. 6) in the eastern Mexico (Mexico-Tuxpan Road, km 216.7). Its very partial  
488 preservation does not make it possible to form an opinion, but its Barremian attribution seems  
489 proved by the presence in the same site of *Holcodiscus* aff. *perezianus* (d'Orbigny, 1850). On

490 the other hand, the variation in rib spacing visible on the last whorl, and the importance of the  
491 interrib spaces in relation to the width of the ribs, is not a character known in *Hemihoplites*.

492

493 This is the same with *Hemihoplites* sp. A reported by Myczynski (1977, pl. 6, fig. 5) in the  
494 Polier Formation of Cuba (El Herete, Sierra del Rosario), which bears 3-4 constrictions per  
495 whorl in the inner whorls, and a change in ornamentation in the last whorl with denser and  
496 prorsiradiate ribs bifurcated close to the ventral margin. Its uppermost Hauterivian attribution  
497 is assumed by the presence of *Pseudothurmannia* sp. in the same layer (not figured), while  
498 some Barremian specimens attributed to *Karsteniceras* sp. are also reported. Pending new  
499 data, these Mexican and Cuban specimens are left in open nomenclature.

500

501 *Hemihoplites?* *popenoi* Murphy, 1975, from the *Shasticrioceras patricki* Zone, is a  
502 *Shasticrioceras* Anderson, 1938 (here *Shasticrioceratidae* nov. fam., see below chapter 5.8)  
503 related species, unrelated to Hemihoplitidae. The *S. patricki* Zone has also delivered  
504 *Kotetishvilia* cf. *compressissima* (d'Orbigny, 1841), index species for the middle lower  
505 Barremian (Fig. 6). It is not shocking to bring *H.? popenoi* close to the genus *Shasticrioceras*,  
506 which contains some taxa with a thick or very thick whorl section [e.g. *Shasticrioceras*  
507 *inflatum* Anderson, 1938, *Shasticrioceras wintunius* (Anderson, 1938)].

508

509 *Hemihoplites* (*Matheronites*) *ridzewskii sachicaensis* Kakabadze and Hoedemaeker, 2004 was  
510 introduced on the basis of a single Colombian specimen of very small size. This specimen has  
511 a morphology very close to the type specimen of *Pseudocrioceras?* *ridzewskii*, and for the  
512 same reasons (see above chapter 5.1) we propose the same assignation in open nomenclature  
513 in the vicinity of the genus *Pseudocrioceras*.

514

515 A unique specimen of *Hemihoplites* sp. has been reported in Antarctica by Thomson (1974).  
516 It was collected in screes in a Keystone Cliff crop section, which stratigraphic attribution is  
517 uncertain, perhaps Aptian due to the presence of *Antarcticoceras* in the same formation  
518 (Thomson 1974, p. 39), or even upper Barremian following the opinion of Mourgues (2007)  
519 based on the distribution of the *Sanmartinoceras* Bonarelli and Nágera, 1921 species. Its thin  
520 ribs, closely spaced and projected towards the front of the shell from the periventral area are  
521 not characters of *Hemihoplites*; thus, pending more data this specimen is left in open  
522 nomenclature.

523

524 '*Hemihoplites*' *perezi* Mourgues, 2007 (*nomen nudum*) was first attributed to the genus  
525 *Antarcticoceras* (sensu Mourgues, 2007) as the last representative of a possible evolutionary  
526 lineage [*'Crioceratites*' *ttofurus* Mourgues, 2007 *nomen nudum* → *Antarcticoceras*  
527 *domeykanum* → '*Antarcticoceras*' *perezi* *nomen nudum*]. In a second time, this species was  
528 assigned to the genus *Hemihoplites* without any explanation by Aguirre-Urreta et al. (2007a),  
529 but the idea of this possible affiliation was already present during the introduction of the  
530 taxon (Mourgues, 2007, pp. 240–241, 246). '*H.*' *perezi* *nomen nudum*, with its lower Aptian  
531 assignation (Fig. 6) and very particular ornamentation with two closely spaced rows of  
532 periventral tubercles (Mourgues, 2007, p.75), clearly does not belong to Hemihoplitidae. On  
533 the other hand, its belonging to the genus *Antarcticoceras* (here *Shasticrioceratidae* fam. nov.,  
534 see below chapter 5.8) is credible and deserves to be considered. It should be noted that the  
535 taxa introduced by Mourgues in his unpublished PhD (2007) are all *nomen nudum* for this  
536 reason. The publication announced by Aguirre-Urreta et al. (2007a, p. 158) to regulate this  
537 taxonomic situation is, to our knowledge, still unpublished to date: it now appears to be  
538 highly desirable.

539



540 The fragmentary and certainly teratological specimen of *Crioceratites* (*Hemihoplites*) n. sp.  
541 ex aff. *C. (H.) soulieri* (Matheron, 1878), figured by Jeletzky (1970) from the Barremian of  
542 British Columbia (Canada, North Pacific Realm), is morphologically closer to the genus  
543 *Colombiceras* Spath, 1923 than to Hemihoplitidae. This specimen is left in open  
544 nomenclature pending new data.

545

#### 546 5.5. The Indonesian 'Hemihoplites'

547

548 In the description of lower Cretaceous ammonites from Western New Guinea (Irian Jaya,  
549 Indonesia), Skwarko and Thieuloy (1989) introduced the species *H. taminabuanensis*,  
550 attributed to the genus *Hemihoplites*, from a high energy level (presence of glauconite and  
551 detrital quartz in the deposit) attemptedly assigned to the Barremian (p. 28). Indeed,  
552 *Hemihoplites taminabuanensis* Skwarko and Thieuloy, 1989 (and also *H. sp.*) shows very  
553 strong morphological affinities with the genus *Hemihoplites*, and especially with *H.*  
554 *feraudianus*. However, the presence of very thin secondary riblets in the Indonesian  
555 specimens, sometimes joining the primary ribs at midflanks to make a fibula pattern (see  
556 Skwarko and Thieuloy, 1989, pl. 4, fig. 3), is not an hemihoplitid character. Thus, pending  
557 more complete specimens and data about their age, the Indonesian '*Hemihoplites*' are left in  
558 open nomenclature.

559

#### 560 5.6. The Indian genus *Pascoeites* Spath, 1933

561

562 *Pascoeites* Spath, 1933 (see Spath, 1933, p. 827, pl. CXXVI, fig. 5, 7, 12), of which the  
563 stratigraphic position was long unclear, was included with doubt in Hemihoplitidae by Wright  
564 (in Arkell et al., 1957). This position has since been followed by the authors, but without

565 further clarification (Klein et al., 2007), particularly because of the uncertain age of the  
566 specimens studied by Spath (*P. budavadensis* Spath, 1933 and *P. crassus* Spath, 1933),  
567 which come from white shales with plants (Raghavapuram Shales Formation) from the Eastern  
568 peninsular India (Budavada village, Nellore District, in the Cauvery Basin). The age  
569 attributed by Spath ('probable Barremian') is essentially based on the presence of very badly  
570 preserved and crushed fossils and attributed by him to Holcodisciidae [*Holcodiscus* cf.  
571 *perezianus*, *H.* cf. *caillaudianus* (d'Orbigny, 1850), *Gymnoplites simplex* Spath, 1933], and  
572 *Hoplites* cf. *borowae* Uhlig, 1883, *H.* cf. *beskidensis* Uhlig, 1883, *H. codazzianus* (Karsten,  
573 1886) and *Lytoceras* sp. cf. *vogdti* Karakasch, 1907. Traditionally, the Raghavapuram Shales  
574 Formation is between the Golapille sandstones below and the Tirupati (Tripetty) sandstones  
575 above (Pandey and Dave, 1998). The Barremian/Aptian boundary known in Kachchh  
576 (between Sivaganga Formation, Ghuneri Member and Dalmiapuram Formation, Ukra  
577 Member) can be extended to the Cauvery Basin between the Golapille Formation and the  
578 Raghavapuram Formation, which implies that the overlying Raghavapuram Formation would  
579 be Aptian (S. Jain, pers. comm.). And thus, the genus *Pascoeites* is not Barremian but Aptian  
580 (Fig. 6) unrelated to the Hemihoplitidae; it is left in open nomenclature awaiting more data.

581

### 582 5.7. Analysis of the critical review

583

584 The 'hemihoplitid-like' morphology is characterized by a platonic evolute shell with  
585 moderately overlapping whorls, and subrectangular whorl section (higher than thick) with a  
586 moderately rapid whorl growth. Such shell morphology takes place in the middle of the 3D  
587 pyramidal representation of the W-D-S morphospace, based on the classical Raup parameters  
588 (Raup, 1966, 1967; Tendler et al., 2015, fig. 7B). The ornamentation is at first well marked  
589 with straight or slightly sinuous ribs, often bifurcated; later the shell becomes smooth (Fig.

590 4A). This simplified morphology appears to be rather widespread, especially in view of the  
591 long list of taxa that have been assimilated to Hemihoplitidae in the literature, but which  
592 actually belong to other groups. This morphology is iterative at Valanginian, Hauterivian,  
593 Barremian and Aptian, and several taxa without any phyletic linkage, including outside  
594 Western Tethys, can develop it by convergence (homeomorphy).

595 Beside the cases of homeomorphy mentioned above (chapters 5.1–5.6), one could also  
596 mention the example of some *Martelites* of the latest Barremian (compare Baudouin et al.,  
597 2012, pl. 14, fig. 1 and Delanoy, 1992, pl. 37, fig. 1, with Delanoy, 1994, pl. 6, fig. 5). The  
598 resemblance is even more striking with the early Hauterivian genus *Theodorites* from Crimea  
599 (here assigned to the Neocomitidae, Endemoceratinae) by its general appearance and its  
600 ornamentation close to *H. feraudianus* (compare Baraboshkin and Mikhailova, 2006, fig. 2b  
601 and c, with Delanoy, 1990b, fig. 4 and 2 respectively), and its ventral area very similar to that  
602 of *Camereiceras limentinus* (compare Baraboshkin and Mikhailova, 2006, fig. 2a, with Bert et  
603 al., 2010, fig. 2b).

604 All these convergent taxa that could be attributed to Hemihoplitinae for morphological  
605 reasons by the authors must now be excluded from this family, which leads to drastically  
606 review the palaeogeographical distribution of this group. Until proven otherwise, there is no  
607 Hemihoplitinae outside the northern and western margins of the Tethyan Realm (including its  
608 Caucasian margin to the east, and the Essaouira Basin in Morocco at the limit of the Proto  
609 Atlantic Ocean to the west).

610

#### 611 5.8. Systematic implications

612

613 As seen above in the critical review (chapter 5.7), some taxa excluded from the  
614 Hemihoplitidae have now to be reassigned; they are the Homeomorphitinae subfam. nov. gen.

