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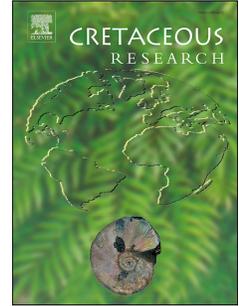
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Size reduction and ornamental oscillation within a Barremian lineage of giant heteromorphic ammonites (Early Cretaceous, northwestern Tethyan margin)

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28 is described: *T. canuti* sp. nov. With respect to an evolutionary perspective under
29 biostratigraphic control, their phylogeny is considered (*M. eigenheeri* -> *T. canuti* sp. nov. ->
30 *T. vandenheckei*). The hypothesis of the origin of the genus *Toxancyloceras* within the
31 *Moutoniceras* is strengthened; this link is consistent both stratigraphically and
32 morphologically. *Moutoniceras* appears to be the oldest known representative of the
33 Ancyloceratidae, which is rooted in the early Barremian. The ontogenetic and evolutionary
34 patterns of the phyletic lineage *Moutoniceras* / *Toxancyloceras* are twofold: the first concerns
35 the ornamental changes (itself determined by three imbricated patterns) and the second
36 involves the adult size. Both patterns determine two evolutionary phases through time: (1) the
37 giant *Moutoniceras* and the progressive disappearance of the tubercles through heterochrony
38 (paedomorphosis), and (2) the drastic size reduction and the reappearance of the tubercles
39 from the “small” *Moutoniceras* to the *Toxancyloceras* (through heterochrony, with
40 peramorphosis and a combination of pseudo-dwarfism, acceleration and graduaptation). The
41 oscillation in disappearance and reappearance of the tubercles demonstrates a possible case of
42 evolutionary reversibility where heterochrony helped by the progenesis impact, favors
43 character repeatability in the evolutionary patterns. The results for the genera *Moutoniceras*
44 and *Toxancyloceras* have significant biostratigraphic implications for the Tethyan Barremian.
45 The status of *T. vandenheckei* as a zonal and subzonal index species (basal upper Barremian)
46 is reinforced, and three new ammonite horizons are defined: the *Moutoniceras eigenheeri*,
47 *Toxancyloceras canuti* and *T. vandenheckei* horizons. The stratigraphic distribution of all
48 their index species is very restricted, indicating a well established evolutionary context.

49

50 **Key-words.** Ancyloceratidae; Barremian; Vocontian Basin; France; Biostratigraphy;
51 Evolution.

52

53 Highlights.

- 54 • The areas studied are in southeastern France and Mallorca (Spain).
- 55 • A new species (*Toxancyloceras canuti* sp. nov.) is described.
- 56 • Review of the Astier collection allows to understand misinterpretations of *T.*
57 *vandenheckei*.
- 58 • Evolutionary patterns and processes of the oldest Ancyloceratidae are explained.
- 59 • 3 biostratigraphic horizons are introduced at the lower/upper Barremian boundary.

60

61 1. Introduction

62 The ammonite family Ancyloceratidae Gill, 1871 (see Klein et al., 2007 for the generally
63 accepted generic content) ranges from late Barremian to late Aptian (Early Cretaceous). In
64 this family, the genus *Toxancyloceras* Delanoy, 2003 is the oldest known representative, as it
65 is present at the base of the lower Barremian (*Toxancyloceras vandenheckei* Zone) with the
66 species *T. vandenheckei* (Astier, 1851). Strong morphological convergences link
67 *Toxancyloceras* to the more recent Aptian *Ancyloceras* s. str. through a variety of forms, but
68 whose phyletic relationship is still poorly known (*Jaubertites* Sarkar, 1955, *Hoheneggericeras*
69 Baudouin et al., 2008, etc.).

70 The origin of the genus *Toxancyloceras* was discussed by Delanoy (2003) and Vermeulen
71 (2005). According to Delanoy (2003, p. 3), it originates in the genus *Emericiceras*
72 (*Emericiceratidae* Vermeulen, 2004), and *T. vandenheckei* (Astier, 1851) is an intermediate
73 species between *Emericiceras emerici* (Léveillé, 1837) and *Gassendiceras alpinum*
74 (d'Orbigny 1850) (*Hemihoplitidae* Spath, 1924). Vermeulen (2005, p. 159-160) considered
75 *Honoratia* Busnardo et al., 2003 (*Emericiceratidae*) as a direct ancestor of *Toxancyloceras*.

76 Bert and Bersac (2014) performed a phylogenetic analysis (Fig. 1) dealing with several taxa
77 (*Toxancyloceras*, *Honnoratia*, *Emericiceras*, *Moutoniceras* Sarkar, 1955 and *Gassendiceras*).

78 The results showed that:

79 - (1) neither *Emericiceras* nor *Honnoratia* can be interpreted as potential ancestors of
80 *Toxancyloceras* (Bert and Bersac, 2014, fig. 3 and 4, p. 262). This position is reinforced by
81 the stratigraphic hiatus of nearly two ammonite zones between the last Emericiceratidae and
82 the first *Toxancyloceras*;

83 - (2) *Gassendiceras* (tested by the older forms *G. essaouirae* Bert and Bersac, 2014
84 and *G. multicoatum* [Sarkar 1955] in Bert and Bersac, 2014, fig. 3, p. 261) cannot be
85 interpreted as a potential descendant of *Toxancyloceras*. Thus Hemihoplitidae and
86 Ancyloceratidae are two independent families;

87 - (3) the early Barremian genus *Moutoniceras* is a sister taxon of *Toxancyloceras*.

88
89
90 This latter result, as well as its strong stratigraphic and morphological consistency, led these
91 authors to consider *Moutoniceras* as an authentic representative of the Ancyloceratidae, rather
92 than as a representative of the Heteroceratidae as it was admitted by a majority of experts
93 until recently (Klein et al., 2007; see Bert and Bersac, 2014, p 264, for a historical account).
94 Thus, to date, *Moutoniceras* is the oldest known Ancyloceratidae. A possible origin of the
95 *Moutoniceras* within the Hauterivian *Pseudomoutoniceras* Autran et al., 1986 was proposed
96 by Vermeulen (2006), but this hypothesis was challenged more recently by the same author
97 (Vermeulen et al., 2010, p. 95) because of the very large stratigraphic gap that exists between
98 these two genera. The review of the literature data (op. cit.) shows that there is a real gap in
99 knowledge regarding the oldest Ancyloceratidae, and especially in their evolutionary
100 modalities, in terms of patterns and processes.

