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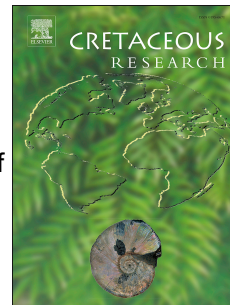
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1 Implications of the ‘hemihoplitid-like’ ammonites iterative morphology in 2 the context of the late Tethyan Barremian (Early Cretaceous)

3
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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 Shasticioceradidae 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 *Pseudoshastrioceras* 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 ploszkiewiczzi* 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. ploszkiewiczzi* → *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 ELU₂U₃I 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 ELU₂U₃I 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 trifold 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 *Pseudoshasticioceras*, 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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1180

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1190

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1192

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1194

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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

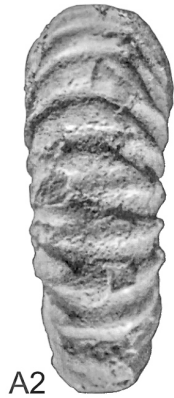
1601 **Figure 7:** Paleogeographic map of the Barremian age showing the distribution of: the north-
1602 west Tethys Hemihoplitidae (stars, the white star points out the Vocontian basin in
1603 southeastern France and also the Lenicostitidae fam. nov.), the Austral Homeomorphitinae
1604 subfam. nov.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

1606

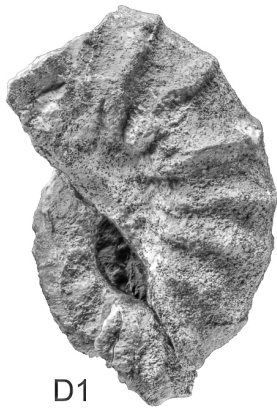
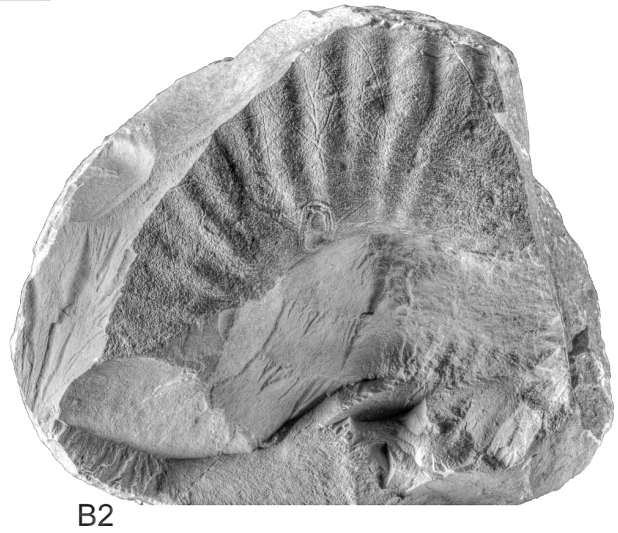
1607 **Figure 8:** The different patterns of homeomorphy in ammonites; numbers 1 to 4 are different
1608 species; circles, squares and triangles are different phenotypes; letters a and b are different
1609 processes; dash-lines separate different environments; **A**, homeomorphy by convergence is
1610 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