615 nov. (with *Homeomorphites aguirreurretae* gen. nov. et sp. nov. [=*Hemihoplites feraudianus*  
616 in Aguirre-Urreta, 2002]) and the Shasticrioceratidae fam. nov. (with the lineage made by  
617 *Shasticrioceras* and *Antarcticoceras*).

618

619 Superfamily: Perisphinctoidea Steinmann, 1890

620 Family: Neocomitidae Salfeld, 1921

621 Subfamily: Homeomorphitinae subfam. nov.

622 *Type genus.* *Homeomorphites* gen. nov.

623 *Generic content.* In the current state of knowledge, this subfamily is monotypic.

624 *Stratigraphic and geographical occurrence.* The Homeomorphitinae subfam. nov. are  
625 restricted to southern hemisphere, especially the Austral Basin (South Patagonia, Argentina  
626 and Chile – Fig. 7). *Homeomorphites* gen. nov. spans from lower Hauterivian to upper  
627 Barremian (see Riccardi and Aguirre-Urreta, 1989; Aguirre-Urreta, 2002).

628 *Discussion.* The succession of species previously assigned to the genus *Hemihoplites* by  
629 Riccardi and Aguirre-Urreta (1989) and Aguirre-Urreta (2002), here *Homeomorphites* gen.  
630 nov., represents a coherent phyletic lineage both in terms of shared morphology and also  
631 stratigraphically as the species show a relatively continuous succession.

632 The Homeomorphitinae subfam. nov. do not have the ontogenic stages common to all the  
633 Hemihoplitidae (see Bert et al., 2013). More, several characters conjointly present, even  
634 sometimes episodic, in *Homeomorphites* gen. nov. (absence of tubercle or bulging of ribs;  
635 spacing of ribs before smooth stage; episodic presence of reinforced ribs and what looks like  
636 constrictions in some specimens; ‘zigzag’ stage; sutural formula with more than one umbilical  
637 lobe U of ELU<sub>2</sub>U<sub>3</sub>I type – clearly visible in Riccardi and Aguirre-Urreta, 1989, text-fig. 4a, 6)  
638 definitely discard the Homeomorphitinae subfam. nov. from the Hemihoplitidae, and more  
639 widely from the Ancyloceratoidea. Actually, these features remember ‘perisphinctid’

640 assemblage of characters. Of course, each of these characters taken separately is not exclusive  
641 of Perisphinctoidea Steinmann, 1890, but their combination allows to consider the  
642 Homeomorphitinae subfam. nov. as the ultimate representatives of the Perisphinctoidea, in the  
643 vicinity of the subfamilies Neocomitinae Salfeld, 1921 and Endemoceratinae Schindewolf,  
644 1966 (Neocomitidae Salfeld, 1921).

645 Compared to the Endemoceratinae *Lyticoceras* Hyatt, 1900 and *Endemoceras* Thiermann,  
646 1964, the suture line is simpler with a trifid narrow and very weakly asymmetrical lateral lobe  
647 L, whereas it is broad and strongly asymmetric in Endemoceratinae. The section is wider and  
648 the ornamentation is usually coarser without periventral tuberculation.

649 The Homeomorphitinae subfam. nov. are morphologically close to the genus *Hatchericeras*,  
650 which was usually classified in the Neocomitinae or even with doubts in the Endemoceratinae  
651 (see Klein, 2005). However, the involute coiling with a relatively high section and narrow  
652 umbilicus, clearly distances *Hatchericeras* from the Homeomorphitinae subfam. nov.

653 The Neocomitinae are really diversified in shell morphology (large to medium size, involute  
654 to evolute or uncoiled morphology) and ornamentation (thin ribs to strong trituberculated ribs  
655 / all identical ribs to differentiated ribs), which makes them hard to effectively and simply  
656 compare or differentiate from other comparable groups. However, compared to Neocomitinae  
657 (in general), the Homeomorphitinae subfam. nov. show much less rib diversity with no real  
658 tubercles or ribs differentiated. Large gerontic Neocomitinae could show change in  
659 ornamentation, to very strong ribs, which is not the case in Homeomorphitinae subfam. nov.

660 On the other hand, in the same way as with Hemihoplitinae and for identical reasons, the  
661 resemblance of *Homeomorphites* gen. nov. with *Theodorites* Baraboshkin and Michailova,  
662 2006 is the result of a morphological convergence. This latter was classified in the  
663 Crioceratitinae Gill, 1871 by Baraboshkin and Mikhailova (2006), between the genera  
664 *Crioceratites* L veill , 1837 (Crioceratitidae Gill, 1871, Ancyloceratoidea) and *Lyticoceras*

665 Hyatt, 1900 (Endemoceratinae), for which Baraboshkin and Mikhailova (2006) assumed a  
666 phyletic link. Such phyletic link could question the *Lyticoceras* as Endemoceratinae, which  
667 are deemed to be linked with the Neocomitidae (Perisphinctoidea).

668

669 Genus *Homeomorphites* gen. nov.

670 *Denomination.* Because of the phenomenon of homeomorphy, which led to confusion with  
671 the genus *Hemihoplites*.

672 *Type species.* *Homeomorphites aguirreurretae* gen. nov. et sp. nov. (= *Hemihoplites*  
673 *feraudianus* in Aguirre-Urreta, 2002).

674 *Specific content.* *Homeomorphites aguirreurretae* gen. nov. et sp. nov., *Ho. ploszkiewiczii*  
675 (Riccardi and Aguirre-Urreta, 1989) and *Ho. varicostatus* (Riccardi and Aguirre-Urreta,  
676 1989).

677 *Stratigraphic and geographical occurrence.* The genus *Homeomorphites* gen. nov. is  
678 currently only known in the Austral Basin (Fig. 7), eastern border of the southern Patagonian  
679 Cordillera (Argentina and Chile), in levels spanning lower Hauterivian (*Favrella americana*  
680 Zone) to upper Barremian (Fig. 6 – between the *Hatchericeras patagonense* and *Colchidites-*  
681 *Sanmartinoceras* zones – see Riccardi and Aguirre-Urreta, 1989 and Aguirre-Urreta, 2002).

682 *Diagnosis.* Dimorphic genus with evolute shell and subquadratic to sub-oval whorl section,  
683 sometimes more compressed in large macroconchs [M]. Flanks and ventral area usually  
684 convex, more or less rounded [M] or flattish [m]. Ornamentation with flexuous ribs, simple or  
685 bifurcated near the umbilical margin (inner whorls) or just above the mid-part of the flanks.  
686 Intercalary ribs sometimes present. Size of the shell (from medium to large) and ribbing  
687 density (from dense to spaced) are different according to the species. On large macroconchs,  
688 the ribs disappear progressively in becoming less marked and more spaced and irregular, and  
689 the body chamber is smooth. Constrictions and reinforced ribs are scarce. Sometimes ‘zigzag’

690 ribs can occur on the ventral area. Suture formula of ELU<sub>2</sub>U<sub>3</sub>I type, with more or less  
691 asymmetric trifid L.

692 *Discussion.* *Homeomorphites* gen. nov. shows dimorphism and a general morphology and  
693 shell size very close to the Hemihoplitinae, especially to *Hemihoplites feraudianus*  
694 (d'Orbigny, 1841). Despite of this, Kakabaze and Hoedemaeker (2004) had previously  
695 refused to assign the Patagonian species to the genus *Hemihoplites* (pp. 82–83) as Lehmann et  
696 al. (2015, p. 238) did more recently. Actually, *Homeomorphites* gen. nov. never shows the  
697 tubercles systematically present in the Hemihoplitinae, nor their ontogenetic stages (see Bert  
698 et al., 2013). Moreover, constrictions, reinforced ribs and 'zigzag' stages (asymmetry of the  
699 ornamentation on the ventral area), although rare in *Homeomorphites* gen. nov., are totally  
700 absent from all Hemihoplitidae. The ribs are spaced just before the smooth part of the body  
701 chamber, which is never the case in *Hemihoplites* (Fig. 4). Finally, the sutura formula is of  
702 'neocomitid' type, while it is of 'ancyloceratid' type in Hemihoplitidae.

703 *Homeomorphites* gen. nov. is more evolute, with a much lower height whorl and a thicker  
704 whorl section than *Hatchericeras*. Adult size seems also larger for *Hatchericeras*.  
705 Ornamentation, on the other hand, is quite comparable in flexuosity and orientation of the  
706 ribs, but with a higher primary bifurcation point, an earlier smooth stage, and a smoother  
707 ventral area in *Hatchericeras*. The suture line is quite different: it is simple, with a relatively  
708 narrow and very weakly asymmetric lateral lobe L in *Homeomorphites* gen. nov., while it is  
709 complex, with a broad, strongly asymmetric lateral lobe L in *Hatchericeras*.

710 Compared with *Theodorites*, the ribs are a bit more flexuous in *Homeomorphites* gen. nov.  
711 and are not as attenuated on the ventral area. *Theodorites* also has periventral tubercles and  
712 peri-umbilical bulges, completely absent in *Homeomorphites* gen. nov.

713 The stratigraphic succession of species of the genus *Homeomorphites* gen. nov. is:  
714 *Homeomorphites ploszkiewiczzi* (*Favrella americana* Assemblage Zone in the upper lower

715 Hauterivian according to Aguirre-Urreta et al., 2007b) → *Ho. varicostatus* (*F. wilckensi* and  
716 *Hatchericeras patagonense* assemblages zones in the upper Hauterivian and lower  
717 Barremian) → *Ho. aguirreurretae* gen. nov. et sp. nov. (non basal upper Barremian). The  
718 evolutionary trend of this group has been described by Aguirre-Urreta (2002), who noted an  
719 increasing body size and coarser ribbing (ribs increasingly spaced in time). To this, one can  
720 add the acquisition of a new ontogenetic stage at the end of growth (smooth stage) by  
721 allometric hypermorphosis (heterochrony in the sense of McKinney, 1988). The general  
722 morphology of the shell remains remarkably stable during this evolution, and the modification  
723 of the ornamentation could be related to the selective drift of the variability of the populations  
724 towards more and more robust forms (Aguirre-Urreta, 2002, p 496).

725

726 *Homeomorphites aguirreurretae* gen. nov. et sp. nov.

727 2002 *Hemihoplites feraudianus* (d'Orbigny, 1841); Aguirre-Urreta: text-fig. 4a, pl. 1–2.

728 *Denomination.* This species is dedicated to Pr. María B. Aguirre-Urreta (University of Buenos  
729 Aires, Argentina), who discovered and described the specimens ascribed to this new species  
730 (2002).

731 *Holotype.* The type specimen designated is the macroconch No. CPBA 19156 (in Aguirre-  
732 Urreta, 2002, pl. 1). It is housed in the Cátedra de Paleontología de Buenos Aires, Ciudad  
733 Universitaria, Pabellón 2, 1428 Buenos Aires, Argentina.