101 New samples from the area of the Barremian stratotype of Angles (southeastern France), in
102 levels dated at the top of the *M. moutonianum* Zone and the basal *T. vandenheckei* Zone, at
103 the transition between the lower and upper Barremian, shed new light on the questions of the
104 *Toxancyloceras* origin and evolution. Other data from the Mallorcan area (Balearic Islands)
105 close gaps in the knowledge about the morphology of the studied species. Seven successive
106 species of *Moutoniceras* and *Toxancyloceras* are identified in the present work, including a
107 new one, and their phylogenetic relationships are considered, based on an evolutionary
108 perspective. Biostratigraphic implications are potentially significant, given the importance of
109 the genera *Moutoniceras* and *Toxancyloceras* in the standard Tethyan ammonite zonation
110 (Reboulet et al., 2014). The index species *T. vandenheckei* is thus revised, taking into account
111 the review of its holotype (Astier collection).

112

113 **2. Geological setting and sections studied**

114 The fossil material studied in the present work is the result of the systematic bed-by-bed
115 sampling of several stratigraphic sections near the Barremian stratotype (southeastern
116 France). Other ex-situ specimens of *Toxancyloceras* are from the Lloseta and Biniamar area
117 (Mallorca, Balearic Islands, Spain). These areas both belong to the Cretaceous of the
118 northwestern Tethyan margin (Fig. 2).

119 The biostratigraphic framework used for the Barremian in this work is the one proposed by
120 the I.U.G.S Lower Cretaceous ammonite working group; the Kilian Group (Reboulet et al.,
121 2014 – see Bert et al., 2008 for historical account). In the present work we also take into
122 account the biostratigraphic proposals of Bert et al. (2008), Bert and Delanoy (2009), and Bert
123 et al. (2010, 2011), which allows a high stratigraphic precision for the area studied (Fig. 3).

124

125 **2.1. The Vocontian Basin**

126 The Southeast France Basin (Fig. 4) is a large subsident intracratonic area, located in the
127 southeast part of the country, between the Massif Central, which borders the West, the Alps
128 that limit the East, the Jura in the North and the Mediterranean Sea in the South. Its Mesozoic
129 sedimentation phase is between the Triassic (late Hercynian orogeny) and the Cretaceous
130 (start of the Alpine orogeny), the Pyrenean-Provencal movements of the Late Cretaceous
131 mark its demise as a basin.

132 Known as the Vocontian Basin (Paquier, 1900) the Southeast basin began its reduction during
133 the Early Cretaceous. Its southern part, in the Barremian stratotype area (near Angles, Alpes
134 de Haute-Provence, southeastern France – red star in Fig. 4), is characterised by pelagic
135 sedimentation with an alternation of marlstones and limestones in decimetric to metric beds.
136 This particular area is very conducive to studies thanks to the abundance and the quality of its
137 outcrops. The continuous sedimentation and good paleontological record reveal the ammonite
138 succession in considerable detail. The deep marine conditions of the Vocontian Basin, largely
139 open to the Alpine Tethys, are reflected in the dominance of ammonites.

140 The Barremian stratotype area belongs to the protected perimeter of the Geological National
141 Nature Reserve of Haute-Provence, managed by the Departmental Council of the Alpes de
142 Haute-Provence. Many field sections were surveyed and studied there for almost two decades,
143 as part of a larger work done by one of us (DB). Some of them have already been published
144 (Bert and Delanoy, 2009; Bert et al, 2008, 2011, 2013). The sections that have provided the
145 majority of the *Toxancyloceras* and *Moutoniceras* specimens studied here are A* and G5 (see
146 below).

147

148 **2.1.1. Field section A* (Fig. 5)**

149 *Previous work:* the Barremian historical stratotype (section A) has been designated by
150 Busnardo in 1963 at the Symposium on the Lower Cretaceous (Busnardo, 1965b). It is located

151 along the road of Angles (Alpes de Haute-Provence, France) where the section A extends
152 approximately 660 m (500 m for the Barremian itself) along two East-West oriented hills.
153 This area has been previously studied by ammonitologists, particularly by Busnardo (1965a),
154 Delanoy (1997) and Vermeulen (2005). The complementary section A* was described for the
155 first time by Bert (2012).

156 *Description:* the trench of the road (section A) allows the entire stratigraphic succession to be
157 seen, from bed No. 1 (upper Hauterivian) to bed No. 232 (lower Aptian), which underlies the
158 Blue Marls Formation. The beds are almost tangential to the road, which allows them to be
159 tracked in good conditions most of the time. Unfortunately, this exposure makes their study
160 quite difficult. In this section, the lower part of the upper Barremian (*T. vandenheckei* and
161 *Gerhardtia sartousiana* zones) is poorly exposed. Firstly because of access difficulties to the
162 section that is along a cliff slope. Secondly because the growth faults disrupt the bed
163 successions and make them impossible to study (see more explanations in Bert, 2012, p. 4).
164 Given these difficulties in section A, a new reference section (denoted A*) was surveyed in
165 the immediate lateral continuity of the stratotype (above the road), where there is no growth
166 fault. For the *T. vandenheckei* Subzone, the bed numbering is the same as for stratotype A.

167

168 **2.1.2. Field section G5 (Fig. 6)**

169 *Previous work:* this outcrop corresponds to the site of “Les Lumières” mentioned by Delanoy
170 (2003, p. 3), near Angles (Alpes de Haute-Provence, southeastern France). Although it
171 allowed the study of several complete specimens of *Toxancyloceras* of the L. Ebbo collection
172 by the latter author, this section was never studied by means of bed-by-bed sampling. Thus,
173 these latter *Toxancyloceras* have been assigned to the *T. vandenheckei* Zone by Delanoy
174 (2003, p. 3, 5) without further detail. The current and more detailed work of this section

175 allows us to characterise the presence of the lower Barremian that was never reported
176 previously (Fig. 6, *M. moutonianum* Zone).

177 *Description:* the field section was surveyed in a small ravine, where the succession is clearly
178 visible from the top of the upper Barremian (*M. moutonianum* Zone) to the *Gassendiceras*
179 *alpinum* Subzone. The section borders the gigantic excavation dig that provided most of the
180 *Toxancyloceras* collected in this section and figured by Delanoy (2003). This intensive
181 sampling almost completely destroyed the structural surface of bed No. G5/85, making it
182 particularly complicated to study. Thus, given the presence of this gigantic excavation, it is
183 very likely that most of the specimens from “Les Lumières” figured by Delanoy (2003) are
184 from bed No. G5/85. The close proximity (a few hundred meters) of the field section G5 from
185 the Angles stratotype (section A*) allows a bed-by-bed correlation between these two
186 sections, which are almost identical.

187

188 **2.2. Mallorca**

189 Mallorca is the largest of the Balearic Islands (East of Spain). Geologically, it is closely
190 related to the Betic System in Southeast Iberian Peninsula. In Mallorca, the Cretaceous is
191 mostly known in the West of the Sierra de Tramuntana but also in the centre of the island
192 (called Es Pla) and in Sierra de Llevant. These Sierras originated in the Alpine orogeny
193 (Colom, 1975). The Lower Cretaceous is formed by *ammonitico rosso* facies, but from the
194 upper Berriasian to upper Barremian the marlstones and limestones of Maiolica facies are
195 dominant. The lower Aptian is absent from the stratigraphical record and the upper Aptian is
196 only present in the Southwest area. After this stratigraphical gap, the Lower Cretaceous is
197 represented by marcasite-rich marls and marly limestones up to the upper Albian. The studied
198 area (see below) is located in the middle part of Tramuntana (red star in Fig. 7).

