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**The ammonites of the Les Ferres Aptian Basin (Lower Cretaceous,
Southeast of France): the genus *Toxoceratoides* (Ancyloceratina,
Helicancyllidae)**

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Abstract:

Toxoceratoides (Ancyloceratina, Helicancyllidae) is a lower Aptian (Lower Cretaceous) small heteromorph ammonoid mainly known by small samples of fragmentary specimens. In the present work, we study a sample of 145 specimens of this genus from the *Deshayesites forbesi*, *Deshayesites deshayesi* and *Dufrenoyia furcata* zones (lower Aptian) of the vicinity of the village of Les Ferres (southeastern France). The taxa recognized (in stratigraphic order) are: *Toxoceratoides* sp., *Toxoceratoides royerianus* (d'Orbigny, 1842) and *Toxoceratoides rochi* Casey, 1961. Their ontogenetic sequence is described; the intraspecific variability of *Toxoceratoides rochi* is considerable and it concerns adult size, coiling, duration of the ontogenetic stages and ornamentation. No sexual dimorphism is recognized. The main evolutionary pattern of the genus consists in the replacement of primitive ribs (here named 'royerianus ribs') by derived ribs ('rochi ribs') on the flexus and retroversum. The genus *Toxoceratoides* could be used as a biostratigraphic tool.

Key words: heteromorph ammonite; evolution; ontogeny; intraspecific variability; heterochronic variation.

1. Introduction

37

38 The Les Ferres Aptian Basin (LFAB) is a small subsident basin nowadays
39 located in the vicinity of the village of Les Ferres, in the Estéron valley (Alpes-
40 Maritimes department, southeastern France, Bersac and Bert, 2019, Fig. 1). The
41 location of the outcrops studied and the lower Aptian litho- and biostratigraphy
42 of the LFAB have been previously described in Bersac and Bert (2019). The
43 LFAB is characterized by relatively thick lower Aptian deposits particularly rich
44 in macrofossils, especially ammonites (fossil cephalopods, Bersac and Bert,
45 2019). The age of these series extends from the *Deshayesites forbesi* Zone (in
46 the sense of Bersac et al., 2012) to the late *Dufrenoyia furcata* Zone (*Dufrenoyia*
47 *dufrenoyi* Subzone, Fig. 2). Its ammonite fauna is remarkable by the significant
48 proportion of heteromorphs of the families Ancyloceratidae Meek, 1876 and
49 Helicancylidae Hyatt, 1894 (=Acrioceratidae Vermeulen, 2004). In the LFAB,
50 the lower Aptian Helicancylidae are only represented by the genus
51 *Toxoceratoides* Spath, 1924 (Bersac and Bert, 2019), which is a small tripartite
52 shelled heteromorph genus (the shell of *Toxoceratoides* is composed of a
53 proversum, a flexus and a retroversum, Casey, 1961a; Aguirre-Urreta, 1986;
54 Avram, 2002; Bulot et al., 2018, Fig. 3). The aim of the present work is to
55 describe and figure the *Toxoceratoides* of the LFAB, based on a sample of 145
56 specimens from the *D. forbesi*-*D. furcata* zones interval.

57

58 2. Material and method

59

60 2.1. Material

61

62 The litho- and biostratigraphic framework based on ammonites of the LFAB and
63 the sections from which the studied material originates are detailed in Bersac
64 and Bert (2019).

65 The material studied is composed of 145 specimens of *Toxoceratoides* from 6
66 sections of the LFAB. The specimens originate from: (1) the top of the
67 Hauterivian-Aptian limestones (*Deshayesites forbesi* Zone, 1 specimen), (2) the
68 *Ammonitoceras* Level of the Pont de la Cerise Member (*Deshayesites*
69 *multicostatus* Subzone of the *Deshayesites deshayesi* Zone, 1 specimen) and (3)
70 from the Les Graous Member (*Deshayesites grandis* Subzone of the *D.*
71 *deshayesi* Zone and *D. furcata* Zone, 143 specimens). They are represented by
72 marly-calcareous internal moulds, mostly deformed and fragmentary. The
73 studied material is curated by the Réserve naturelle nationale géologique de
74 Haute-Provence (RNNGHP, Digne-les-bains, France). The list of the studied
75 specimens is given in Supplementary Appendix.

76

77 2.2. Method

78

79 The terminology used for describing the studied specimens and the criteria for
80 determining them are based on the works of Frau et al. (2017) and Bulot et al.
81 (2018). The variable H is the whorl height at the middle of the flexus (Fig. 3).

82 The ontogenetic sequence of the genus *Toxoceratoides* shows 3 successive
83 stages (Fig. 3):

84 - Stage *i* (Bulot et al., 2018, p. 189) is adorned with uniform, simple and
85 atuberculate ribs or ribs bearing a single ventrolateral tubercle.