734 *Type locality.* The Río Ghio locality, in the eastern border of the southern Patagonian  
735 Cordillera (Argentina).

736 *Type Level.* The Río Belgrano Formation.

737 *Stratigraphic and geographical occurrence.* The geographical distribution is the same as for  
738 the genus (Fig. 7). Stratigraphically, *Ho. aguirreurretae* gen. nov. et sp. nov. is recorded in



739 levels of the upper Barremian, just between the *Hatchericeras patagonense* and the  
740 *Colchidites-Sanmartinoceras* zones (Fig. 6 – see Aguirre-Urreta, 2002).

741 *Diagnosis.* Dimorphic species, macroconch [M] of large size (D=210 mm) and microconch  
742 [m] reaching D=70–80 mm. Evolute shell with section compressed for [M] or subrectangular  
743 for [m]. Umbilical shoulder and flanks rounded [M] or flattish [m]. Ventral area slightly  
744 convex. Ornamentation with strong ribs, usually flexuous; they cross the venter without any  
745 weakening. Ribs are simple or bifurcated from the umbilical margin (inner whorls) or just  
746 below the midflank. On the macroconch, the ribs disappear progressively in becoming less  
747 marked and more spaced and irregular; the end of the phragmocone and the body chamber are  
748 smooth. Constrictions and reinforced ribs are scarce. Suture with L slightly deeper than E,  
749 moderately wide and asymmetrically trifid.

750 *Discussion.* Morphologically, *Homeomorphites aguirreurretae* gen. nov. et sp. nov. shows  
751 dimorphism and a general morphology and size of the shell very close to *Hemihoplites*  
752 *feraudianus* (d'Orbigny, 1841). Despite of this, the former lacks the tubercles systematically  
753 known in the latter. Moreover, the constrictions and reinforced ribs, albeit rare, are not an  
754 hemihoplitid character. Finally, the ribs are spaced just before the smooth part of the body  
755 chamber, which is never the case in *Hemihoplites feraudianus*. These differences are also  
756 discriminating against all other species of Hemihoplitinae, with a distinct ontogenic trend [i.e.  
757 *H. astarte*, *H. cornagoae*, *Camereiceras limentinus*, *C. marchandi*, *C. breistrofferi*, and the  
758 representatives of the genus *Pachyhemihoplites*].

759 *Homeomorphites aguirreurretae* gen. nov. et sp. nov. is larger in size than *Ho. varicostatus*  
760 gen. nov. and *Ho. ploszkiewiczzi* gen. nov. The ribbing density is also different as *Ho.*  
761 *aguirreurretae* gen. nov. et sp. nov. shows more spaced and coarser ribs than the two other  
762 species of the genus.

763 *Hatchericeras patagonense* Stanton, 1901 has a higher whorl section and a more closed  
764 umbilicus than *Homeomorphites aguirreurretae* gen. nov. et sp. nov. Ornamentation, on the  
765 other hand, is quite comparable in flexuosity and orientation of the ribs, but with an earlier  
766 smooth stage (80–100 mm versus 200 mm in diameter) and a smoother ventral area in  
767 *Hatchericeras patagonense*. The suture line is simpler and quite different with a narrower and  
768 more trifid symmetrical lobe L in *Homeomorphites aguirreurretae* gen. nov. et sp. nov.

769 Compared with *Hatchericeras argentinense* Stanton, 1901, *Ho. aguirreurretae* gen. nov. et sp.  
770 nov. has a more evolute coiling, a lower whorl height and a different ornamentation: the ribs  
771 are stronger, spaced and not attenuated on the ventral area.

772 Compared with *Theodorites theodori* Baraboshkin and Michailova, 2006 and *Th. drushitsi*  
773 Baraboshkin and Michailova, 2006, the ribs are a little more flexuous in *Homeomorphites*  
774 *aguirreurretae* gen. nov. et sp. nov. and are not as attenuated on the venter. Both species of  
775 *Theodorites* also have periventral tubercles and peri-umbilical bulges, completely absent in  
776 *Homeomorphites aguirreurretae* gen. nov. et sp. nov.

777

778 Family: Shasticrioceratidae fam. nov.

779 Type genus. *Shasticrioceras* Anderson, 1938.

780 Generic content. *Shasticrioceras* Anderson, 1938 (and its synonym *Backraceras* Mourgues,  
781 2007 *nomen nudum*) and *Antarcticoceras* Thomson, 1974.

782 Stratigraphic and geographical occurrence. The Shasticrioceratidae fam. nov. have a circum  
783 Pacific repartition from Arctic Canada to California (western USA) and to Chile and Japan  
784 (Fig. 7). The family is also known in the Austral Basin in Antarctica. *Shasticrioceras* occurs  
785 in lower Barremian (Chile) and lower and upper Barremian-lowermost Aptian (California).  
786 *Antarcticoceras* occurs in upper Barremian and lower Aptian (see Mourgues, 2007, p. 162 –  
787 Fig. 6).

788 *Discussion.* The genus *Shasticrioceras* was originally classified in Hemihoplitidae (Anderson,  
789 1938; Murphy, 1975) and more recently in the ‘catch-all’ family Megacrioceratidae  
790 Vermeulen, 2006 (see Klein et al., 2007), but its phyletic relationships have never been very  
791 clearly established to support these propositions [note that in our point of view, the  
792 Megacrioceratidae are a probable synonym of the family Hamulinidae Gill, 1871 because of  
793 the very close relationships between *Megacrioceras doublieri* (Jaubert, 1856) and the genus  
794 *Hamulina* d'Orbigny, 1850]. The genus *Shasticrioceras* has long been known in the lower and  
795 upper North American Barremian (Murphy, 1975) and Japan (Matsukawa and Obata, 1993).  
796 Mourgues (2007) reported it more recently in Chile.

797 *Antarcticoceras* was originally left in open nomenclature by Thomson (1974), then was  
798 placed with doubt in the Ancyloceratidae by Klein et al. (2007). This genus was assumed  
799 Aptian by Thomson (1974), but would rather be upper Barremian according to Mourgues  
800 (2007).

801 In the constrained geographic context of the Chañarcillo Basin (Chile), besides the fact that  
802 the coiling and the shape of the ribs between *Shasticrioceras* and *Antarcticoceras* are very  
803 close with a very particular morphology of the ventral area whose flat ribs are framed by a  
804 peri-ventral punctiform tubercle, a phyletic link between both these two genera can be  
805 established with the simple acquisition, very early in ontogeny, of an additional tubercle at the  
806 top of the flanks very close to the periventral tubercle. This hypothesis is also supported by the  
807 representation by Murphy (1975, fig. 25) of a *Shasticrioceras roddai* Murphy, 1975 showing  
808 a large (adult?) specimen with lateral and periventral tubercles very close together on the  
809 topflanks. In Japan, Matsukawa and Obata (1993) also reported the lower Barremian  
810 *Shasticrioceras intermedium* Matsukawa and Obata, 1993 with 2-3 tubercles on the main ribs  
811 at adult stage. Finally, the attribution by Mourgues (2007) (1) of the upper Barremian  
812 (*Antarcticoceras domeycanum* Zone) species *A. domeycanum* (Bayle and Coquand, 1851) to

813 the genus *Antarcticoceras* (previously ?*Parancyloceras* Spath, 1924a in Klein et al., 2007),  
814 and (2) the description of *A. perezii* Mourgues, 2007 *nomen nudum* (later assigned to the genus  
815 *Hemihoplites*) at the base of the lower Aptian ('*Hemihoplites*' *perezii* Zone) with tubercles  
816 very close together in the periventral and topflank areas, typical of the *Antarcticoceras*, makes  
817 possible to fill the stratigraphic and morphological hiatus with the genus *Shasticrioceras* and  
818 to classify them together within the same family: the Shasticrioceratidae fam. nov.

819

## 820 **6. Discussion about the phyletic position of *Lenicostites* gen. nov.**

821

822 *Lenicostites* gen. nov. has a morphology close to Hemihoplitinae, however it departs from it  
823 by ontogeny and a number of characters (see above chapter 4). Is this morphological  
824 proximity a reflection of a phyletic link, or does it only reflect homeomorphy just as the  
825 above examples? Several hypotheses have to be considered.

826

827 *6.1. Hypothesis (1): Lenicostites gen. nov. as an ancestor of the Hemihoplitinae or an*  
828 *offshoot of Gassendiceras*

829

830 In the hypothesis where *Lenicostites* gen. nov. were the ancestor of the Hemihoplitinae, given  
831 their stratigraphic appearance, they would derive directly from the first *Gassendiceras* cf.  
832 *essaouirae* present on the northwestern Tethyan margin, to make the link next with  
833 *Camereiceras breistrofferi*, which is the oldest known *Camereiceras* at the top of the  
834 *Gassendiceras alpinum* Subzone. On the other hand, if *Lenicostites* gen. nov. were an  
835 offshoot of the Tethyan Gassendiceratinae, they would have at least a common ancestor: the  
836 only possible candidate is the top-early Barremian Moroccan *G. essaouirae*. These  
837 hypotheses come up against a number of objections concerning (1) ontogenesis and

838 ornamentation, (2) adult size, (3) coiling, (4) evolutionary rhythms, and (5) stratigraphic  
839 coherence:

840 - (1) The Hemihoplitidae share a common ontogenetic trajectory and the  
841 Hemihoplitinae follow the constant trend initiated by their ancestor Gassendiceratinae. This  
842 trajectory is respected in Hemihoplitidae also in case of major evolutive changes such as the  
843 reversion of the heterochrony trend that lead to the appearance of *Pseudoshasticroceras*, and  
844 later with the appearance of the helical coiling in *Imerites* Rouchadzé, 1933 (Fig. 1; Bert et  
845 al., 2009; Bert, 2014, p. 155–157). In these examples, the Barremense and Camereiceras  
846 stages are still present or little modified for mechanical reason (i.e. the presence of the helical  
847 coiling). Thus, in the case of *Gassendiceras* (the ancestors) and *Camereiceras* (the  
848 descendents), both genera have in common the Heberti stage in their innermost whorls,  
849 followed by the Barremense and Camereiceras stages (Fig. 5 – see Bert et al., 2006 for the  
850 extensive description of these stages). This trend and the associated trituberculate ontogenetic  
851 stages are totally absent in the supposed intermediates *Lenicostites* gen. nov. (Fig. 2–3),  
852 which does not fit with the hypothesis of a phyletic link between these genera. Moreover, if  
853 we consider the loss and complete subsequent recovery of these ontogenetic stages as a  
854 possibility, it would mean accepting an exact characters reversibility through time, which is in  
855 total contradiction with the Dollo's rule of the irreversibility of evolution.