199 As they are collected ex-situ (see below), the specimens from Mallorca were not taken into
200 account when considering the biostratigraphic part, but they were used (1) to enlarge the
201 understanding of the morphology of the species studied (the fossils studied are often
202 fragmentary due to the heteromorphic state of the shells, thus there is a real need to increase
203 the number of specimens), and (2) for palaeobiogeographical purpose.

204

205 **2.2.1. Can Negret Quarry**

206 *Previous work:* the quarry was studied only recently in a work conducted by one of us
207 (Juárez-Ruiz and Matamales-Andreu, unpublished), who described the Cretaceous ammonite
208 biozonation of the area and part of the representative taxa.

209 *Description:* this active quarry, which represents the largest mining enterprise in the Balearic
210 Islands, is located near the town of Lloseta, in the middle of Tramuntana. Can Negret is the
211 richest Cretaceous fossil locality in Mallorca and one of the most abundant in Spain, with
212 more than 220 recognised ammonite species. Unfortunately, the activity of the quarry and the
213 extreme deformation of the series (common in most of the Mallorcan Cretaceous sites) make
214 it almost impossible to carry out accurate bed-by-bed sampling. However many ammonite
215 zones from the upper Valanginian to upper Albian are recognised by their index species and
216 faunal association, including the *M. moutonianum* and *T. vandenheckei* zones.

217

218 **2.2.2. Lloseta-Biniamar area**

219 *Previous work:* several small and dispersed Cretaceous outcrops in the area between Lloseta
220 and Biniamar were studied or mentioned from the end of the 19th Century (Hermite, 1879;
221 Nolan, 1895). The area near Lloseta is especially famous for having delivered the type
222 specimen of *Kotestishvilia sauvageaui* (Hermite, 1879). Fallot (1910, 1922) and Fallot and
223 Termier (1923) also mentioned some species near this town. Wiedmann (1962a, 1962b, 1964,

224 1967) described some Valanginian, Barremian and Albian ammonites from this area.
225 Recently, Juárez-Ruiz and Matamales-Andreu (unpublished) recognised most of the
226 ammonite zones from the upper Valanginian to the upper Barremian, and they found taxa
227 previously unknown in Mallorca, including taxa also unreported in Spain.

228 *Description:* this area shows some dispersed outcrops, which are hard to study because they
229 are usually covered by cultivated land. The stratigraphy can be studied only with faunal
230 association in *ex situ* samples in most of the cases. However, some small sections are located
231 from the *Kotetishvilia compressissima* to *T. vandenheckei* zones, which are especially rich in
232 ammonites in most of their beds.

233

234 **3. Material**

235 The explanations about the material studied, and an overview of the Astier collection, which
236 contains the holotype of the index species *Toxancyloceras vandenheckei*, are in the additional
237 online material of the present work.

238

239 **4. Systematic paleontology**

240 The detailed systematic part (including the description of *Toxancyloceras canuti* sp. nov. and
241 the revisions of *T. vandenheckei* and *Moutoniceras eigenheeri*) and the photographic figures
242 of the studied material are in the additional online material of the present work.

243

244 **5. Results: phylogenetic and evolutionary perspective under patterns and processes**

245 The new data exposed in the present study strengthens the phyletic link Bert and Bersac
246 (2014) proposed, based on a cladistic analysis (Fig. 1) between the genera *Moutoniceras* and
247 *Toxancyloceras*. It appears that this link is consistent both stratigraphically and
248 morphologically. The stratigraphic data obtained in the Vocontian Basin (southeastern

249 France) shows that the genus *Moutoniceras* disappeared with the tuberculate species *M.*
250 *eigenheeri* at the very end of the early Barremian, stratigraphically just below the First
251 Occurrence (FO) of the genus *Toxancyloceras* (beginning in the upper Barremian). In the
252 Barremian stratotype area of Angles the latter genus appears only one bed higher from the
253 former (Figs. 5, 6), so a real continuity exists from a stratigraphic point of view between these
254 two genera. On the other hand, the general morphology of the large tripartite ancyloceratic
255 shell is very close to *Moutoniceras* and *Toxancyloceras*. Actually, in the beds around the
256 boundary between the lower and upper Barremian of this area, there are no other large
257 ancyloceratic ammonites aside from these two genera. Under these conditions, the following
258 phylogenetic succession (from the oldest to the youngest) can be established: *M. eigenheeri* ->
259 *T. canuti* sp. nov. -> *T. vandenheckei*.

260
261 Paleontological and stratigraphic data, resulting from analytical systematics, enable us to
262 highlight ontogenetic and evolutionary patterns in this phyletic lineage. This succession is
263 completed for the lower Barremian by older *Moutoniceras* species. More data about the
264 development of the *Moutoniceras* species are required to make an accurate cladistic analysis,
265 which requires further research into the *Nicklesia pulchella*, *K. compressissima* and *M.*
266 *moutonianum* zones (lower Barremian). In any case, the species of the genus *Moutoniceras*
267 need a revision under intraspecific variability and evolutionary perspectives. In summary, the
268 evolution of *Moutoniceras* / *Toxancyloceras* goes through a decrease in adult size from the
269 upper *M. moutonianum* Zone (Fig. 8), and also by heterochronies in the duration of the
270 different ontogenetic stages (Fig. 9), and finally by modification of the tubercles, which
271 oscillate between appearance and disappearance (Fig. 9):

272 - The adult size seems relatively stable between *M. nodosum* (lower part of *K.*
273 *compressissima* Zone – H=1160 mm) and *M. moutonianum* (lower *M. moutonianum* Zone –

274 H=1280 mm), and also probably in *M. berti* (upper part of *K. compressissima* Zone).
275 However, in the upper part of the *M. moutonianum* Zone the adult size of *M. marii* is reduced
276 significantly (pseudo-dwarfism / progenetic process, in the sense of Dommergues et al.,
277 1986). Although no sufficiently complete specimen of this latter species is known to date, the
278 height of around 600-700 mm is assumed by data collected by one of us [DB]. The
279 tuberculation is present on the outer whorl of the coil (bituberculate pattern) and at the top of
280 the shaft in *M. nodosum* (peri-ventral tubercles reduced to the state of bulges on the rest of the
281 shaft). It then regresses gradually from *M. berti* to *M. marii*. In *M. berti*, the tuberculation is
282 represented by peri-ventral clavi individualized on the outer whorl of the coil (the only
283 currently known part of the shell in this species) and in very discrete lateral tubercles. In *M.*
284 *moutonianum*, there are only mere peri-ventral bulges at the turn of the outer coil and the
285 shaft. Finally, the tuberculation seems to disappear completely on the coil and the shaft in *M.*
286 *marii*.