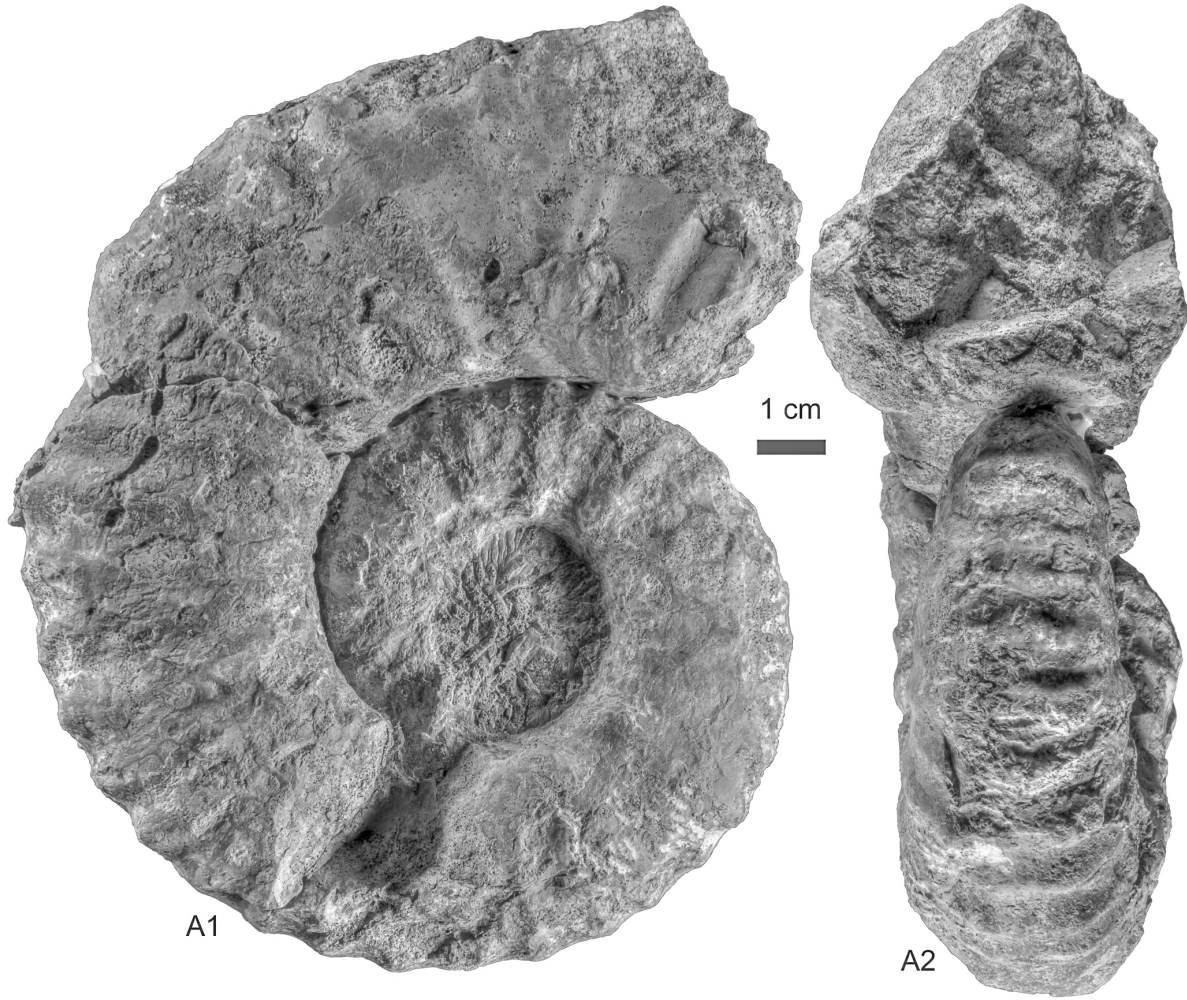
1625 special case of parallel evolution shifted in time is known, for example, in *Gregoryceras*,
1626 which finally repeated the morphology known in its ancestor *Peltoceratoides* (see Bonnot,
1627 1995; Bert, 2004, 2014).