856 - (2) It has been shown (Bert et al., 2013) that the *Gassendiceras* species reach a large  
857 size, around or above 350 mm in diameter. It is the same with the macroconchs of  
858 *Camereiceras* (D=325 mm for *C. limentinus* in Delanoy, 1990a, pl. 6), including the older  
859 species of this genus (D=300 mm for *C. breistrofferi* in Bert, 2014a, fig. 20a). However, this  
860 is not the case for *Lenicostites* gen. nov., which is much smaller with a body chamber that  
861 starts at around 110 mm in diameter with the ornamental stage change. In mollusks, the size  
862 seems more subject to the stabilizing effect of the natural selection than the ornamental

863 characters (Mayr, 1963), thus in a phyletic relationship hypothesis, it is rather unlikely that  
864 *Lenicostites* gen. nov. would break this stability otherwise than being a progenetic  
865 micromorph. In such an hypothesis, or if *Lenicostites* gen. nov. were an offshoot of  
866 *Gassendiceras*, they would share at least the early Heberti ontogenetic stage with octagonal  
867 section and trituberculate ribs known in innermost whorls of every Hemihoplitidae (or a  
868 modified version of it), or the strongly tuberculate Barremense stage that immediately  
869 succeed it. This is clearly not the case.

870 - (3) With regard to coiling, the different species of the genus *Gassendiceras*  
871 systematically have heteromorphic shells, which is also the case for the older *Camereiceras*  
872 (whorls are crioconic non-joined in macroconchs, and tripartite or crioconic in microconchs –  
873 see Bert and Delanoy, 2000; Bert et al., 2006; Bert, 2012a, 2014a). To be more precise, the  
874 evolutionary trend from *Gassendiceras* to *Camereiceras* is towards the progressive loss of  
875 heteromorphy, fully achieved in *C. limentinus*. On the contrary, at the same time, in  
876 *Lenicostites* gen. nov. the shell is constantly plan-spiral with systematically contiguous  
877 whorls, which discards it from the *Gassendiceras/Camereiceras* coiling trend.

878 - (4) The evolution of *Lenicostites* gen. nov. appears to be essentially in stasis, with no  
879 particular morphological differentiation visible between the oldest and most recent known  
880 forms, despite the stratigraphic departure of almost two ammonite subzones. In the  
881 assumption that *Lenicostites* gen. nov. would be intermediate between *Gassendiceras* and  
882 *Camereiceras*, or an offshoot of *Gassendiceras*, this sudden and transient stasis would be very  
883 difficult to explain in comparison with the high speed of evolutionary changes known in  
884 Hemihoplitidae (both the ancestral Gassendiceratinae and the derived Hemihoplitinae), whose  
885 succession of species allows to establish successions of biostratigraphic horizons (Fig. 1 – see  
886 Bert et al., 2008; Bert and Bersac, 2013; Bert, 2014).

887 - (5) The succession *Lenicostites* gen. nov. / *Camereiceras* could be stratigraphically  
888 coherent (*L. rusticus* gen. nov. is still present together with *C. limentinus* and could, for  
889 example, give *C. breistrofferi* by cladogenesis), but the stratigraphic data available on the  
890 northwestern margin of the Tethys show that *Lenicostites* gen. nov. appear at the same time as  
891 their supposed ancestor, *Gassendiceras*. This observation remains problematic in the context  
892 of the hypothesis of an ancestor-descendant relationship. That said, a possible common  
893 ancestor for *Gassendiceras* and *Lenicostites* gen. nov., or the hypothesis of *Lenicostites* gen.  
894 nov. as an offshoot of *Gassendiceras*, are not discarded only stratigraphically, but they are  
895 mostly ontogenetically (see above point 1): the common ontogenetic development of  
896 Hemihoplitidae (Heberti, Barremense, etc. stages) is not only present in the Tethyan late  
897 Barremian *Gassendiceras*, but also in their Moroccan ancestors (*Gassendiceras essaouirae*) at  
898 the top-early Barremian (see Bert and Bersac, 2013), long before the appearance of  
899 *Lenicostites* gen. nov.

900

901 In summary, to consider the hypothesis of *Lenicostites* gen. nov. as an ancestor of the  
902 Hemihoplitinae would lead to imagine a period of evolutionary stasis separated from two  
903 phases of rapid evolutionary changes by two major breaks. The first rupture could only be the  
904 result of a very sudden progeny, with abrupt regression of the size and major reconfiguration  
905 of the shell, which would lead to the loss of heteromorphy between the Tethyan *G.* cf.  
906 *essaouirae*, or Moroccan *G. essaouirae*, and *L. rusticus* gen. nov. Cases of progenesis,  
907 sometimes involving extensive restructuring of the organism, have been described  
908 (Dommergues et al., 1986, p. 345–348; Landman et al., 1991; Bert, 2004, p. 121–122). On the  
909 other hand, they do not explain the total loss of the ontogenetic stages (especially those  
910 known in the innermost whorls of every Hemihoplitidae) and the second break between *L.*  
911 *rusticus* gen. nov. and *C. breistrofferi*, with a complete reverse restructuring and the sudden

912 reappearance of the ancestral ontogenetic stages (Heberti and Barremense stages). This  
913 inverse and exact restructuring would be a violation of Dollo's rule of the irreversibility of  
914 evolution (Dollo, 1893; Gould, 1970), which goes beyond the simple repeatability or the  
915 iterative evolution of certain characters (see for example Bert et al., 2018, p. 182); as such it  
916 would be highly unlikely. All the arguments developed above are likely to rule out  
917 *Lenicostites* gen. nov. from the Hemihoplitidae.

918

919 *6.2. Hypothesis (2): Lenicostites gen. nov. as an 'hemihoplitid-like' homeomorph*

920

921 As stated above (chapters 4, 6.1), it is now clear that *Lenicostites* gen. nov. is not linked with  
922 the Hemihoplitidae: on the one hand, this genus is not at the origin of the *Camereiceras*,  
923 which succeed directly to the *Gassendiceras* in the upper part of the *G. alpinum* Subzone by  
924 the reduction of the Barremense stage in the inner whorls and by the centripetal development  
925 of the *Camereiceras* stage (Bert et al., 2006, 2013; Bert and Bersac, 2013). And on the other  
926 hand, *Lenicostites* gen. nov. is not derived from the *Gassendiceras*, of which it is not an  
927 offshoot.

928 As *Lenicostites* gen. nov. is independent of Hemihoplitidae, it represents a pure case of  
929 homeomorphy. In the same way, there is no reason to think that *Lenicostites* gen. nov. may be  
930 related, other than by the same phenomenon of homeomorphy, to Homeomorphitinae subfam.  
931 nov. or to other groups detailed above (chapter 5), especially because of the important  
932 geographical, stratigraphic and phyletic hiatuses, and apomorphies specific to these groups. In  
933 the current state of knowledge, *Lenicostites* gen. nov. could be considered as a cryptogenic  
934 taxon. It could possibly have a migratory origin (?) given its simultaneous appearance in the  
935 south-east of France with *Gassendiceras* under favorable climatic and paleogeographic  
936 conditions (Bert and Bersac, 2014).



937 Reasons for this particular widespread homeomorphism could be linked to the simplified  
938 generalist ‘hemihoplitid-like’ morphology, making it easily reproducible. Considering the  
939 Pareto optimality theory applied to ammonites (Tendler et al, 2015), the 3D morphospace  
940 occupation of ammonoid shell, based on the Raup’s parameters, occurs in a square pyramid  
941 with 5 vertices. Each of these extreme point of the Pareto space corresponds to archetype  
942 morphology optimized with respect to a single task (constraint). Tendler et al. (2015) have  
943 inferred these constraints as hydrodynamic efficiency, shell economy, rapid growth and size  
944 (including compactness). As said above (chapter 5.7), the ‘hemihoplitid-like’ shell  
945 morphology takes place in the middle of the pyramid. Such a position fits generalist  
946 morphologies, in the zone of maximum equilibrium between the different constraints that  
947 govern the construction of ammonite shells, namely a Pareto-optimal solution. It is therefore  
948 expected that the morphologies at the equilibrium of the constraints (knowing that this  
949 optimum can vary depending on the environment) are the easiest to reproduce and therefore  
950 the most often imitated (convergence). As this, such occupation position in the W-D-S  
951 morphospace is mainly explained by convergence over Pareto-optimal solutions, rather than  
952 only phylogenetic relationships (Tendler et al., 2015, p. 11).

953

### 954 *6.3. Homeomorphy as a result of convergence, parallelism or iterative evolution?*

955

956 It is well known that ammonites are a remarkable model for the study of phenotypic  
957 evolution, even if only their shell is accessible. This shell secreted by accretion performs the  
958 development of structures and morphologies sufficiently diversified to allow the  
959 paleontologists not only to recognize the different taxa and evolutionary patterns, but also to  
960 try to understand their processes. However, due to its nature and construction, the shell of  
961 ammonites necessarily develops sooner or later homeomorphies between different taxa that

962 may or may not belong to different lineages and/or at very different times. Examples of  
963 homeomorphy in ammonites are numerous and have been the source of many discussions (see  
964 for example Kennedy and Cobban, 1976, p. 41–42, Monnet et al., 2015, p. 97 and Walton and  
965 Korn, 2017 with references). The consequences of this phenomenon and their perception by  
966 the researchers (with all the risks of producing polyphyletic taxa), had already been noted by  
967 Kilian in 1910: they can have major implications on phylogenetics, systematics and on the  
968 understanding of the evolutionary fact. In this respect, the case of *Lenicostites* gen. nov. is  
969 demonstrative of a peculiar ammonite, since it presents a part of the diagnostic characters of  
970 Hemihoplitinae but with a discordant stratigraphic distribution, which, without a more in-  
971 depth study, could have led to some wrong conclusions with respect to the evolution and  
972 classification of the whole group (e.g. Vermeulen, 1996, 2005).

973 In a very Darwinian framework, it is expected that the external constraints of abiotic  
974 (environmental factors) and biotic (intra- or interspecific competition) factors constrained  
975 adaptation of the morphology of the ammonites shell (adaptive selection). It is generally  
976 accepted that homeomorphy between two forms could be the result of a morphofunctional  
977 adaptation linked to a similar way of life and thus to the occupation of the same ecological  
978 niche. The influence of these extrinsic constraints has often been overestimated with respect  
979 to internal constraints (construction, development and of course also genetic, but this aspect  
980 inaccessible in ammonites can only be deduced), whereas the evolution of organisms is an  
981 equilibrium between various mutually interacting processes (see Monnet et al., 2015).  
982 Understanding these constraints, and the relationships among them, is necessary to understand  
983 the causes of homeomorphy, which can be expressed according to different evolutionary  
984 phenomena, either convergence or parallelism (not mutually exclusive). The case of iteration  
985 is a little different, and although it is usually considered as a form of convergence, it can

986 sometimes be a mixture of both and in this case be very constrained by intrinsic factors (see  
987 below the example of the *Gregoryceras* Spath, 1924a).