86 - Stage *ii* presents an '*alternation of (...) primary ribs and atuberculate*
87 *intercalatories*' (Bulot et al., 2018, p. 189). The main ribs are tuberculate and
88 attenuated on the siphonal area. They are usually separated by one or more
89 atuberculate intercalary ribs but can be more rarely contiguous. The intercalary
90 ribs are generally not attenuated on the siphonal area. Stage *ii* can be subdivided
91 in an early part named here 'stage *iia*' with bituberculate main ribs (lateral and
92 lateroventral tubercles, see Bulot et al., 2018, fig. 2R) and a late part named here
93 'stage *iib*' with trituberculate main ribs (laterodorsal, lateral and lateroventral
94 tubercles).

95 - Stage *iii* (Bulot et al., 2018, p. 189) is represented by various types of ribs: (1)
96 simple and atuberculate ribs named here ‘rochi ribs’ because they predominate
97 in the species *Toxoceratoides rochi* Casey, 1961 (Frau et al., 2017; Bulot et al.,
98 2018); (2) bifid ribs with a laterodorsal tubercle named here ‘royerianus ribs’
99 because they predominate in the species *Toxoceratoides royerianus* (d’Orbigny,
100 1842) (Bulot et al., 2018); and (3) ribs with intermediate pattern (single with a
101 laterodorsal tubercle or atuberculate and bifid).

102 According to Bulot et al. (2018), the species *Toxoceratoides royerianus* evolves
103 toward the species *Toxoceratoides rochi* by the replacement of ontogenetic stage
104 *iii*’s royerianus ribs by rochi ribs and by the change in shape of stage *ii*’s
105 lateroventral tubercles. Thus, we consider the proportion of rochi ribs relative to
106 the total number of ribs of stage *iii* as a diagnostic character. We calculated such
107 proportion for the samples of each lithostratigraphic unit of the LFAB when
108 possible. We studied the distributions of H and of the proportion of rochi ribs
109 through frequency histograms and a Shapiro-Wilk normality test (Hammer and
110 Harper, 2006) for the only significantly larger subzonal sample (over 30
111 specimens), namely the sample from the *D. furcata* Subzone. They were
112 performed using the software PAST version 2.17c (Hammer et al., 2001,
113 <http://folk.uio.no/ohammer/past/>).

Our taxonomic approach is based on a ‘palaeobiologic’ concept of the species rather than a typologic concept (see discussions about these concepts in Bert, 2013; De Baets et al., 2015).

The database of the studied specimens is available in Supplementary Appendix.

3. Results

3.1. Descriptive paleontology

Order Ammonoidea Zittel, 1884

Suborder Ancyloceratina Wiedmann, 1966

Superfamily Ancyloceratoidea Gill, 1871

Family Helicancylidae Hyatt, 1894

Taxonomic considerations about the family-group name Helicancylidae. The opinions of recent authors differ on the suprageneric classification of *Toxoceratoides*: it could belong to the family Helicancylidae (Bert, 2009), to the family Acrioceratidae (Vermeulen, 2004; Bulot in Vincent et al., 2010; Frau et

al., 2017) or to the subfamily Helicancylinae of the family Ancyloceratidae (see Casey, 1961a; Aguirre-Urreta, 1986; Kakabadze and Hoedemaeker, 2004; Kakabadze in Klein et al., 2007, footnote p. 94). Here, we consider that the genus *Toxoceratoides* belongs to a family distinct from the Ancyloceratidae on the basis of the phylogenetic arguments developed by Bert (2009), and we use the family-group name Helicancyllidae for the following reasons:

- (1) following Bert (2009) and Bulot (in Vincent et al., 2010), we consider that the family-groups Helicancyllidae and Acrioceratidae share the same taxonomic content and that both the two names designate the same family;

- (2) the family-group names Helicancyllidae and Acrioceratidae meet all the requirements of availability outlined in Articles 11 and 12 of the International Code of Zoological Nomenclature (ICZN). Both are thus available in the sense of the ICZN (see also Article 10.6);

- (3) according to the Principle of Priority (ICZN, Article 23), the name Helicancyllidae, Hyatt, 1894 has seniority on the name Acrioceratidae, Vermeulen, 2004.

Toxoceratoides sp.

Fig. 4A

151

152 2019 *Toxoceratoides* sp. - Bersac and Bert, p. 155, fig. 12.

153

154 *Material* (see *Supplementary Appendix*). 1 specimen from the top of the
155 Hauterivian-Aptian limestones (Bed 400 of CLE section, *Deshayesites forbesi*
156 Zone).