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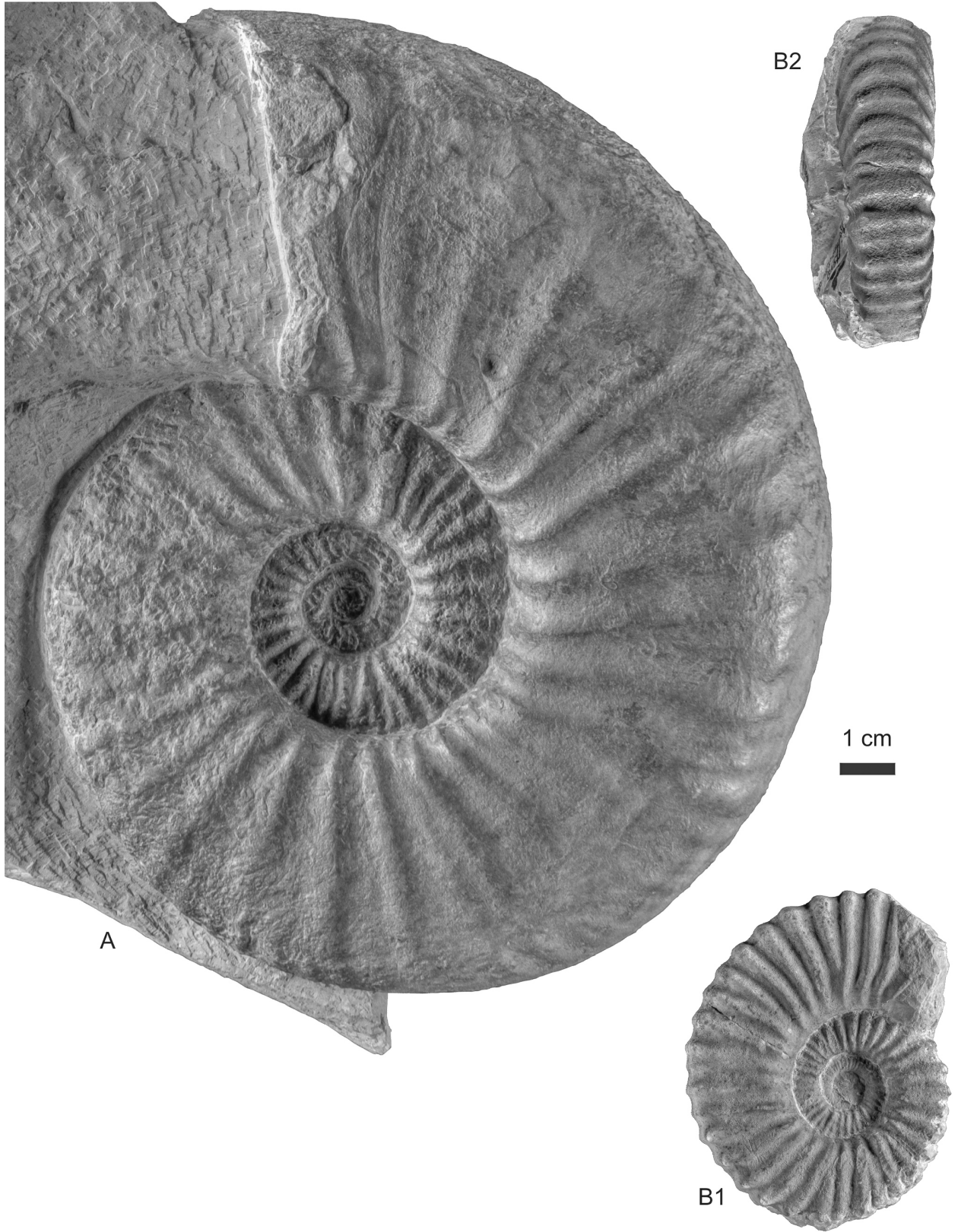