988 Convergence and parallel evolution are a main source of homoplasy, and following Serb and  
989 Eernisse (2008) they are distinct concepts (Fig. 8). Convergence appears to be the  
990 independent evolution of similar structural or functional components in two or more unrelated  
991 lineages. The homeomorphs given by evolutionary convergence do not share a common  
992 ancestor and they have evolved convergently to the same morphology, mainly because of  
993 adaptation to similar conditions (Fig. 8A – external constraints, see above).

994 In parallel evolution (Fig. 8B–C), two (or more) lineages have similar ancestral phenotype  
995 and the descendants have evolved in trajectories towards similar morphology. Parallel  
996 evolution assumes that the same common developmental processes are independently  
997 involved between the lineages (intrinsic factor), and thus is more frequent in closely related  
998 organisms. Parallel evolution would also be subject to natural selection, but obviously when  
999 the genome is still close between the lineages, they will be more likely to evolve identically in  
1000 the same environment (Tintant, 1963, p. 474–475).

1001 Iterative evolution uses the notion of repeatability of the phenotypic traits (Fig. 8D–E). This  
1002 repeatability is usually argued by an adaptive response to changes in environmental cycles  
1003 (Milankovitch, 1941), and thus would be totally dependent on external constraints (selection  
1004 pressure – Bayer and McGhee, 1984). Examples show that ammonite lineages that have  
1005 evolved iteratively are from generalist pools, rather distributed in pelagic environments,  
1006 which have drifted to more specialized forms in platform edge environments (see the example  
1007 of *Physodoceras* Hyatt, 1900 in Hantzpergue, 1987, p. 520). The counter-example of the  
1008 *Gregoryceras*, which have evolved from the *Peltoceratoides* Spath, 1925, shows that iterative  
1009 evolution can also be expressed as a result of an evolutionary crisis (punctuated event of  
1010 proteromorphosis type in the sense of Guex, 2006), which leads to the reappearance of

1011 ancestral characters (here the duplicated ventral tubercles, specific to *Peltoceratoides*, at the  
1012 end of the lineage in *Gregoryceras* – Bonnot, 1995; Bert, 2004, 2014). In this case, the  
1013 morphological iteration is linked to a common genetic inheritance (internal constraint) and  
1014 everything happens as if the punctuated event would reset the evolutionary trend and revive it  
1015 on the same bases, which finally lead to homeomorphy by evolutionary parallelism shifted in  
1016 time.

1017

1018 It does not seem possible to invoke a phenomenon of parallel evolution between *Lenicostites*  
1019 gen. nov. and *Hemihoplites*, nor an evolutionary iteration like the *Physodoceras* or the  
1020 *Gregoryceras* examples. On the one hand, there is no phyletic proximity between *Lenicostites*  
1021 gen. nov. and the Hemihoplitinae (see the arguments developed above in chapters 4, 6.1), and  
1022 on the other hand the general common morphology between these groups is rather generalist  
1023 in a Pareto-optimal solution and does not require to invoke great ecological adaptations  
1024 towards a constrained specialization. Finally, the most appropriate model in this case is that of  
1025 homeomorphy given by evolutionary convergence, which also supposes that the external  
1026 constraints are the strongest to reproduce this type of generalist ‘hemihoplitid-like’ simplified  
1027 morphology.

1028

## 1029 **7. The principle of Gause applied to *Lenicostites* gen. nov.: a matter of competitive** 1030 **replacement in favor of Hemihoplitinae**

1031

1032 The principle of competition for the struggle for existence is at the root of the Darwinian  
1033 theory, where ‘*the extinction of ancient forms is the almost inevitable consequence of the*  
1034 *production of new forms*’ (Darwin, 1859, reprint of 2008, p. 410). Competition is an  
1035 extremely complex phenomenon subtended by the interaction of two different processes:

1036 exploitation (the use of a resource in necessarily limited quantity) and interference (the  
1037 interaction between the organisms affecting their reproduction or their survival). Interspecific  
1038 competition has been studied in laboratory on various groups (e.g. paramecium for Gause,  
1039 1935, beetles for Park, 1962) and experimental results have shown that in a given stable  
1040 environment, two species that use the same type of limited resource cannot coexist for a very  
1041 long time, which tends systematically to extinction of the least 'fit' species because of the  
1042 competitively superior species (Benton, 1996; Stanley, 2008). There are many examples of  
1043 the Gause principle of competitive replacement that have allowed it to be generalized  
1044 (Maynard-Smith, 1983; Rosenzweig, 1995; Simpson, 1953; Stanley, 1979; Stebbins, 1974),  
1045 but the concept of aptitude is not always very clear. Park's experimental work (1962) has  
1046 shown that the result of competition between two species depends both on intrinsic factors but  
1047 also on the environment, which may be more or less favorable to one or the other species. It  
1048 turns out that the surviving species is not systematically the most favored at the beginning,  
1049 nor the most representative in number of individuals, even if it is the most expected and the  
1050 most frequent case. This could be explained by the fact that, in a natural environment (Case  
1051 and Taper, 2000), competition between two species reduces the both population densities,  
1052 which decreases local adaptation (local adaptation concerns all changes in the frequency of  
1053 genes, and the resulting phenotype, in response to selective pressures associated with the local  
1054 environment). Despite the fact that this leaves room for a certain amount of chance, the  
1055 strength of interspecific competition also depends on phenotypic similarity and plasticity:  
1056 greater phenotypic variability seems to induce a reduction in the negative effect of  
1057 interspecific competition for the concerned taxon (Burgess et al., 2013, with references;  
1058 Morten and Twitchett, 2009).

1059 In paleontology, these competitive interactions are still poorly studied, especially in  
1060 ammonites, and most often after mass extinction events (Benton, 1996; Morten and Twitchett,

1061 2009; Hautmann et al., 2015). However, according to some authors (Benton, 1996; Stanley,  
1062 1974, 2008), the role of competition has generally been exaggerated by paleontologists, and it  
1063 would only play a minor role in most ecological communities because of the regulating action  
1064 of predation, which would exert a pressure such as to desaturate the ecological niches.  
1065 Although sessile communities, such as bivalve mollusks, are more susceptible to the effects of  
1066 predation than to competition, the same is not true for vagile forms such as mammals,  
1067 trilobites, or ammonites, which are subject to a high rate of evolution (Stanley, 1974), and for  
1068 which competition is likely to play an important role in terms of evolutionary divergence (the  
1069 ‘centrifugal force of evolution’ of Mayr, 1963). Thus, the rate of evolution is as high as  
1070 competitive interactions between species is intense. As this, every successful adaptation of  
1071 one species is done at the expense of the other species living in the same ecological niche. In  
1072 other words, as stated in the Red Queen theory, the permanent evolution of a species is  
1073 necessary to answer the fitness of the other species with which it co-evolve to avoid  
1074 extinction (Van Valen, 1973): in the Darwinian frame, only the fittest species would survive  
1075 in such a run.

1076  
1077 By the foregoing, and based on the principle of morphology linked to functional needs in  
1078 ammonites (e.g. Westermann, 1996; Lukeneder, 2015) and on the constraints highlighted by  
1079 the Pareto-optimal theory (Tendler et al., 2015), it is reasonable to think that the morphology  
1080 of *Lenicostites* gen. nov. suggests that it occupied an ecological niche very similar to  
1081 *Hemihoplites feraudianus* and adults microconchs of Hemihoplitinae with smooth ribbed  
1082 body chamber (*Camereiceras marchandi* and *C. limentinus* – see Fig. 5B, C). *Lenicostites*  
1083 gen. nov. was not contemporaneous with *H. feraudianus*, but it was with *C. marchandi* and  
1084 *limentinus*, which was a favorable condition for the establishment of interspecific  
1085 competition. As seen above, *Camereiceras* has characteristics generally associated with better

1086 competitiveness compared to *Lenicostites* gen. nov.: (1) the adult size of *Camereiceras* is  
1087 larger, which presumably conferred it certain advantages in terms of defense against predation  
1088 (Tendler et al., 2015, p. 6), increased food competition, increased success in mating and  
1089 reproduction, increased individual longevity, and better energy use (see also Monnet et al.,  
1090 2015, p. 116, with references); (2) Hemihoplitinae are much more dynamic with a higher  
1091 evolutionary rate (rapid succession of species), while *Lenicostites* gen. nov. seems to be in a  
1092 period of evolutionary stasis; (3) in terms of representativeness, *Camereiceras* is much more  
1093 abundant than *Lenicostites* gen. nov. in the deposits, which suggests that its reproductive rate  
1094 was higher (higher fitness); (4) preliminary studies (work in progress) show that  
1095 *Camereiceras* has an extraordinarily wide intraspecific variability (combination of both  
1096 heterochronies and multipolar variations in the sense of Bert, 2014a, b), between forms highly  
1097 tuberculate in the inner whorls and forms much more slender. In any case, this variability is  
1098 much higher than that of *Lenicostites* gen. nov., where it concerns the robustness of  
1099 ornamentation only (see description). This high difference in variability between the two  
1100 groups could explain that *Camereiceras* has better supported competition with *Lenicostites*  
1101 gen. nov. by a lesser impact of its negative effects. Of course, with only partial  
1102 paleontological data (external ammonites shell) there is no guarantee that this example is  
1103 evidenced or random, but here we interpret the disappearance of *Lenicostites* gen. nov., very  
1104 soon after they meet the re-coiled Hemihoplitinae (*Camereiceras marchandi* and *C.*  
1105 *limentinus* – Fig. 5), by the effect of interspecific competition: in this hypothesis, *Lenicostites*  
1106 gen. nov. is a victim of the Gause Principle as it lost the Red Queen race.