157

158 *Description*. The specimen is a fragment of flexus and retroversum with $H = 9$
159 mm. Only one side of the specimen is preserved and its width cannot thus be
160 measured. Its ventral area is not preserved. The ornamentation is only composed
161 of royerianus ribs (slightly rursiradiate, thin, relatively dense and arising in pairs
162 from a laterodorsal tubercle). Apart the laterodorsal tubercle, these ribs do not
163 bear additional tubercle. The septal suture is not observable. The proportion of
164 rochi ribs is 0% (Table 1).

165

166 *Discussion*. This specimen is quoted in Bersac and Bert (2019, p. 157, fig. 12). It
167 originates from a bed (Bed 400 of CLE section) assigned to the lower part of the
168 *D. forbesi* Zone. Its ornamentation corresponds to the ontogenetic stage *iii*. The
169 specimen shows primitive characteristics with a proportion of rochi ribs of 0%

(ornamentation of its stage *iii* only represented by royerianus ribs). This specimen may correspond to a primitive form of *Toxoceratoides*, just like those figured by Avram (2002, pl. 1, figs. 9a, b, 12a-c, pl. 2, figs. 9, 12) and Delanoy et al. (2008, pl. 11, fig. 4a, b). Our specimen differs from the lower Aptian small heteromorph genus *Volgoceratoides* Mikhailova and Baraboshkin, 2002 (Mikhailova and Baraboshkin, 2002, p. 544) by its less distant ribs and its lower position of the rib furcation point on the flexus and proversum. The imprecise biostratigraphic position and the very fragmentary state of preservation of the studied specimen prevent us to identify it at species level.

Biostratigraphic distribution. *Deshayesites forbesi* Zone of the LFAB.

Toxoceratoides royerianus (d'Orbigny, 1842)

Fig. 4B-G

2019 *Toxoceratoides* aff. *royerianus* - Bersac and Bert, p. 155, 163, 164, figs. 5, 7, 10, 12, pl. 3, figs. 13-16.

For an extensive synonymy of this species, see Bulot et al. (2018).

188

189 *Material* (see *Supplementary Appendix*). 1 specimen from Bed 405 of VAL
190 section (*D. multicosatus* Subzone, *D. deshayesi* Zone) and 10 specimens from
191 the *Toxoceratoides* Bed (*D. grandis* Subzone, *D. deshayesi* Zone) of GRS1,
192 CLE and CHP sections. These 11 specimens were identified as *Toxoceratoides*
193 aff. *royerianus* in Bersac and Bert (2019).

194

195 *Description of the material of the D. multicosatus Subzone (D. deshayesi Zone).*
196 The specimen No. SBC.06061-00003/VAL066 (Fig. 4B) is the only
197 Helicancyliidae we collected in the *D. multicosatus* Subzone (*D. deshayesi*
198 Zone) of the LFAB. It was identified as *Toxoceratoides* aff. *royerianus* in
199 Bersac and Bert (2019, fig. 7). This specimen is a fragment of flexus and
200 retroversum with H=13.9 mm. Only one side of the specimen is preserved. The
201 ornamentation of the flexus is represented by thick and straight main ribs
202 bearing lateroventral and smaller lateral tubercles. The shape of the lateroventral
203 tubercles is conical, slightly sagittally compressed. It is not possible to
204 determine if these ribs bear or not a laterodorsal tubercle since the
205 ornamentation is poorly preserved on the dorsal margin of the flexus. These
206 main ribs are separated by one straight, thin and atuberculate intercalary rib.
207 This ornamentation corresponds to the stage *ii*. On the retroversum, stage *ii* is

replaced by stage *iii*. Its ribs are simple and atuberculate (rochi ribs) or arise in pairs from a laterodorsal tubercle (royerianus ribs). The peristome is not preserved and the septal suture is not observable. The proportion of rochi ribs is 42.85% for this specimen (Table 1).

Description of the material of the D. grandis Subzone (D. deshayesi Zone). The 10 specimens of the *D. grandis* Subzone (*D. deshayesi* Zone) are all fragments but it is nevertheless possible to follow their ontogeny from a specimen to another. H has been measured only on 5 specimens; it varies from 7.2 mm to 11.7 mm with a mean value of 10.04 mm (Table 1).

The ornamentation is visible from a whorl height of 1 mm and corresponds to the stage *iia* (Fig. 4F). It is represented by simple, uniform, straight and rectiradiate ribs attenuated on the siphonal area. These ribs bear a lateroventral and a smaller lateral tubercle.

From a whorl height of 2.7 mm (Fig. 4F), ornamentation changes and corresponds to stage *iib*: the ribs become slightly prorsiradiate and the siphonal area becomes smooth to subsmooth. The main ribs bear a laterodorsal, a lateral and a larger lateroventral tubercle. This latter can be conical or claviform. Two main ribs are separated from each other by a single thin and atuberculate intercalary rib (Figs 4F, G).