287
288 - *M. eigenheeri* (top of the *M. moutonianum* Zone, in the new *M. eigenheeri* Horizon
289 in this work): the adult size of *M. eigenheeri* continues its reduction compared to *M. marii* (H
290 around 500-600 mm) with a large spiral part of about 200 mm in diameter. The tubercles,
291 which were missing in *M. marii*, reappear on the early whorls of the coil (bituberculation with
292 the fibula pattern) and the shaft (peri-ventral tubercles). The acquisition of the lateral
293 tubercles on the shaft is very discreet, but this is new for the genus *Moutoniceras* on this part
294 of the shell (lateral tubercles are known in *M. nodosum* but only on the outer coil). It is here
295 that the trituberculation known in the immediately more recent *Toxancyloceras* begins to
296 occur. This trituberculation appears however in a very fleeting manner at the very top of the
297 shaft (the peri-dorsal bulges are very discreet). There are four ontogenetic stages in *M.*
298 *eigenheeri*: (1) the inner part of the coil with differentiated ribs; (2) the outer part of the coil

299 with all identical ribs; (3) the shaft with ribs differentiated again; and (4) the hook with a
300 more irregular ornamentation.

301

302 - *T. canuti* sp. nov. (lower part of the *T. vandenheckei* Zone and Subzone, in the new
303 *T. canuti* Horizon, in this work): the adult size is a little further reduced ($360 < H < 550$ mm), as
304 the spiral part reduces (110-140 mm). This implies an increase of the shell curvature and an
305 increase in the whorl height growth. The main ribs of the coil and the shaft become
306 systematically trituberculate; however the tubercles never become strongly expressed. The
307 four ontogenetic stages are still present, although there are some changes from *M. eigenheeri*:
308 (1) the inner part of the coil has strong differentiated ribs and regular alternation between
309 main and intercalary ribs. The new pattern with looped ribs is likely an evolution of the
310 pattern with fibula ribs known in *M. eigenheeri*: the lower tubercle closes the fibula and forms
311 the loop; (2) the alternation of main / intercalary ribs of the outer part of the coil becomes
312 much less regular. As in *M. eigenheeri*, the intercalary ribs maintain their strengthened
313 appearance on the venter and on the peri-ventral margin, where they are sometimes even
314 slightly tuberculate; (3) the shaft has differentiated ribs, but the number of intercalary ribs
315 increases; and (4) the hook is almost identical.

316 - *T. vandenheckei* (lower part of the *T. vandenheckei* Zone and Subzone, in the new *T.*
317 *vandenheckei* Horizon, in this work): the adult size is reduced and seems to be stabilised (H
318 around 425 mm), as well as the spiral uncoiled part (95-160 mm). In terms of ornamentation,
319 the intermediate bituberculate ribs, which were ornamental remains of *Moutoniceras*,
320 disappear. At the same time the tubercles become stronger on the main ribs, while the peri-
321 ventral strengthening of the intercalary ribs becomes anecdotal. There are no more than three
322 ontogenetic successive stages during growth since the stage with differentiated ribs invaded
323 the entire coil.

324

325 To summarize, two imbricated evolutionary trends are highlighted in the *Moutoniceras* /
326 *Toxancyloceras* lineage. The first major trend concerns the ornamental changes, itself
327 determined by three imbricated patterns (Fig. 9):

328 - (1) An ornamental oscillation of the appearance (*M. nodosum*), regression (*M. berti*,
329 more in *M. moutonianum*), disappearance (*M. marii*), then reappearance (*M. eigenheeri*) and
330 finally increasing amplification (*T. canuti* sp. nov., more in *T. vandenheckei*) of the
331 tuberculate pattern over time. This oscillation is adjusted by: (1) the retardation of the
332 ornamentation (the progressive disappearance of the tuberculation by the extension of the
333 non-tuberculate young stage during ontogenesis – stage 1 in Fig. 9), which is a
334 pedomorphosic process; and (2) by the acceleration of the ornamentation (invasion of the
335 tuberculate pattern increasingly early through ontogenesis), which is a peramorphic process.

336 - (2) A differentiation of the ornamentation in main and intercalary ribs, increasingly
337 clear in *M. eigenheeri* and the subsequent species. The tuberculation becomes more present
338 and powerful on the main ribs over time, to become a true trituberculate pattern in
339 *Toxancyloceras* (by the acquisition of the lower tubercles and the generalisation of the median
340 tubercles on the main ribs).

341 - (3) A mitigation and disappearance of the marginal strengthening of the intermediate
342 ribs. This evolutionary trend (as for the previous pattern) likely corresponds to graduaptation.
343 This term was introduced by Chaline (1999) to designate the adaptations of a characteristic
344 that take place gradually under the pressure of natural selection. These iterative and reversible
345 changes (as this is the case here for the *Moutoniceras* / *Toxancyloceras* lineage) are
346 understood under the model of the punctuated equilibrium/disequilibrium (Chaline, 1984,
347 1987) in the sense of a continuous and flexible adaptation to environmental changes, possibly
348 causing minimal genome changes.

349
350 The second major evolutionary trend of this group regards the reduction in adult size
351 throughout the transition from *Moutoniceras* to *Toxancyloceras* (Fig. 8), which seems to be
352 expressed by a decrease in the duration of the different stages in a rather balanced way. This
353 could be interpreted in terms of heterochronies (accelerated progenesis = pseudo-dwarfism in
354 the sense of Dommergues et al., 1986). It is important to note that, as this is usually the case
355 for numerous heteromorph ammonites species (see Bert, 2014), the adult size is subject to
356 variation from one specimen to another (see the systematic part in the online additional
357 material), thus, the evolutionary trend recognised here concerns only the maximal possible
358 reached size.

359

360 **6. Discussion**

361 *Moutoniceras marii* and *M. eigenheeri* are both at the limit of the two phases recognised in
362 the evolution of the lineage formed by the *Moutoniceras* and the *Toxancyloceras* species.
363 Obviously, the *Toxancyloceras* morphology is already predefined in *Moutoniceras* where
364 there already exists a tendency to form tubercles. In addition, the peri-ventral bulges on
365 smooth ribs, which persist in earlier *Toxancyloceras*, are an inherited trait of the
366 *Moutoniceras*.

367 Thus, from a merely taxonomic point of view, the choice could have been made to separate
368 the small *Moutoniceras* species (*M. marii* and *M. eigenheeri*) from their giant ancestors. This
369 proposition would have been coherent in evolutionary terms, since the use of evolutionary
370 progenesis events are usually used to separate taxa at the genus-group level (Dommergues et
371 al., 1986). There were two taxonomic options: either (1) we group *M. marii* and *M. eigenheeri*
372 to the *Toxancyloceras* to match the generic cut-off with the drastic reduction in the size of *M.*
373 *marii*; (2) either we group *M. marii* and *M. eigenheeri* into a separate genus (the genus

374 *Ewaldiceras* proposed by Vermeulen in 2003 for the latter species) separate from
375 *Moutoniceras* and *Toxancyloceras*.