1107

## 1108 **8. Conclusions**

1109

1110 The evolution, biostratigraphy and systematics of the ammonite family Hemihoplitidae is  
1111 nowadays well known. Concerning the subfamily Hemihoplitinae, the genus *Camereiceras* is  
1112 derived from the genus *Gassendiceras* (Gassendiceratinae) in the top *Gassendiceras alpinum*  
1113 Subzone (Bert and Bersac, 2014). The older *Camereiceras* retain some characters from their  
1114 ancestor (ornamentation pattern, general heteromorphic morphology and, above all, their  
1115 ontogenetic stages), and their microconchs have an adult simplified morphology with smooth  
1116 identical ribs. Later (in the *Camereiceras limentinus* Subzone), *Camereiceras* gives rise to  
1117 *Hemihoplites*, of which the evolution shows a progressive reduction of the tubercles to give  
1118 finally the simplified morphology known in *H. feraudianus* with weak tubercles. All this  
1119 evolution is actually restrained to the north-west Tethyan margin (Fig. 7) at the early late  
1120 Barremian only (*T. vandenheckei* and *G. sartousiana* zones – Fig. 1). In this context, the  
1121 genus *Lenicostites* gen. nov. that suddenly appears in the middle *T. vandenheckei* Subzone with  
1122 its simplified morphology very close to *Hemihoplites feraudianus* (compare Fig. 2–3 with  
1123 Fig. 4) is unexpected because of its older age of three ammonites subzones, contemporary of  
1124 the genera *Gassendiceras* and *Camereiceras* (in several occurrences according to new data  
1125 collected in southeastern France – this work). Despite its large stratigraphic range,  
1126 *Lenicostites* gen. nov. appears to be monospecific (*L. rusticus* gen. nov.) and in evolutionary  
1127 stasis, unlike the Hemihoplitinae that show a high evolutionary rate. It is undeniable that  
1128 Lenicostitidae fam. nov. are morphologically very close to Hemihoplitinae, however, the  
1129 stratigraphic, ontogenetic, evolutionary and systematic analyses show that there is no  
1130 connection between these families and that the resemblance is purely a case of homeomorphy,  
1131 as they occupies the same solution in the morphological space of the Pareto optimality theory  
1132 applied to ammonites (Tendler et al., 2015): the ‘hemihoplitid-like’ morphology.

1133



1134 In the light of the *Lenicostites* gen. nov., it is possible to re-examine the numerous  
1135 occurrences of Hemihoplitinae reported in the literature in localities sometimes very distant  
1136 from each other and from the Tethyan domain or even from the upper Barremian, which are  
1137 sometimes contradictory with the evolutionary history of the group. The critical review of  
1138 these reports allows a drastic revision and clarification of the systematic and paleogeographic  
1139 distribution of Hemihoplitinae as a whole: until proven otherwise, there is no Hemihoplitinae  
1140 outside the north and west margins of the Tethyan Realm (including its Caucasian margin in  
1141 the east, and the Essaouira Basin in Morocco at the limit of the Proto Atlantic Ocean in the  
1142 west). Actually, the ‘hemihoplitid-like’ morphology is iterative at the Valanginian,  
1143 Hauterivian, Barremian and Aptian in several taxa without any phyletic links, which develop  
1144 it by homeomorphy.

1145 For example, it is now certain that the genus ‘*Hemihoplites*’ reported in Patagonia (Argentina  
1146 – Riccardi and Aguirre-Urreta, 1989; Aguirre-Urreta, 2002) actually corresponds to a genus  
1147 of ammonite endemic to the Austral Basin, identified here under *Homeomorphites* gen. nov.,  
1148 which evolves locally from the early Hauterivian to the late Barremian by allometric  
1149 hypermorphosis (heterochrony).

1150 In the same way, it is possible to propose a direct phyletic link from *Shasticrioceras* to  
1151 *Antarcticoceras* based on data from Chañarcillo Basin (Chile – Mourgues, 2007). This  
1152 evolution is done by the simple acquisition of an additional tubercle at the top of the flanks  
1153 very early during ontogeny. The attribution of the species *A. domeycanum* (late Barremian) to  
1154 the genus *Antarcticoceras* and the description of *A. perezii* nomen nudum at the base of the  
1155 early Aptian make possible to fill the stratigraphic and morphological hiatus between the both  
1156 two genera and to classify them together within the same family: the Shasticrioceratidae fam.  
1157 nov.

1158

1159 These examples, which are independent from the Hemihoplitidae, show that the shared  
1160 ‘hemihoplitid-like’ morphology is widespread, generalist and thus easily reproducible under  
1161 the Pareto optimality theory (Pareto-optimal solution in the zone of maximum equilibrium  
1162 between the different constraints that govern the construction of ammonite shells).  
1163 Homeomorphy is common in ammonites, and in the case of *Lenicostites* gen. nov. it is due to  
1164 convergence (Fig. 8A) rather than parallelism (Fig. 8B–C) or iterative evolution (Fig. 8D–E).  
1165 Such homeomorphy could be the result of a morphofunctional adaptation related to similar  
1166 living conditions (external constraints). The appearance of *Camereiceras* with a non-  
1167 heteromorphic shell (Fig. 5B–C) established favorable conditions for interspecific  
1168 competition. *Camereiceras* has characteristics generally associated with better  
1169 competitiveness compared to *Lenicostites* gen. nov.: larger adult size (Tendler et al., 2015),  
1170 better evolutionary dynamics, probably higher reproductive rate and greater intraspecific  
1171 variability (see Monnet et al., 2015, p. 116, with references.). Thus, the disappearance of  
1172 *Lenicostites* gen. nov., very soon after they meet the re-coiled Hemihoplitinae (*Camereiceras*  
1173 *marchandi* and *C. limentinus*), could be interpreted as the effect of interspecific competition,  
1174 to go so far as a complete competitive replacement: in this hypothesis, *Lenicostites* gen. nov.  
1175 is a victim of the Gause Principle as it lost the Red Queen race (the permanent evolution of  
1176 species being necessary to answer the fitness of the other species with which it co-evolve to  
1177 avoid extinction – Van Valen, 1973).

1178

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1192

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1552

### 1553 **Figure captions**

1554 **Figure 1:** Biostratigraphic chart of the upper Barremian (see references in the text), with the  
1555 repartition and phylogeny of the Hemihoplitidae compared to the Lenicostitidae fam. nov. In  
1556 the Hemihoplitinae the species of the genera *Camereiceras* and *Hemihoplites* are: **1**,  
1557 *Camereiceras breistrofferi* (uncoiled shell); **2**, *Camereiceras marchandi* (tight uncoiled shell);  
1558 **3**, *Camereiceras limentinus* (fully coiled shell); **4**, *Hemihoplites cornagoae* (fully coiled  
1559 shell); **5**, *Hemihoplites astarte* (fully coiled shell); **6**, *Hemihoplites feraudianus* (fully coiled  
1560 shell).

1561

1562 **Figure 2:** *Lenicostites rusticus* gen. nov. from the upper Barremian (Lower Cretaceous) of  
1563 southeastern France. **A**, the holotype (4141351) figured by Vermeulen (1996, pl. 3, fig. 2–5),  
1564 from the Saint Martin ravine section (bed 20) in the neritic domain (*Gerhardtia sartousiana*  
1565 Zone, *Camereiceras limentinus* Subzone and Horizon); **B**, body chamber of an adult specimen  
1566 in two parts (RNNGHP.DBT.04007-A'/149-4.AJ49) from bed A'/149-4 in the pelagic  
1567 domain (*Toxancyloceras vandenheckei* Zone and Subzone); **C**, robust specimen from the  
1568 'Camereiceras limentinus beds' in the neritic domain (RNNGHP.DBT.04171-MAN.BB34),  
1569 section MAN (*Gerhardtia sartousiana* Zone, *Camereiceras limentinus* Subzone and  
1570 Horizon); **D**, robust specimen (RNNGHP.SBC.06050-TAI/99.TAI155) from bed TAI/99 in  
1571 the neritic domain (*T. vandenheckei* or *G. sartousiana* Zone); **E**, slender specimen  
1572 (RNNGHP.DBT.04007-A\*/149-3.BA54) from bed A'/149-4 in the pelagic domain  
1573 (*Toxancyloceras vandenheckei* Zone and Subzone).

1574

1575 **Figure 3:** Nearly complete robust adult of *Lenicostites rusticus* (Vermeulen, 1996) gen. nov.  
1576 (RNNGHP.SBC.06050-TAI/99.TAI153) from the upper Barremian (Lower Cretaceous, *T.*  
1577 *vandenheckei* Zone or *C. limentinus* Subzone) of section TAI/99, southeastern France. **A1**,  
1578 lateral view; **A2**, ventral view.

1579

1580 **Figure 4:** *Hemihoplites feraudianus* from the upper Barremian (Lower Cretaceous) of  
1581 southeastern France (Angles area), *Gerhardtia sartousiana* Zone, *Hemihoplites feraudianus*  
1582 Subzone and Horizon; **A**, macroconch specimen with smooth stage (RNNGHP.DBT.04007-  
1583 G12b/336.BA68); **B**, microconch adult specimen (RNNGHP.DBT.04173-GRY/903b.BA67).

1584

1585 **Figure 5:** *Camereiceras* from the upper Barremian (Lower Cretaceous) of southeastern  
1586 France; **A**, macroconch specimen of *Camereiceras limentinus* from La Gaude (*Gerhardtia*  
1587 *sartousiana* Zone, *Camereiceras limentinus* Subzone and Horizon – RNNGHP.DBT.06065-  
1588 VA/11b.BB32) in the neritic domain; **B**, microconch adult specimen of *Camereiceras*  
1589 *limentinus* from the Angles area (*Gerhardtia sartousiana* Zone, *Camereiceras limentinus*  
1590 Subzone and Horizon – RNNGHP.DBT.04173-GRY/883a.BB30) in the pelagic domain; **C**,  
1591 microconch adult specimen of *Camereiceras marchandi* from the Angles area  
1592 (*Toxancyloceras vandenheckei* Zone, *Gassendiceras alpinum* Subzone, *Camereiceras*  
1593 *marchandi* Horizon –RNNGHP.DBT.04007-A\*/156-15.BB29), note the uncoiling of the last  
1594 whorl (body chamber).

1595

1596 **Figure 6:** Correlation of the biostratigraphic charts between the north-west Tethys, the  
1597 Chañarcillo and Neuquén Basins (Chile and Argentina), Patagonia (Austral Basin) and  
1598 California, with repartition of the ammonites with ‘hemihoplitid like’ morphology. See text  
1599 for the bibliographic references and explanations.

1600

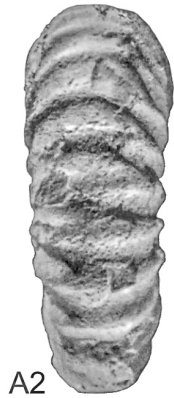
1601 **Figure 7:** Paleogeographic map of the Barremian age showing the distribution of: the north-  
1602 west Tethys Hemihoplitidae (stars, the white star points out the Vocontian basin in  
1603 southeastern France and also the Lenicostitidae fam. nov.), the Austral Homeomorphitinae  
1604 subfam. nov. (squares), and the Circum-Pacific Shasticrioceratidae fam. nov. (hexagons).  
1605 Data from literature (see text), map modified after Barron et al. (1981).