At the beginning of the flexus, stage *iib* is abruptly replaced by stage *iii* (Bersac and Bert, 2019, pl. 3, figs. 13, 14). Its ornamentation is represented by slightly rursiradiate ribs that can be of royerianus, rochi or intermediate type. Most of the specimens exhibit a mixture of each type of ribs (Fig. 4C1-D2, Bersac and Bert, 2019, pl. 3, figs. 15, 16). One specimen (SBC.06061-00006/CHP038, Fig. 4E1, E2) exhibits some ribs bearing a discrete lateroventral tubercle. The royerianus ribs seem to predominate on the flexus and the beginning of the retroversum whereas the rochi ribs seem to be more frequent on the distal part of the retroversum (Fig. 4C1, C2). On the proversum, the flexus and the retroversum, the dorsal area is adorned with dense and thin ribs concave towards the peristome. No specimen has its peristome preserved. The septal suture is not observable. The proportion of rochi ribs has been measured on 4 specimens: it ranges from 30% to 61.53% and is 47.88% on average (Table 1).

Remarks on the biostratigraphic position of T. royerianus in its type-stratum. *T. royerianus* was recently revised by Bulot et al. (2018) on the basis of topotype material from the *Argiles à Plicatules* (a lower Aptian formation of the Paris Basin, see Corroy, 1925; Amédéo and Matrimon, 2004; Bersac and Bert, 2015, 2018, 2020). Bulot et al (2018, fig. 3) argued that this formation ranges from the *D. forbesi* Zone to the *Epicheloniceras martini* Zone and that *T. royerianus*

cannot thus be precisely dated. We do not agree on this point. We studied the material figured by Bulot et al. (2018, excepting the specimen figured fig. 3(3)) and numerous additional representatives of *T. royerianus* from the *Argiles à Plicatules* deposited in various French public institutions (a list of these institutions is given in Bersac and Bert, 2015, p. 270).

Actually, the taphonomic characteristics of the whole *Toxoceratoides* of the *Argiles à Plicatules* we could study are the same as those of the sample of the *D. deshayesi* Subzone's small pyrite ammonites (*D. deshayesi* Zone, Bersac and Bert, 2015, 2018). The *Toxoceratoides* are thus part of this taphopopulation and are assigned to the *D. deshayesi* Subzone too. Moreover, we consider that the syntype of *Megatyloceras ricordeanum* (d'Orbigny, 1850) and the lectotype of *Deshayesites deshayesi* (d'Orbigny, 1841) (respectively figured in Bulot et al., 2018, figs. 3(1) and 3(2)) are contemporaneous and assigned to the *D. deshayesi* Subzone too (see Bersac and Bert, 2015, 2018 for explanations).

Concerning the taxonomic identification of the specimens figured by Bulot et al. (2018), we disagree about the following determinations proposed by these authors:

- The specimen figured under *Dufrenoyia* sp. in Bulot et al. (2018, fig. 3(4)) is in our opinion a *Deshayesites* whose characters fall into the range of variability of *D. deshayesi* (see Bersac and Bert, 2015).

- The specimen figured under *Epicheloniceras* sp. (Bulot et al., 2018, fig. 3(6)) bears neither the trituberculate ribs nor the ventral depression typical of this genus. We interpret it as a robust representative of *Cheloniceras cornuelianum* (d'Orbigny, 1842) (see Bersac and Bert, 2018); its taphonomic characteristics are those of the *D. deshayesi* Subzone's small pyritic ammonites of the *Argiles à Plicatules*.

- The specimen figured under *Dufrenoyia* gr. *dufrenoyi* (Bulot et al., 2018, fig. 3(5)) is indeed a representative of the genus *Dufrenoyia* Kilian and Reboul, 1915, but its black matrix clearly differs from that of the specimens of the *D. deshayesi* Subzone of the *Argiles à Plicatules*. This indicates that this specimen does not belong to the *D. deshayesi* Subzone of this formation but comes from a different level (for a discussion on the presence of the genus *Dufrenoyia* in the *Argiles à Plicatules* see Bersac and Bert, 2018). It is to note that this *Dufrenoyia* belongs to the famous Swiss paleontologist François-Jules Pictet de la Rive's (1809-1872) collection (Lionel Cavin, personal communication) and not to the Antoine Pictet's collection ('A. Pictet' coll. in Bulot et al., 2018, caption of fig. 3(5)).

In our opinion, the specimens figured by Bulot et al. (2018, figs. 2, 3) do not contradict the fact that the topotype material of *T. royerianus* is assigned to the *D. deshayesi* Subzone (*D. deshayesi* Zone). This age is consistent with the

observations Bulot et al. (2018, p. 193) made in southern France, where ‘*T. royeri* occurs in the upper part of the *D. forbesi* Zone’ (the Bersac et al.’s (2012) *D. deshayesi* Subzone corresponds to the upper part of the Reboulet et al.’s (2014, 2018) *D. forbesi* Zone, Fig. 2).