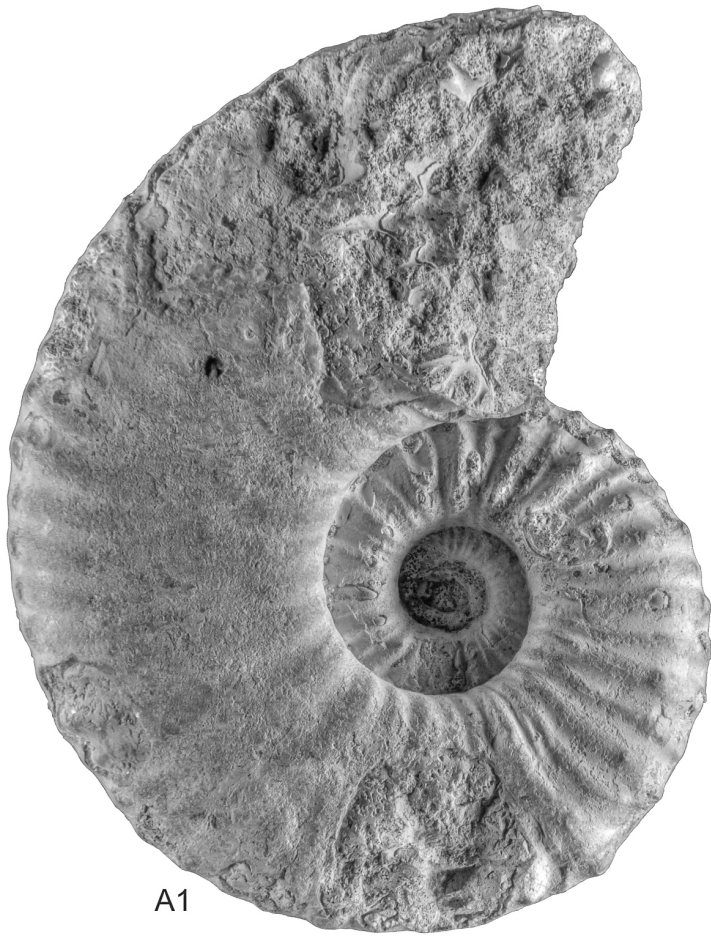
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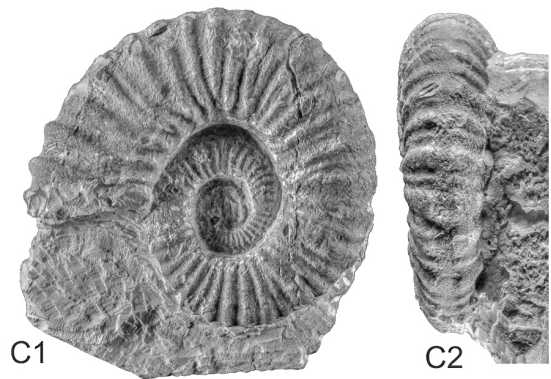
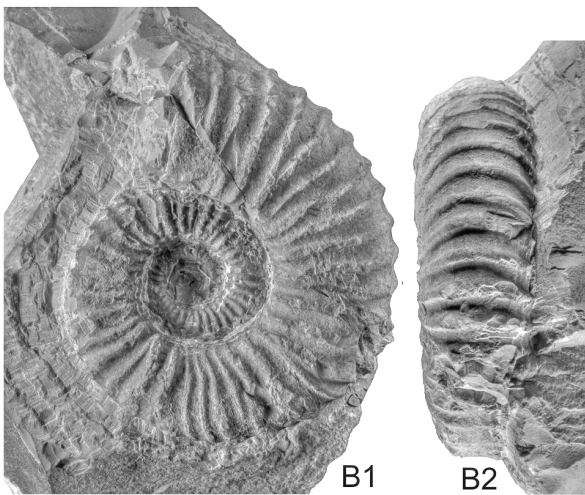