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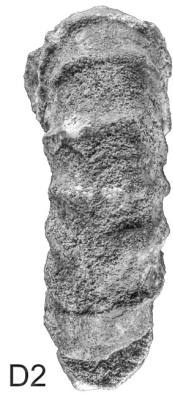
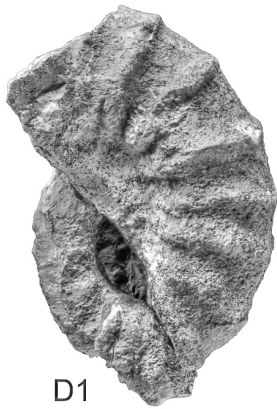
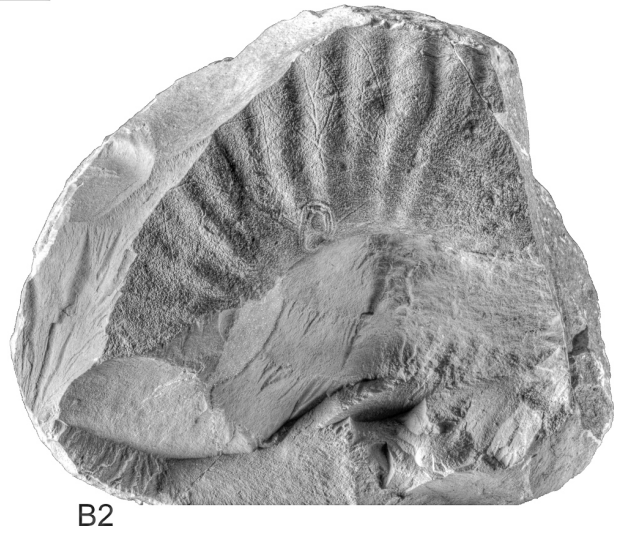
1607 **Figure 8:** The different patterns of homeomorphy in ammonites; numbers 1 to 4 are different  
1608 species; circles, squares and triangles are different phenotypes; letters a and b are different  
1609 processes; dash-lines separate different environments; **A**, homeomorphy by convergence is  
1610 given by evolution of independent processes (a and b) towards similar morphology (circles) in  
1611 two or more unrelated lineages (here 1-2 and 3-4), mainly because of adaptation to similar  
1612 conditions (external constraints). This is the case for example with the *Lenicostites* gen. nov.  
1613 and Hemihoplitinae; **B and C**, homeomorphy by parallel evolution is given when the  
1614 descendants of the same ancestral phenotype (species 1, square) have evolved in trajectories  
1615 towards a similar morphology (circle). Here, the same common developmental processes  
1616 was involved independently (a – intrinsic factor). See for example the parallel evolution of  
1617 two Devonian ammonoid families (Auguritidae Bogoslovski, 1961 and Pinacitidae Hyatt,  
1618 1900) in Monnet et al. (2015); **D**, iterative evolution can be given by adaptive convergence,  
1619 which gives the repeatability of the phenotypic traits (extrinsic factor). In that case (see the  
1620 example of *Physodoceras* in Hantzpergue, 1987), ammonite lineages 2 and 3 have evolved  
1621 iteratively in platform edge environment (whatever the processes involved, a or b) from the  
1622 generalist pelagic pool 1; **E**, iterative evolution can be also given by evolutionary crisis  
1623 (punctuated event of proteromorphosis type – intrinsic factor), which leads to the  
1624 reappearance of ancestral phenotype (circle), whatever the processes involved, a or b. This

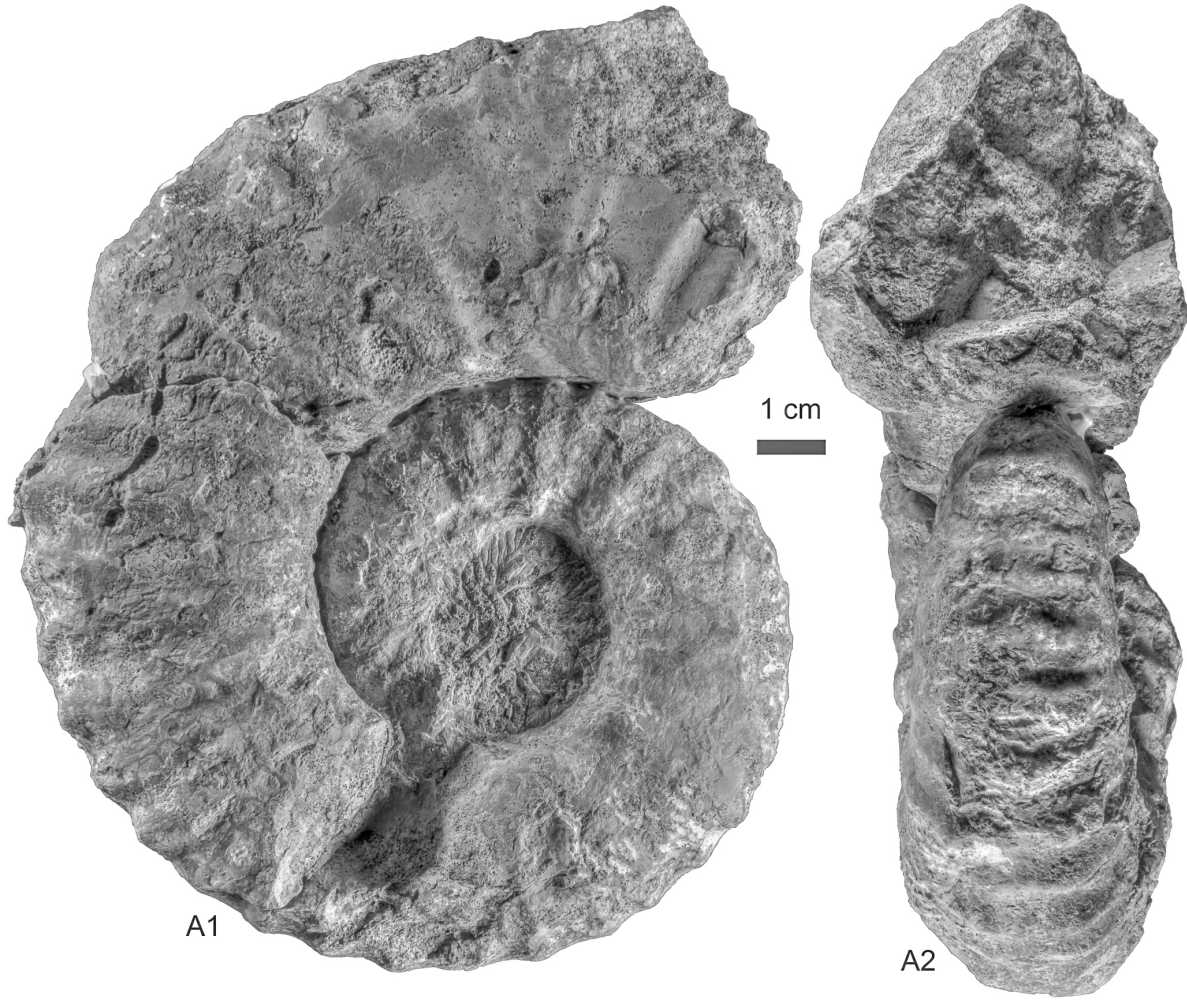
1625 special case of parallel evolution shifted in time is known, for example, in *Gregoryceras*,  
1626 which finally repeated the morphology known in its ancestor *Peltoceratoides* (see Bonnot,  
1627 1995; Bert, 2004, 2014).

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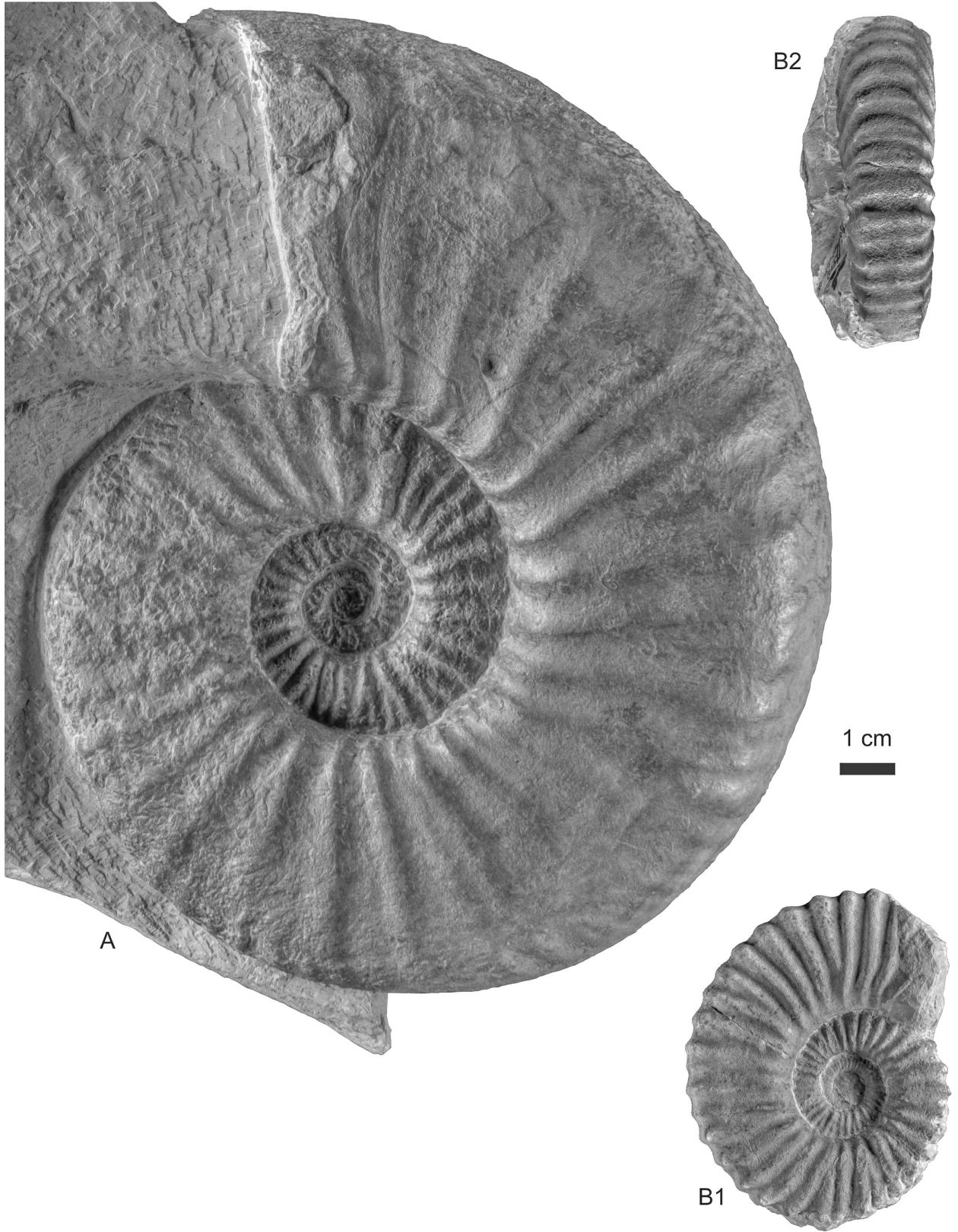
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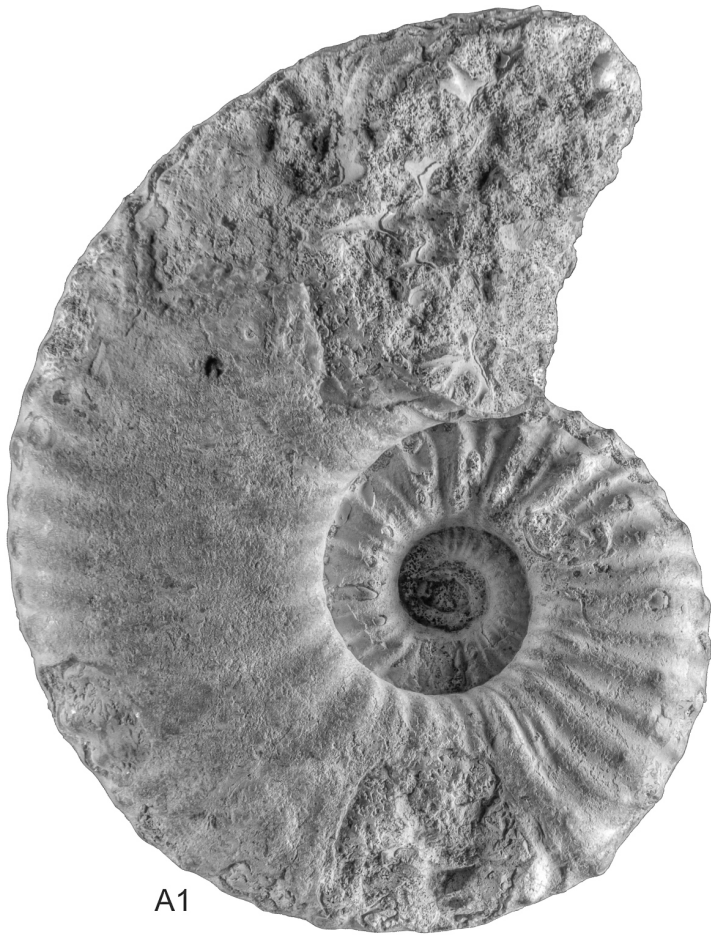