Evolutionary characters of the Toxoceratoides of the D. deshayesi Zone in the literature. Some specimens figured in the literature and assigned to the *D. deshayesi* Zone have their flexus and retroversum preserved, which allows comparisons with the material of the LFAB:

- One specimen from the *Chelonicerias parinodum* Subzone (= *D. multicosatus* Subzone in Bersac et al., 2012) of southern England was figured under *T. royerianus* by Casey (1960, pl. VI, figs. 2a, 2b). Its retroversum seems to exhibit a mixture of royerianus and rochi ribs. Following Bulot et al. (2018, p. 190), we consider this specimen as a *T. royerianus*.

- The specimen figured under *T. aff. royerianus* by Conte (1999, fig. 6) originates from Serviers-et-Labaume (southern France) lower Aptian’s Bed 2 (‘*Serviers-la-Baume*’, ‘*niveau 2*’ in Conte, 1999, p. 11, fig. 1). This bed seems to be assigned to the *D. grandis* Subzone because it has provided *Deshayesites* Kasansky, 1914 identified as *Deshayesites grandis* var. *lacertosus* Casey, 1964 and *Deshayesites vectensis* Spath, 1930 by Conte (1999, p. 11). The specimen of

308 *Toxoceratoides* from Bed 2 bears a majority of royerianus ribs, thus we consider
309 it as a representative of *T. royerianus*.

310 - The specimens identified under *Toxoceratoides subproteus* Casey, 1961 by
311 Casey (1980, p. 651, pl. CIII, fig. 3) and under *Tonohamites decurrens* Spath,
312 1924 by the same author (1960, pl. V, fig. 3; 1961a, pl. XXI, fig. 2B) originate
313 from Scaphites Beds' Bed 15 ('bed 3' in Casey, 1961b, p. 510) of Atherfield
314 Bay (Isle of Wight, southern England, see Casey et al., 1998, p. 517-519), which
315 is the last bed of the *D. grandis* Subzone in this section. Following Bulot et al.
316 (2018), we consider these specimens as representatives of the genus
317 *Toxoceratoides* and not *Tonohamites* Spath, 1924. Contrary to the specimens of
318 the *D. grandis* Subzone of the LFAB, these English specimens bear a majority
319 of rochi ribs on their stage *iii* and we thus assign them to *T. rochi*. Consequently,
320 the *Toxoceratoides* of the *D. grandis* Subzone of the LFAB (Vocontian Basin)
321 bear more primitive characters (significant proportion of royerianus ribs and
322 thus low proportion of rochi ribs) than the *Toxoceratoides* of the upper *D.*
323 *grandis* Subzone of Atherfield (Anglo-Paris Basin) that bear a significant
324 proportion of rochi ribs. If one supposes that the evolution of the proportion of
325 rochi ribs is synchronous between the Vocontian Basin and the Anglo-Paris
326 Basin, the *Toxoceratoides* of the LFAB's *Toxoceratoides* Bed are slightly earlier
327 within the *D. grandis* Subzone than the *Toxoceratoides* of Scaphites Beds' Bed
328 15 of Atherfield. These elements suggest that *T. royerianus* occurs at least from

the *D. deshayesi* Subzone to the *D. grandis* Subzone (*D. deshayesi* Zone) and that the transition between *T. royerianus* and *T. rochi* may occur within the *D. grandis* Subzone.

- The specimen identified as *Toxoceratoides royerianus* from the *Audouliceras renauxianum* Subzone (upper *D. deshayesi* Zone) of the Middle Volga area (Central Russia) by Baraboshkin and Mikhailova (2002, pl. VI, fig. 6) presents an irregular alternation of main trituberculate and atuberculate ribs on its proversum and a flexus and retroversum bearing a mixture of possible *rochi* and intermediate or *royerianus* ribs. This specimen is remarkable by the presence of a spire with whorls in contact (this latter character seems to be uncommon in *Toxoceratoides*, see Aguirre-Urreta, 1986; Avram, 2002; Frau et al., 2017; Bulot et al., 2018). As far as we know, no other Helicancyliidae from the *A. renauxianum* Subzone of the Middle Volga area has been figured or described. In our opinion, additional data on the lower Aptian Helicancyliidae from this area are required to identify this specimen to the species level.

Discussion on the identification of the Toxoceratoides from the D. multicostatus and D. Grandis subzones of the LFAB. Following Frau et al. (2017) and Bulot et al. (2018), the main diagnostic characters of *T. royerianus* (*'T. royeri'* in Bulot et al., 2018) are (1) the predominance of stage *iii*'s *royerianus* ribs whereas *rochi*

ribs predominate in its daughter species *T. rochi* and (2) the lateroventral tubercles of stage *ii* that are less prominent and less flattened in *T. royerianus* than in *T. rochi*.