376 Unfortunately, neither of these solutions is really satisfactory. In the former, morphological
377 coherence would be lost since *M. eigenheeri* and *M. marii* have an ornamentation strongly
378 rooted in the *Moutoniceras* morphology (this is especially the case for *M. marii*). They do not
379 have the apomorphies known in the more recent *Toxancyloceras*, and especially the
380 trituberculate pattern, which is a diagnostic criterion for defining the genus (discriminative
381 character). The second solution has the disadvantage of pulverizing the group by introducing
382 a third artificial taxon to create the link which doesn't make much sense in terms of
383 palaeobiology and clearly poses a problem in overestimating biodiversity. These risks have
384 been evaluated and criticised by several authors from other ammonites groups (see a review in
385 Bert, 2014).

386 Ideally, it is better to foster generic cuts to major changes in the evolutionary rhythms. So the
387 choice was made in the present work to maintain *M. marii* and *M. eigenheeri* in the genus
388 *Moutoniceras*, with the interest of maintaining a certain nomenclatural stability, and also to
389 reserve this taxonomic hyphenation of the genus-group level for another major morphological
390 aspect in the evolution of the group: the appearance of the trituberculate pattern. All this
391 shows that even if taxa of the genus-group level are essential to separate formally
392 phylogenetic lineages, they are also very conventional. Thus, they should not be used to
393 measure biodiversity without some care to ensure they were introduced on a solid
394 phylogenetic basis, taking into account the variability of species and evolutionary data (Bert,
395 2014).

396

397 When interpreting (see above, chapter 5) the two major evolutionary patterns of the
398 *Moutoniceras* / *Toxancyloceras* lineage in terms of heterochronies, it is understood that two

399 evolutionary processes are underlying these patterns in the history of this group. The first is
400 paedomorphic and concerns the large sized *Moutoniceras*, in which it causes the progressive
401 reduction in tuberculation by retardation of the ontogeny with the disappearance of
402 ornamental stages (Fig. 9). However, during this process the morphology and the adult size
403 remain remarkably stable (Fig. 8). The second process is peramorphic and, determines the
404 second phase of the evolutionary history of the group (small *Moutoniceras* species and
405 transition to the genus *Toxancyloceras* – Fig. 9): an increasingly early appearance of the
406 ontogenetic stages (acceleration). Between these two phases, the start of the size reduction is
407 effective from *M. marii* and is quite sudden, usually corresponding to a progenesis
408 (interpreted here as pseudo-dwarfism in the sense of Dommergues et al., 1986). This change
409 in size also corresponds to the minimum expression of the tubercles, which reappear later
410 (oscillation) and are strengthened to give the *Toxancyloceras* morphology. It is tempting to
411 interpret this progenetic phenomenon as a result of environmental stress, e.g. due to
412 environmental changes. At the same time, the maximum regressive (named SbB3 in Arnaud,
413 2005) occurs, which corresponds to the top-early Barremian peak of $\delta^{18}\text{O}$ (Baudin et al.,
414 2009), corresponding with a “drastic” decrease in temperature.

415
416 It is very interesting to consider the ornamental oscillation, with the gradual disappearance
417 and then reappearance of the tuberculate pattern along the evolutionary trend of the group.
418 Ornamental oscillation implies that some evolutionary patterns are ultimately not completely
419 irreversible and that they are certainly subject to external variations (Guex, 2016). This is the
420 very idea of the graduaptation (see above chapter 5), which designates the adaptations of a
421 characteristic that take place gradually under the pressure of natural selection. If these
422 conditions are reversed, some evolutionary trends seem able to reverse also, even to oscillate,
423 but not without resulting in some internal upheavals requiring morphological adaptations.

424 And that's what seems to happen here with the progenetic event of *M. marii*, which causes the
425 reduction in size and the heterochrony inversion (peramorphosis *versus* paedomorphosis
426 previously).

427 Evidence appears to suggest that this oscillation occurs as a possible case of evolutionary
428 reversibility, which at first glance seems to contradict the Dollo law on the irreversibility of
429 evolution (Dollo, 1893; Gould, 1970). Although genetic (Marshall et al., 1994) and molecular
430 experimentations (Bridgham et al., 2009) seem to show the veracity of this law, exceptions
431 have already been reported in literature, often based on heterochrony (eg. Collin and Cipriani,
432 2003; Diogo and Woods, 2012; Kerney et al 2011; Whiting et al., 2003; see review in Wiens,
433 2011), to the extent that its relevance could be questioned (Collin and Miglietta, 2008). In any
434 case, and as Gould stated (1970), Dollo Law strictly concerns the impossibility for the
435 organisms (or a sufficiently complex biological structure) to return to their ancestral state
436 using the same complete but reversed path (to a question of probabilities based on
437 complexity). However, Dollo Law doesn't objectively exclude the possibility of certain
438 characteristics returning to an ancestral state, regardless of the function they occupied before.
439 Without being a real violation of Dollo Law in the strict sense (Gould, 1970), the example of
440 *Moutoniceras* / *Toxancyloceras* shows that there may be a form of repeatability in the
441 evolutionary patterns in ammonites. It is here favored by heterochrony (due to the progenesis
442 impact), as it was demonstrated with the re-evolution of coiling in some gastropods of the
443 family Calyptraeidae (Collin and Cipriani, 2003). Besides the developmental process
444 highlighted by heterochrony, it is also tempting to think that some of these iterative
445 phenomena may cause minimal modifications of the genome and may occur through
446 epigenetic processes, whose influence seems to be confirmed as might suggest some recent
447 studies (Goudarzi et al., 2016).

448

449 **Remarks about the dimorphism in the *Moutoniceras* / *Toxancyloceras* lineage:** in the
450 literature data, the dimorphism has never been demonstrated for the genera *Moutoniceras* and
451 *Toxancyloceras* (Delanoy et al., 1995). The specimens studied in the present work do not
452 document it either, even if size variation is observed between some specimens. There is no
453 evidence that this size variation could be due to dimorphism, especially because the extreme
454 variants seem to be linked by intermediates. This size variation very likely corresponds to the
455 intraspecific “normal” variation, as it is known for other genera of heteromorph ammonites
456 (see for example Delanoy, 1997 for the genus *Heteroceras* d’Orbigny, 1849). Of course, this
457 non-documentation does not mean that the dimorphism is absent from these genera, but that
458 further research is needed to highlight it.