Jo





1 cm



| STAGES | NE Tethys | | Chañarcillo and Neuquén Basins | | Patagonia | California | Ammonites with hemihoplitid like morphology | |
|-------------|-----------|-------------------------------------|--|--|-------------------------------------|--|--|--|
| | ZONES | SUBZONES | ZONES | SUBZONES | ZONES | ZONES | | |
| APTIAN | UPPER | <i>Hypacanthoplites jacobii</i> | | <i>Hypacanthoplites</i> sp. | | <i>Peltoiceras deeckeii</i> | | |
| | | <i>Acanthoplites nolani</i> | <i>Diadochoceras nodosocostatum</i> | | | <i>Australiceras hallei</i> | | |
| | | <i>Parahoplites melchioris</i> | | | | | | |
| | | <i>Epicheloniceras martini</i> | <i>Epicheloniceras bustorfi</i> <i>Epicheloniceras gracile</i> <i>Epicheloniceras debile</i> | | | | | |
| | | <i>Dufrenoyia furcata</i> | <i>Dufrenoyia dufrenoyi</i> <i>Dufrenoyia furcata</i> | | | <i>Tropaeum magnum</i> | | |
| | | <i>Deshayesites deshavesi</i> | <i>Deshayesites grandis</i> <i>Deshayesites multicostatus</i> <i>Deshayesites deshavesi</i> | | <i>Ancyloceras</i> sp. | | ? | |
| | LOWER | <i>Deshayesites forbesi</i> | <i>Deshayesites forbesi</i> <i>Deshayesites fittoni</i> | | | | <i>Shastrioceras poniente</i> | |
| | | <i>Deshayesites fissicostatus</i> | <i>Deshayesites obsoletus</i> <i>Deshayesites fissicostatus</i> | <i>Antarcticoceras perzi</i> | | | | |
| | | <i>Imerites giraudi</i> | <i>Pseudocrioceras feradiamus</i> <i>Gerhardia waagenioides</i> <i>Martelites sarasini</i> <i>Imerites giraudi</i> | | | <i>Colchidites-Sanmartinoceras</i> | | |
| | | <i>Gerhardia sartousiana</i> | <i>Hemihoplites feradiamus</i> <i>Gerhardia provincialis</i> <i>Camericeras limentinus</i> | <i>Antarcticoceras domykannum</i> | | | <i>Homeomorphytes aguirre-uretae</i> gen. nov. et sp. nov. | |
| | | <i>Toxancyloceras vandenheckei</i> | <i>Gassidiceras alpinum</i> <i>Toxancyloceras vandenheckei</i> | | | | <i>Shastrioceras rodai</i> | |
| | | <i>Moutoniceras moutonianum</i> | | | <i>S. africanum insignicostatum</i> | <i>Hatchericeras patagonense</i> | | |
| BARREMIAN | UPPER | <i>Kotetishvilia compressissima</i> | <i>Holcodiscus caillaudianus</i> <i>Holcodiscus fallax</i> | <i>Moutoniceras</i> sp. | | | | |
| | | <i>Nicklesia pulchella</i> | | <i>Emericeras</i> | <i>Emericeras aff. otto-hassi</i> | | <i>Shastrioceras patricki</i> | |
| | | <i>Kotetishvilia nicklesi</i> | | <i>Shastrioceras</i> | | | | |
| | LOWER | <i>Taveraidiscus hugii</i> | <i>Psilotissotia colombiana</i> <i>Taveraidiscus hugii</i> | <i>Paraspiticeras groeberi</i> | | | | |
| | | <i>Pseudothurmannia ohmi</i> | <i>Pseudothurmannia pietetti</i> <i>Pseudothurmannia ohmi</i> | | | <i>Favella wilckensi</i> | <i>Hertleinites aguilae</i> | |
| | | <i>Crioceratites balearis</i> | <i>Crioceratites angulicostatus</i> <i>Crioceratites irenkei</i> <i>Crioceratites binelli</i> <i>Crioceratites balearis</i> | <i>Diamantoceras diamantensis</i> | | | | |
| HAUTERIVIAN | UPPER | <i>Plesiospitidiscus ligatus</i> | | <i>Crioceratites schlagintweitii</i> | | | | |
| | | <i>Sibaynella sayni</i> | | <i>Spinidiscus riccardii</i> | | ? | | |
| | | <i>Lyticoceras nodosoplicatum</i> | | <i>Weav. vacuense</i> <i>Hopl. gentilii</i> | | <i>Aegocrioceras patagonicum</i> | | |
| | LOWER | <i>Crioceratites loryi</i> | <i>Olcostephanus jeannoti</i> <i>Crioceratites loryi</i> | <i>Holcoptychites neuquensis</i> | | <i>Olcostephanus laiocostata</i> <i>Hol. agricensis</i> <i>Hol. neuquensis</i> | <i>Favella americana</i> | |
| | | <i>Acanthodiscus radiatus</i> | | | | | | |
| | | | | | | | | |

LENCOCERATIDAE

- Lencoceras* gen. nov. (France)
- Walpenites* ? *saclicensis* (Columbia)
- Pachyhemihoplites*
- Camericeras*
- Hemihoplites*
- Hemihoplites feradiamus*
- HEMIOPHITINAE** (NW Tethys)
- Homeomorphytes* gen. nov. (Argentina)
- Makutinites* gen. nov. (Zabuland)
- Hatchericeras* (Austral Basin)

ENDEMO CERATINAE

- Theodorites* (Crimea)
- Inserta sedis *'Hemihoplites' mexicanum* (Mexico)