The *Toxoceratooides* of the *D. grandis* Subzone of the LFAB have a stage *iii* characterized by a mixture of royerianus and rochi ribs, with a significant proportion of royerianus ribs. We thus assigned them to *T. royerianus*.

The only specimen of *Toxoceratooides* from the *D. multicostatus* Subzone of the LFAB has a stage *iii* characterized by a mixture of royerianus and rochi ribs too. Because (1) this specimen exhibits evolutionary characters of *T. royerianus*, because (2) it is temporally located between two populations of *Toxoceratooides* with the same evolutionary characters (earlier topotype *T. royerianus* from the *D. deshayesi* Subzone of the Paris Basin and later *T. royerianus* of the *D. grandis* Subzone of the LFAB) and because (3) these two latter populations are both identified as *T. royerianus*, we identified this specimen as *T. royerianus* too, despite its fragmentary state of preservation.

Biostratigraphic distribution. *Deshayesites deshayesi*, *Deshayesites multicostatus* and *Deshayesites grandis* subzones (*Deshayesites deshayesi* Zone).

368 *Toxoceratoides rochi* Casey, 1961

369 Figs. 4H-P4, 5, 7

370

371 2011 *Tonohamites* sp. - Bert and Bersac, fig. 42

372 2019 *Toxoceratoides rochi* - Bersac and Bert, p. 155, 165, figs. 5, 9, 10, 12, 15,

373 pl. 5, figs. 1-4

374 For an extensive synonymy of this species, see Frau et al. (2017).

375

376 *Material* (see *Supplementary Appendix*). 130 specimens from the *D. furcata*

377 Subzone and 3 specimens from the *D. dufrenoyi* Subzone (*D. furcata* Zone)

378 from GRS1, CHP and GRO sections.

379

380 *Description of the sample of the D. furcata Subzone*. Most of the 130 specimens

381 of this sample are fragmentary but they allow a good overview of the

382 ontogenetic sequence. The sample is characterized by a very important

383 morphological disparity.

384 The two subcomplete specimens of the sample are 82.7 mm (SBC.06061-

385 00001/GRS398, Fig. 4P1-P4) and 73.8 mm (SBC.06061-00001/GRS383, Fig.

5J) in total length. H was measured for 60 specimens, including 57 specimens from GRS1 section (Supplementary Appendix). Most of the specimens are deformed, which implies that the value of H has to be considered as an estimation. This values varies by a factor of two (from 8 to 16.7 mm) with an average around 13 mm. According to the fitted normal curve of its histogram, the distribution of H seems bimodal (Fig. 6) but it does not significantly depart from normality ($p=0.512$). Specimens with small whorl height are exemplified by SBC.06061-00001/GRS206 (Fig. 5A1, A2) and SBC.06061-00001/GRS366 (Fig. 5G); intermediate specimens are illustrated by SBC.06061-00001/GRS287 (Fig. 4L) and SBC.06061-00001/GRS591 (Fig. 5I); larger ones are represented by SBC.06061-00001/GRS198 (Fig. 5Q1, Q2) and SBC.06061-00001/GRS527 (Fig. 5D).

The shell is planispiraled (no helical specimen was observed). The earliest developments of the proversum are observable from a whorl height of 0.8 mm (Fig. 7I, J, L) and they never exhibit any spiral. The proversum is more or less curved. The angle between the proversum and retroversum is variable from a specimen to another: SBC.06061-00001/GRS580 (Fig. 5O1) and SBC.06061-00001/GRS221 (Fig. 5H1) have a rather narrow angle, whereas SBC.06061-00001/GRS284 (Fig. 4H) and SBC.06061-00001/GRS383 (Fig. 5J) have an open angle. The retroversum seems to reach a significant length in some specimens (Fig. 7G).

407 The ornamentation and duration of the ontogenetic stages vary significantly
408 from a specimen to another:

409 - Stage *i* is composed of dense and thin ribs that can be atuberculate or bear a
410 discrete lateroventral tubercle. These ribs do not attenuate when crossing the
411 siphonal area. This stage is generally present in the earliest part of the
412 proversum (Fig. 7I, L), but its duration strongly varies from a specimen to
413 another: it can be very short (Fig. 4J1-J4), intermediate (Fig. 4P1-P4, Fig. 5C)
414 or more rarely can be present on nearly the entire proversum. In this last case,
415 the specimens have a very slender shape (Fig. 7G, H).