459

460 **7. Biostratigraphic implications**

461 Some biostratigraphic implications can be drawn from the understanding of the relationship
462 between the genera *Toxancyloceras* and *Moutoniceras* at the turn of the early and late
463 Barremian in the northwestern Tethyan margin. On the one hand, the revision of the classic
464 species *T. vandenheckei* reinforces its status as index for the *T. vandenheckei* zone and
465 subzone (lower upper Barremian). On the other hand, the review of *M. eigenheeri* and the
466 discovery of *T. canuti* sp. nov., which was confused in the past with *T. vandenheckei* for
467 various reasons (see above, chapter 4), allow us to propose three new biostratigraphic
468 horizons for the Vocontian Basin (Fig. 3): the *M. eigenheeri* Horizon at the top of the lower
469 Barremian (*M. moutonianum* Zone), and the *T. canuti* and *T. vandenheckei* horizons at the
470 lower upper Barremian (*T. vandenheckei* Zone and Subzone). The stratigraphic distribution of
471 all the index species proposed in the present work (Fig. 3) is very restricted and now precisely
472 known. The importance of their being part of an evolutionary context is now well established

473 (this work, Figs. 8 and 9). The relative frequency of these species, in respect to the other
474 contemporary ammonite faunas, makes them serious and legitimate candidates to the status of
475 index species. Finally, the presence of representatives of the *Moutoniceras* and
476 *Toxancyloceras* genera over a large geographical area, coupled with the discovery of *T. canuti*
477 sp. nov. from Spain (Mallorca) to Tyrol (= *T. vandenheckei*, fig. 8a-b in Lukeneder, 2012) and
478 Hungary (Fözy and Janssen, 2009, fig. 5b, 5f-g), suggests a high potential of correlation for
479 these horizons on the whole northwestern Tethyan margin.

480

481 ***Moutoniceras eigenheeri* Horizon (new)**

482 *Index species: Moutoniceras eigenheeri* (Vermeulen, 2003), which is revised in the present
483 work. This species is currently known in the Vocontian Basin only, but as it is the mother-
484 species of *T. canuti* sp. nov., it could potentially extend to the same area.

485 *Reference section:* the section G5 of the Angles area (southeastern France, Vocontian Basin)
486 is chosen as the reference section of the *M. eigenheeri* Horizon. The index species is present
487 in the beds 78, 80 and 82, which are equivalent to the stratotype beds 141, 143-1a and 143-1c
488 respectively (sections A, A' and A*, see Figs 5 and 6 and Bert, 2012).

489 *Status:* this horizon is defined by the First Occurrence (FO) of its index-species. In fact, the
490 latter is present in the uppermost thick bed of the lower Barremian in the stratotype area, and
491 the horizon corresponds to the total distribution of the index species. In 2009, Reboulet et al.
492 restored the division of the *M. moutonianum* Zone into two horizons: a *Coronites darsi*
493 Horizon at the base, and a *Heinzia caicedi* Horizon at the top. The latter horizon encompasses
494 the upper half of the *M. moutonianum* Zone; however, *Heinzia caicedi* (Karsten, 1856) is
495 virtually absent from the basin, where the horizon is rendered of difficult use. The latter
496 species is almost exclusively present in the platform borders where the levels are often quite
497 condensed. Compared to the reference zonal scheme (Reboulet et al., 2014), the *M. eigenheeri*

498 Horizon is more recent than the *H. caicedi* Horizon, as the disappearance of *M. eigenheeri*
499 coincides with the end of the lower Barremian. It immediately precedes the appearance of *T.*
500 *canuti* sp. nov., which serves as index species of the overlying horizon: the first one of the
501 upper Barremian.

502 *Faunal assemblage*: the ammonites are relatively scarce at the top of the lower Barremian. In
503 spite of that, *M. eigenheeri* is relatively abundant (often in fragments) with respect to other
504 ammonite faunas of the *M. eigenheeri* Horizon, where it is the most significant and easy-to-
505 use ammonite for non-specialists. The index species is associated with numerous
506 Barremitidae; the holcodiscids are well represented with *Holcodiscus uhligi* (Karakasch,
507 1907) and *Parasaynoceras* sp.; *Kotetishvilia sauvageaui* (Hermitte, 1890) and *Silesites vulpes*
508 (Matheron, 1880) are also present.

509

510 ***Toxancyloceras canuti* Horizon (new)**

511 *Index species*: *Toxancyloceras canuti* sp. nov., which is introduced and described in an
512 evolutionary context in the present work. It is known currently in southeastern France, in
513 South Tyrol, in Hungary and in Spain (Mallorca), where the new horizon could be used.

514 *Reference section*: the field section A* is chosen as reference for the *T. canuti* Horizon. The
515 index species is present in beds No. 144 and 145. It may be present in the small beds No. 143-
516 2 and 143-3 (where the change in lithology known at the lower/upper Barremian boundary
517 occurs), but so far these beds have delivered no fossils. The *T. canuti* Horizon corresponds to
518 the beds No. 84 and 85 of the neighbouring section G5 (see Figs 5 and 6).

519 *Status*: this horizon is defined by the FO of its index species immediately above the last thick
520 beds of the lower Barremian in the stratotype area (Angles, southeastern France), and the
521 horizon corresponds to the total distribution of the index species. The choice to place the *T.*
522 *canuti* Horizon into the upper Barremian instead of the lower Barremian does not modify the

523 lower limit of the *T. vandenheckei* Zone. The first reason is that *T. canuti* sp. nov. has often
524 been confused with *T. vandenheckei* (see synonymy, chapter 4), and therefore the *T.*
525 *vandenheckei* Zone was already starting *de facto* with the appearance of *T. canuti* sp. nov. The
526 second reason is that the ammonite fauna of the *T. canuti* Horizon is closer to that of the
527 upper of *Heinzia sayni* Hyatt, 1903, which was used as index of the first zone of the upper
528 Barremian in the past (Vermeulen, 1997). The acceptance of the *T. canuti* Horizon as the
529 lowest horizon of the upper Barremian at the basis of the *T. vandenheckei* Zone requires only
530 very slight modification of its definition. It no longer starts with its index species, but with the
531 emergence of the *Toxancyloceras* genus (in the evolutionary context *Moutoniceras* ->
532 *Toxancyloceras*), which ultimately facilitates its recognition by non-ammonite specialists.
533 *Faunal assemblage:* the *T. canuti* Horizon undoubtedly marks the appearance of the
534 *Toxancyloceras*. *T. canuti* sp. nov., which is relatively abundant, appears simultaneously with
535 rare specimens of *Heinzia sayni*. Note the extreme scarcity of the Holcodisciidae (scarce
536 *Holcodiscus uhligi* and *Parasaynoceras* sp.), and the total disappearance of the *Moutoniceras*.
537 Present in this horizon are also: *Macroscaphites rakusi* (Uhlig, 1883) ([m&M]), *Kotetishvilia*
538 *sauvageaui*, *Silesites vulpes* and numerous Barremitidae.