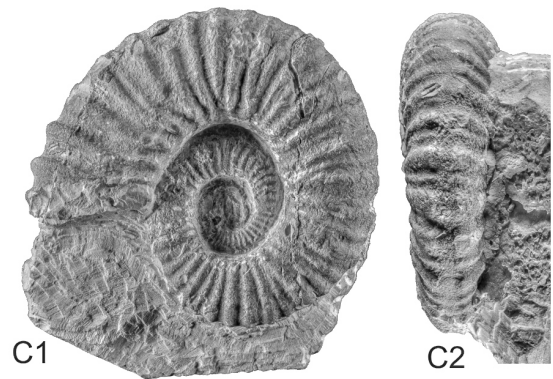
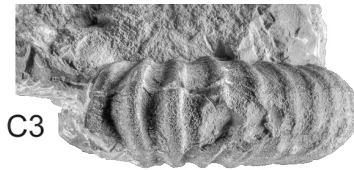
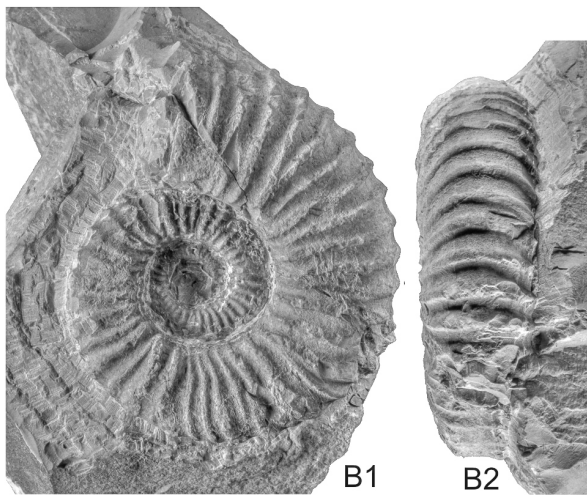
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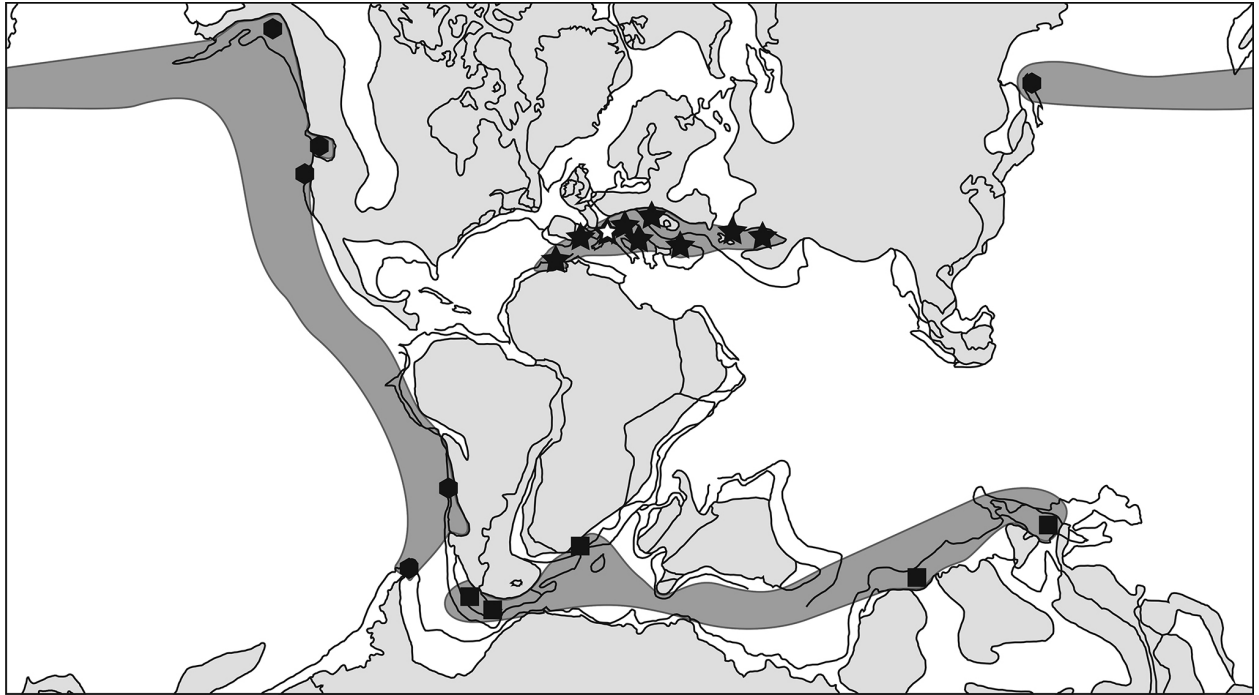




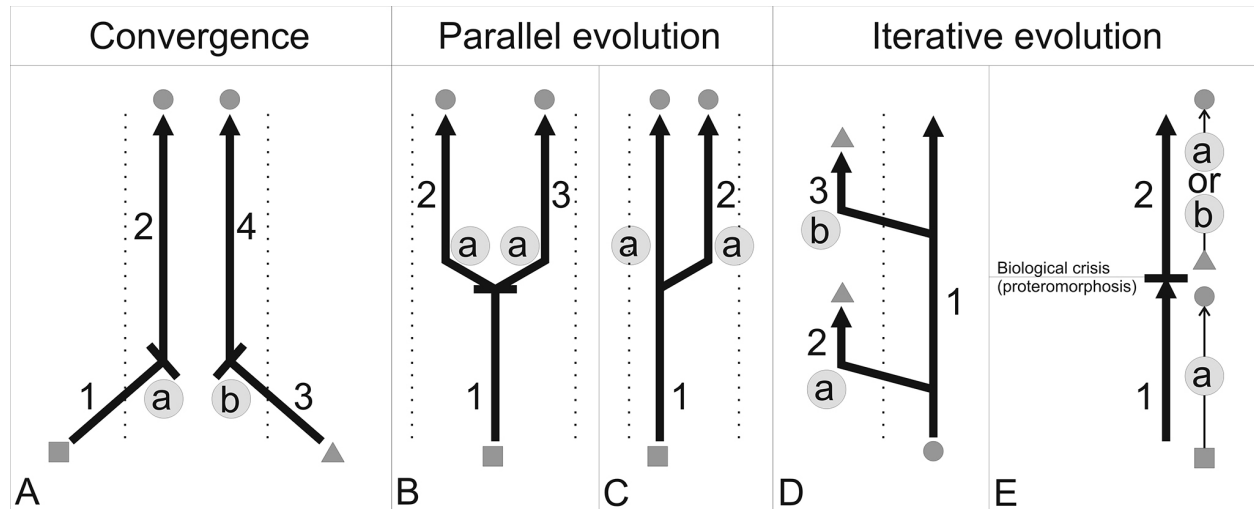
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STAGES	ZONES	SUBZONES	HORIZONS	AMMONITES
BARREMIAN pars. UPPER	<i>Imerites giraudi</i>	<i>Pseudocrioceras waagenioides</i>		<b>DOUVILLEICERATIDAE</b>
		<i>Martelites sarasini</i>		
		<i>Imerites giraudi</i>	<i>Heteroceras emerci</i> <i>Imerites giraudi</i> <i>Imerites dichotomus</i>	
	<i>Gerhardtia sartousiana</i>	<i>Hemihoplites feraudianus</i>	<i>Pseudoshasticioceras autrani</i>	
			<i>Pseudoshasticioceras magnini</i>	
			<i>Pseudoshasticioceras bersaci</i>	
		<i>Hemihoplites feraudianus</i>		
		<i>Gerhardtia provincialis</i>	<i>Hemihoplites astarte</i>	
			<i>Gerhardtia provincialis acme</i>	
			<i>Gerhardtia provincialis FAD</i>	
		<i>Camereiceras limentinus</i>	<i>Gerhardtia sartousiana acme</i>	
			<i>Camereiceras limentinus</i>	
			<i>Camereiceras marchandi</i>	
		<i>Gassendiceras alpinum</i>	<i>Camereiceras breistrofferi</i>	
			<i>Gassendiceras alpinum</i>	
	<i>Gassendiceras alpinum</i>			
	<i>Toxancyloceras vandenheckei</i>	<i>Toxancyloceras vandenheckei</i>		
		<i>Toxancyloceras canuti</i>		