416 - Stage *ii* is represented by tuberculate main ribs and atuberculate intercalary
417 ribs. The ribs are generally simple, straight, rectiradiate or prorsiradiate and
418 attenuated on the siphonal area (Fig. 4M). The main ribs first bear a lateral and a
419 lateroventral tubercle (stage *iiia*). They are rarely separated by one or more
420 atuberculate intercalary ribs. Thereafter, a laterodorsal tubercle arises on the
421 main ribs and the intercalary ribs become more frequent (stage *iiib*, Fig. 4N1-
422 N3). Rarely, the main ribs can be looped (Fig. 5Q1) or the intercalary ribs may
423 be absent (Fig. 5C, D). Alternation between main and intercalary ribs is
424 generally regular (Fig. 4K, O1-O3), but it can be irregular in some cases. In both
425 stages *iiia* and *iiib*, the lateroventral tubercles are larger than the other tubercles.
426 They are conical or claviform but their shape is altered by *post mortem*

deformation. Transition between stages *ii*a and *ii*b is very variable from a specimen to another. Stage *ii* ends between the beginning (Fig. 5O1) and the end of the flexus (Fig. 5F1, F2).

- Stage *iii* is in most of the cases composed of simple, dense, straight, flattened or sharp uniform ribs (rochi ribs, Fig. 7A, B1). They can be attenuated (Fig. 5E) or not (Fig. 5K1, K2) on the ventral area. They rarely bear a lateroventral tubercle (generally discrete, Fig. 5E), or lateral and lateroventral tubercles (Fig. 5F1, F2). Some specimens exhibit rare royerianus ribs (Fig. 7C).

The dorsal area of the proversum, the flexus and the retroversum bear thin and dense ribs, concave toward the peristome (Fig. 4J2, N3, O3). No specimen has its peristome preserved. Septa can be observed on several specimens but the suture line is too poorly preserved to be studied. The phragmocone can occupy the whole proversum and the beginning of the flexus (Figs. 4P2, 5H1, O1, 7A, F). On several specimens, the last septum is located in the proversum (Figs. 4J1, L, N1, 5L).

The proportion of rochi ribs was calculated for 52 specimens, including 51 specimens from GRS1 section. In this last section, the mean proportion of rochi ribs varies from 91.59% to 96.17% from Bed 99 to Bed 106, with a total mean value of 94.52% (Table 1). The histogram of rochi ribs proportion shows a

continuous, unimodal and strongly negatively skewed distribution (Fig. 8). It significantly departs from normality ($p=0$).

Description of the sample of the D. dufrenoyi Subzone. Only 3 specimens were collected in the *D. dufrenoyi* Subzone. SBC06061/00001/GRS586 (GRS1, Bed 110), figured in Bert and Bersac (2011, fig. 42) and SBC06061/00001/GRS728 (GRS1, Bed 113) are fragments of proversum adorned with dense, straight, uniform and prorsiradiate ribs bearing a discrete lateroventral tubercle (stage *i*). SBC06061/00001/GRS731 (GRS1, Bed 113 figured Fig. 7O) is a very poorly preserved fragment of proversum, flexus and retroversum. The proversum bears trituberculate ribs separated by one or two intercalaries. The ornamentation on the flexus and retroversum cannot be studied and the proportion of rochi ribs cannot be calculated.

Variability and homogeneity of the Toxoceratoides of the D. furcata Zone of the LFAB. As far as possible, ammonite populations have to be studied from a restricted stratigraphic interval in order to avoid time-averaging (see discussion in de Baets et al., 2015, p. 363). This is the case of our sample, which is restricted to the *D. furcata* Subzone, excepting 3 poorly preserved specimens

from the *D. dufrenoyi* Subzone. The following interpretations are thus based on the sample of the *D. furcata* Subzone only.

This sample has a very important morphological disparity. This variability is continuous and similar in every beds (Fig. 9). In GRS1 section, which provides most of the specimens of the *D. furcata* Subzone, changes from a bed to another are limited to a slight increase of H and a slight increase of the proportion of rochi ribs (Table 1). The value of H allows estimating adult size in tripartite ammonites (see discussion in Bersac and Bert 2020). Consequently, we consider a progressive increasing adult size of the *Toxoceratoides* through the *D. furcata* Subzone of the LFAB.

We interpret the morphological disparity of the sample of the *D. furcata* Zone as being driven by several processes (Fig. 9):

- The variation in duration of the ontogenetic stages: this corresponds to a process of heterochronic type that plays a significant role in ammonoid intraspecific variability in general (De Baets et al., 2015; Vennari and Aguirre-Urreta, 2019);

- The variation of the ornamentation of each ontogenetic stage: within each stage, there is a variation in rib density and in the number of intercalary ribs. This kind of ‘multipolar’ variability is extensively documented among ammonoids (Bert, 2013, De Baets et al., 2015). In stage *iii*, this variability

concerns in addition the proportion of rochi ribs. This proportion continuously varies from a specimen to another (Fig. 8). Its strongly negatively skewed distribution (which thus significantly departs from normality) can be due to the fact that the proportion of rochi ribs in this sample tends toward the value of 100%, without, naturally, exceeding it.