539

540 ***Toxancyloceras vandenheckei* Horizon (new)**

541 *Index species:* *Toxancyloceras vandenheckei* (Astier, 1851), which is revised in the present
542 work. This species is currently known in southeastern France, Spain (incl. Mallorca),
543 Slovakia, Italy, and maybe in South Tyrol and Japan.

544 *Reference section:* the field section A* is chosen as the reference for the *T. vandenheckei*
545 Horizon. The index species appears there from bed No. 146. This level corresponds to bed
546 No. 86 of the neighbouring section G5 (see Figs 5 and 6).

547 *Status:* this horizon is defined by the FO of its index species, and the horizon corresponds to
548 the total distribution of its index species as understood in the present work. *T. vandenheckei*,
549 now revised, is strengthened as index species for the *T. vandenheckei* Zone and Subzone. On
550 the other hand, while it is now recognised that *T. vandenheckei* does not appear at the base of
551 its zone, it is not necessary to rename it the “*T. canuti* Zone”. Indeed, the lower limit of an
552 interval zone, of which the use has been recommended by the IUGS Lower Cretaceous
553 Ammonite Working Group (Reboulet et al., 2011, p. 790), is defined by a horizon (Thierry,
554 1997). In this case, it is not mandatory that a horizon starts with its index taxon (unlike a
555 distribution zone, for example).

556 *Faunal assemblage:* *T. vandenheckei* is common in the horizon of which the ammonite fauna
557 is very similar to the *T. canuti* Horizon. *Heinzia sayni* specimens however, become more
558 frequent, while Holcodisciidae become scarcer. As in the previous horizon, *Macroscaphites*
559 *rakusi* ([m&M]), *Kotetishvilia sauvageoui*, *Silesites vulpes* and numerous Barremitidae are
560 present.

561

562 **8. Conclusions**

563 The new data from several stratigraphic sections near the Barremian stratotype (the Angles
564 area in southeastern France) and from the Lloseta and Biniamar area (Mallorca, Balearic
565 Islands, Spain), allow us to demonstrate that the upper Barremian ammonite genus
566 *Toxancyloceras* originates in the lower Barremian *Moutoniceras*. The genus *Moutoniceras*
567 disappeared with the tuberculate species *M. eigenheeri* at the very top of the lower Barremian,
568 just below the FO of *T. canuti* sp. nov., which is the oldest species of the genus
569 *Toxancyloceras* at the base of the upper Barremian. Thus, *Moutoniceras* is now the oldest
570 currently known representative of the ammonite family Ancyloceratidae, and this genus

571 cannot be considered as a Heteroceratidae. Of course, this classification does not exclude the
572 hypothesis that the Heteroceratidae themselves probably derive from the Ancyloceratidae.

573 This new data sheds new light on the comprehension of the *Moutoniceras* and
574 *Toxancyloceras*. Especially, the revision of the species *M. eigenheeri* and *T. vandenhecki*, and
575 a new species (*T. canuti* sp. nov.) is described. *T. vandenhecki* is considered in the historical
576 context of the acquisition of the Astier collection by the Natural History Museum of London,
577 and its holotype is figured here for the first time other than by a drawing. The examination of
578 this latter specimen, which is not totally identical with the original drawing of 1851, partly
579 explains some misinterpretations of the species. Seven successive species of *Moutoniceras*
580 and *Toxancyloceras* are considered and their phylogeny is established as follow: *M. nodosum*
581 -> *M. berti* -> *M. moutonianum* -> *M. marii* -> *M. eigenheeri* -> *T. canuti* sp. nov. -> *T.*
582 *vandenhecki*. However, more data about the development of the *Moutoniceras* species is
583 required to make an accurate cladistic analysis, which requires further research into the
584 *Nicklesia pulchella*, *K. compressissima* and *M. moutonianum* zones (lower Barremian). In any
585 case, the species of the genus *Moutoniceras* need revision with consideration into the
586 perspectives of intraspecific variability and evolutionary.

587

588 Biostratigraphically, the status of *T. vandenhecki* as zonal and subzonal index at the base of
589 the upper Barremian is reinforced, and three new ammonite horizons are defined: the
590 *Moutoniceras eigenheeri*, *Toxancyloceras canuti* and *T. vandenhecki* horizons. The
591 stratigraphic distribution of all their index species is very restricted, forming part of a well
592 established evolutionary context.

593

594 There are two phases in the evolutionary history of the *Moutoniceras* / *Toxancyloceras*
595 lineage, underlined by two processes. The first is pedomorphosis and it concerns the large

596 *Moutoniceras* species with the progressive disappearance of the tubercle pattern over time
597 through a retardation of the ontogeny and the disappearance of ornamental stages (Figs. 8, 9).
598 The second process is peramorphosis with the acceleration of the ornamentation in the small
599 *Moutoniceras* species and the *Toxancyloceras* (Figs. 8, 9). Between these two phases occurs a
600 progenesis with the quite sudden reduction in adult size effective from *M. marii*. This size
601 reduction is interpreted here as pseudo-dwarfism (in the sense of Dommergues et al., 1986)
602 where the duration of the different ontogenic stages decreases. This change in size also
603 corresponds to the pattern of minimum expression of the tubercles, which reappear later
604 (oscillation). This progenesis is concomitant with some environmental changes (maximum
605 regressive of the late Barremian, and “drastic” decrease in temperatures) and it would be
606 tempting to correlate the two phenomenon.

607 The oscillation of the tuberculate pattern is adjusted by: (1) a process of paedomorphosis
608 (retardation of the ornamentation with extension of the non-tuberculate young stage during
609 growth that implies the progressive disappearance of the tuberculation); and (2) by a
610 peramorphic process (acceleration of the tuberculate pattern, which appears increasingly early
611 through ontogenesis). Finally, two other ornamental patterns are related to graduaptation
612 processes. The first is the differentiation in main and intercalary ribs, with the increase of the
613 tuberculation to a true trituberculate pattern (in *Toxancyloceras*). The second is the mitigation
614 and disappearance of the marginal strengthening of the intermediate ribs.

615 The ornamental oscillation of the tuberculate pattern could act a possible case of evolutionary
616 reversibility. Actually, the Dollo law is not violated as this latter does not objectively exclude
617 the possibility for certain characteristics to return to an ancestral state, regardless of the
618 function they occupied before. Here, the example of *Moutoniceras* / *Toxancyloceras* shows
619 that there exist a form of repeatability in the ammonites evolution favoured by the
620 heterochronies.

621

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636

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907

908

909 **CAPTION OF THE FIGURES:**

910

911 **Fig. 1.** Strict consensus tree computed with statistics (Bootstrap values and BREMER
912 support) (Consistency Index CI = 0.643; Retention Index RI = 0.712; Adjusted homoplasy Aj
913 = 3.45) by Bert and Bersac, 2014, to test some hypothesis about the origin of the
914 Hemihoplitidae. *Toxancyloceras vandenheckei* and *Moutoniceras moutonianum* appear to be
915 sister-taxa, without any link with the Hemihoplitidae (the clade *Fissicostaticeras* /
916 *Gassendiceras*). The table of characters is given in Bert and Bersac (2014, appendix).