SHASTRIOCERATIDAE

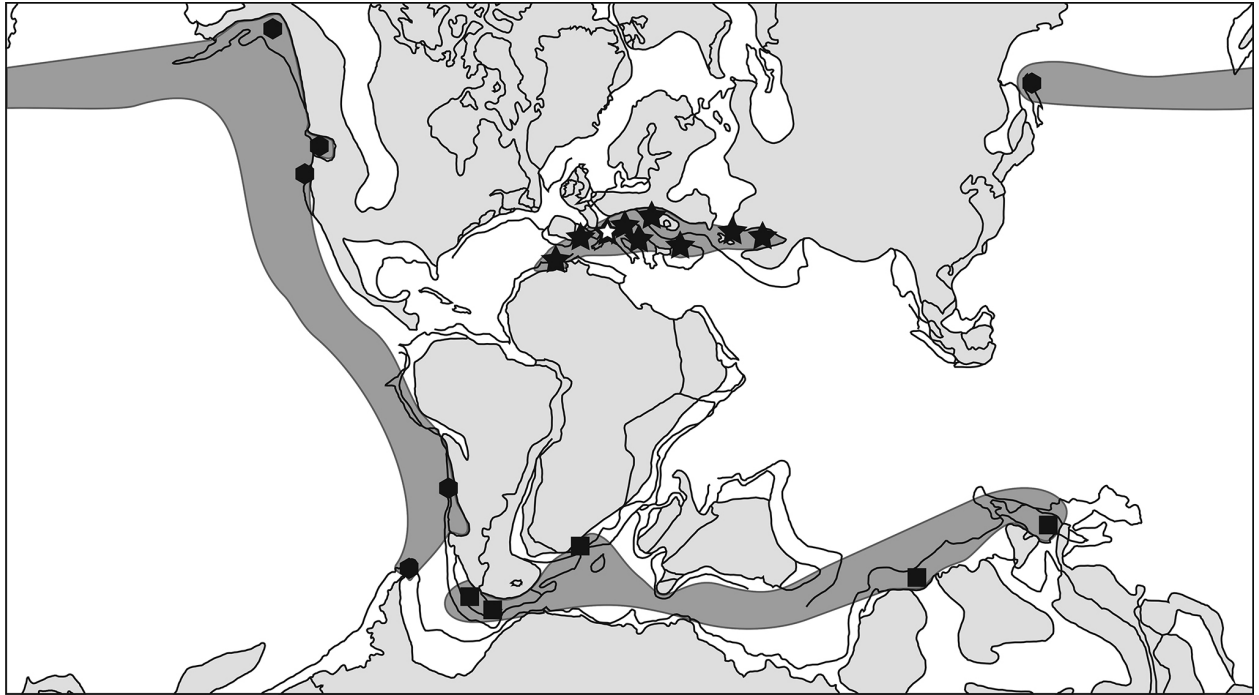
- Antarcticoceras* (Antarctica)
- Antarcticoceras perzi* (Chile)
- Shastrioceras popanoi* (California)
- Shastrioceras* (Chile)
- Shastrioceras* (California)