917

918 **Fig. 2.** Palaeogeographic map of the Western Tethyan Realm at the Barremian, modified after
919 Bert and Bersac, 2014 (reconstructed from Barron et al., 1981, and Dercourt et al., 2000),
920 with the position of the Vocontian Basin (southeastern France), and the Balearic Islands
921 (Spain).

922
923 **Fig. 3.** Barremian biostratigraphy of the stratotype area (southeastern France), according to
924 Reboulet et al. (2014) completed by the data of Bert et al. (2008, 2009, 2010, 2011). The three
925 new horizons are in red (*Moutoniceras eigenheeri*, *Toxancyloceras canuti* and *T.*
926 *vandenheckei*). Note that the *Hemihoplites astarte* Horizon replaces the *H. casanovai* Horizon
927 of Bert et al., 2008, because of the objective synonymy of *H. casanovai* Delanoy, 1992 with
928 *H. astarte* (Fallot and Termier, 1923) (new unpublished data – forthcoming work).

929
930 **Fig. 4.** Palaeogeographic map of the Vocontian Basin (southeastern France – modified after
931 Arnaud, 2005). The red star points out the Barremian stratotype area near Angles.

932
933 **Fig. 5.** Outcrop section A* near Angles (stratotype of the Barremian stage, southeastern
934 France). ME: *Moutoniceras eigenheeri* Horizon; TC: *Toxancyloceras canuti* Horizon; TV: *T.*
935 *vandenheckei* Horizon; GA: *Gassendiceras alpinum* Horizon.

936
937 **Fig. 6.** Outcrop section G5 in the Angles area (southeastern France). ME: *Moutoniceras*
938 *eigenheeri* Horizon; TC: *Toxancyloceras canuti* Horizon; TV: *T. vandenheckei* Horizon; GA:
939 *Gassendiceras alpinum* Horizon.

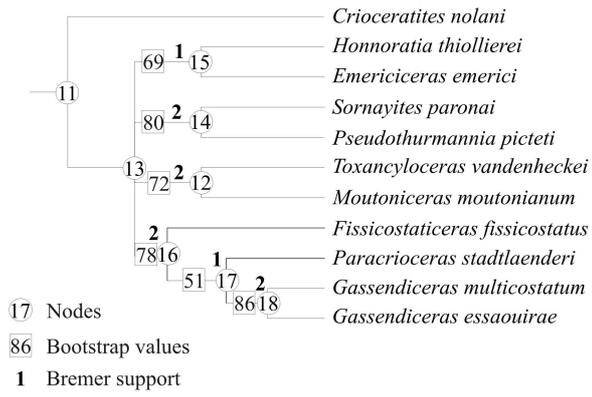
940
941 **Fig. 7.** Simplified geological map of Mallorca (Balearic Islands, Spain). The red star points
942 out the outcrops studied in the Sierra Tramuntana.

943

944 **Fig. 8.** Size and reconstructed morphology of the successive species of the lineage
945 *Moutoniceras* / *Toxancyloceras*. The ammonites are at the scale. From left to right (the oldest
946 to the youngest) are: **a**, *Moutoniceras nodosum*; **b**, *M. berti*; **c**, *M. moutonianum*; **d**, *M. marii*;
947 **e**, *M. eigenheeri*; **f**, *Toxancyloceras canuti* sp. nov. and **g**, *T. vandenheckei*. The numbers
948 correspond to the ontogenetic stages explained in Figure 9. Original drawings by José Juárez-
949 Ruiz.

950

951 **Fig. 9.** Ontogeny and heterochronies within the *Moutoniceras* / *Toxancyloceras* lineage. The
952 ornamental stages are: **1**, Tubercle less ribs, which are ventrally reinforced; **2**, Fibulate /
953 looped rib pattern (tuberculate); **3**, Coil with differentiated ribs (regular alternation of
954 trituberculate / smooth ribs); **4**, Bituberculate pattern (coil); **5**, Tubercle-less ribs; **6**,
955 Bituberculate pattern (shaft); **7**, Irregular trituberculate pattern (shaft); **8**, Bend and hook (this
956 stage is considered here as an ‘adult variation’ without any evolutionary implications – see
957 Delsol, 1977). See text, chapter 5, for explanations.



ACCEPTED MANUSCRIPT



ACCEPTED

Standard Tethyan ammonite zonation of Reboulet et al. (2014) with the biostratigraphic proposals of Bert et al. (2008, 2009, 2010, 2011)				Distribution of the <i>Moutoniceras</i> / <i>Toxancyloceras</i>							
Stages	Zones	Subzones	Horizons	<i>M. nodosum</i>	<i>M. berti</i>	<i>M. moutonianum</i>	<i>M. marii</i>	<i>M. eigenheeri</i>	<i>T. canuti</i> sp. nov.	<i>T. vandenheckei</i>	
BARREMIAN	upper	<i>Imerites giraudi</i>	<i>Pseudocrioceras wagenioides</i>								
			<i>Martelites sarasini</i>	<i>Leptoceratoides puzosianum</i>							
				<i>Heteroceras emerici</i>							
			<i>I. giraudi</i>	<i>I. giraudi</i>							
				<i>I. dichotomus</i>							
		<i>Pseudoshasticioceras autrani</i>									
		<i>Gerhardtia sartousiana</i>	<i>Hemihoplites ferudianus</i>	<i>P. magnini</i>							
				<i>P. bersaci</i>							
				<i>H. ferudianus</i>							
			<i>G. provincialis</i>	<i>H. astarte</i>							
				<i>G. provincialis climax</i>							
			<i>G. provincialis</i>								
			<i>Camereiceras limentinus</i>	<i>G. sartousiana</i>							
		<i>C. limentinus</i>									
		<i>Toxancyloceras vandenheckei</i>	<i>Gassendiceras alpinum</i>	<i>C. marchandi</i>							
	<i>C. breistrofferi</i>										
	<i>G. alpinum</i>										
	<i>T. vandenheckei</i>		<i>T. vandenheckei</i>								
			<i>T. canuti</i>								
	lower	<i>Moutoniceras moutonianum</i>	<i>M. eigenheeri</i>								
			<i>Heinzia caicedi</i>								
			<i>Coronites darsi</i>								
		<i>Kotetishvilia compressissima</i>	<i>Subtorcapella defayae</i>								
			<i>H. communis</i>								
			<i>Nicklesia didayana</i>								
		<i>Nicklesia pulchella</i>	<i>Holcodiscus fallax</i>								
			<i>Kotetishvilia nicklesi</i>								
<i>Taveraidiscus hugii auctorum</i>		<i>Psilotissotia colombiana</i>									
		<i>T. hugii auctorum</i>									