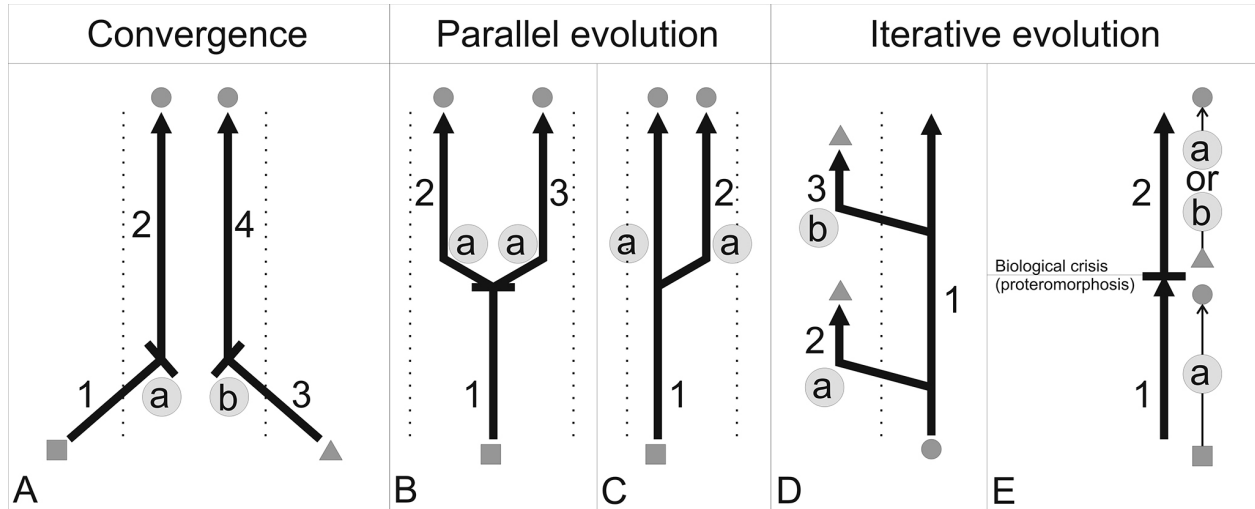
HOMEOMORPHITINAE

- Inserta sedis *Hemihoplites cf. feradiamus* (Mexico)
- Inserta sedis *Hemihoplites* sp. (Cuba)
- Inserta sedis *Hemihoplites* sp. (Antarctica)

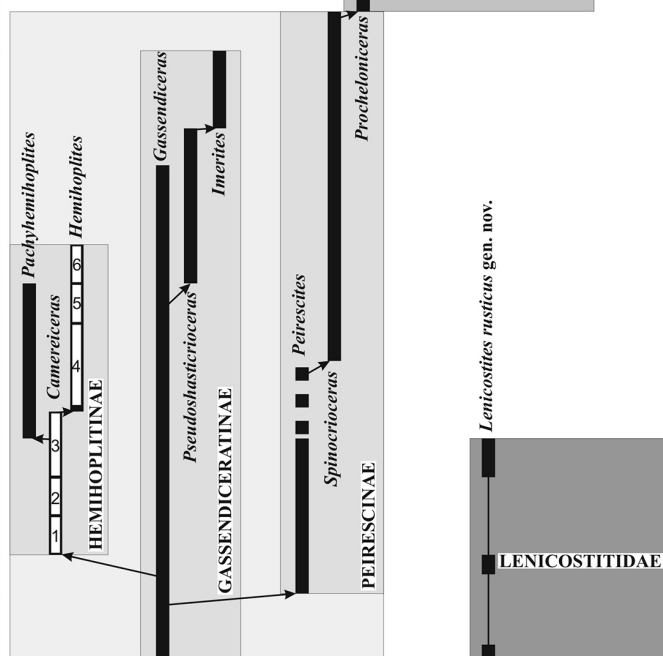
HETEROCERATIDAE

- Martelites* (NW Tethys)
- Turkmeniceras* (Caucasus)
- DESHAYESITIDAE**





| STAGES | ZONES | SUBZONES | HORIZONS | AMMONITES | | | |
|--------------------------|------------------------------------|-------------------------------------|--|---------------------------|-----------------------|--------------------------|--------------------|
| BARREMIAN pars. UPPER | <i>Imerites giraudi</i> | <i>Pseudocrioceras waagenioides</i> | | DOUVILLEICERATIDAE | | | |
| | | <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> | HEMIHOPLITINAE | HEMIHOPLITIDAE | | |
| | | | <i>Pseudoshasticioceras magnini</i> | | | | |
| | | | <i>Pseudoshasticioceras bersaci</i> | | | | |
| | | | <i>Hemihoplites feraudianus</i> | | | | |
| | | <i>Gerhardtia provincialis</i> | <i>Hemihoplites astarte</i> | GASSENDICERATINAE | | GASSENDICERATIDAE | |
| | | | <i>Gerhardtia provincialis acme</i> | | | | |
| | | | <i>Gerhardtia provincialis FAD</i> | | | | |
| | | | <i>Gerhardtia sartousiana acme</i> | | | | |
| | | <i>Camereiceras limentinus</i> | <i>Camereiceras limentinus</i> | PEIRESCINAE | | | PEIRESCINAE |
| | | | <i>Camereiceras marchandi</i> | | | | |
| | | | <i>Camereiceras breistrofferi</i> | | | | |
| | | | <i>Gassendiceras alpinum</i> | | | | |
| | <i>Toxancyloceras vandenheckei</i> | <i>Gassendiceras alpinum</i> | <i>Gassendiceras alpinum</i> | LENICOSTITIDAE | | | |
| | | | <i>Toxancyloceras vandenheckei</i> | | | | |
| | | <i>Toxancyloceras vandenheckei</i> | <i>Toxancyloceras vandenheckei</i> | | | | |
| | | | <i>Toxancyloceras canuti</i> | | | | |
| | | | <i>Toxancyloceras canuti</i> | | | | |



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