- The delayed disappearance of a character through ontogeny: it could explain the presence of ribs with lateroventral and/or lateral tubercles (characteristic of the main ribs of stage *ii*) in some specimens' stage *iii*. Such phenomenon was described in the lower Aptian ammonite genus *Cheloniceras* Hyatt, 1903 (Bersac and Bert, 2018);

- *H* varies in a continuous way by a factor 2 and its distribution does not significantly depart from normality (Fig. 6), which suggests a variation of the adult size in the same way. Such significant variation has already been documented among heteromorph tripartite ammonites (Landman, 1987; see discussion in Bersac and Bert, 2020);

- The variation of coiling (more or less curved proversum, variable angle between proversum and retroversum). This kind of variability among heteromorph ammonites has already been described (Kakabadze, 2004; Bert, 2013; Delanoy et al., 2013; Bersac and Bert, 2020), especially in other representatives of the family Helicancylidae (*Helicancylus bonarellii* (Leanza,

1970) in Aguirre-Urreta, 1986, p. 292, fig. 13A-F; *Toxoceratoides nagerai*
(Leanza, 1970) in Aguirre-Urreta, 1986, p. 298, fig. 16A-D, 17A-D).

The variability of the sample of the *D. furcata* Subzone appears to be continuous and involves processes already observed in other ammonite monospecific samples. Consequently, we interpret this sample as being monospecific. Such continuous variability is not involved by sexual dimorphism (see Bert, 2013, 2019 for a description of the various rules of ammonoid intraspecific variability).

Although they are fragmentary, we have no argument to taxonomically isolate the three specimens of the *D. dufrenoyi* Subzone from the rest of the sample.

Taxonomic attribution and consequences. The sample of *Toxoceratoides* of the *D. furcata* Zone of the LFAB is characterized by the predominance of rochi ribs in its stage *iii*; its biostratigraphic position is also similar to that of *T. rochi* in its type locality (Frau et al., 2017, p. 340). For these reasons, we assigned this sample to *T. rochi*.

This interpretation implies that the disparity of *T. rochi* encompasses morphologies corresponding to several species of *Toxoceratoides*, but also morphologies that are atypical among *Toxoceratoides* and which are often

524 assigned to other genera of Helicancylidae. Therefore, slender specimens with
525 long stage *i* (i.e. with feebly tuberculate proversum, Fig. 7G) resemble the genus
526 *Tonohamites*. Among the Helicancylidae, co-occurrence of specimens with
527 feebly tuberculate proversum and specimens with tuberculate proversum was
528 already observed in the *D. grandis* Subzone of southern England by Casey
529 (1960, 1961a). This author assigned the feebly tuberculate specimens to the
530 genus *Tonohamites* and the tuberculate specimens to the genera *Tonohamites*
531 and *Toxoceratoides*. Specimens with a stage *ii* essentially composed of main ribs
532 (i.e. without intercalaries, Fig. 5D) mimic representatives of the genus
533 *Helicancylus* Gabb, 1869 or the species *Toxoceratoides krenkeli* Förster, 1975
534 (Förster, 1975; Aguirre-Urreta, 1986). Fragments with such ornamentation from
535 the *C. parinodum* Subzone (= *D. multicostatus* Subzone of Bersac et al., 2012)
536 and the *D. grandis* Subzone of southern England were described under
537 *Toxoceratoides* cf. *fustiformis* (von Koenen, 1902) by Casey (1961a, p. 83, pl.
538 XVII, fig. 4). Large sized robust specimens resemble *Toxoceratoides stefanescui*
539 Avram, 2002 (Avram, 2002, this species is regarded as a junior synonym of *T.*
540 *rochi* by Frau et al., 2017). Specimens with slender stage *ii* (main ribs separated
541 by several intercalaries, Figs. 5H, 7A) are similar to *Toxoceratoides transitorius*
542 Avram, 2002. Small fragments of proversum bearing a stage *i* look like
543 *Toxoceratoides emericianum* (d'Orbigny, 1842), etc.

Biostratigraphic distribution. *Dufrenoyia furcata* and *Dufrenoyia dufrenoyi* subzones (*Dufrenoyia furcata* Zone) and probably upper part of *Deshayesites grandis* Subzone (*Deshayesites deshayesi* Zone) of southern England.

3.2. Evolutionary patterns of the *Toxoceratoides* of the LFAB (Fig. 10)

The interpretations proposed in this chapter are based on data from the LFAB only. The proportion of rochi ribs in the *D. furcata* Zone could have been quantified in several beds only in GRS1 section (Table 1): we thus have studied the evolution of this character only in this section.

3.2.1. From the *D. forbesi* Zone to the *D. grandis* Subzone

In this interval, the *Toxoceratoides*:

- belong to the species *T. royerianus*;
- have a small population. In the *D. forbesi* Zone and the *D. multicostatus* Subzone, the population size of *Toxoceratoides* could have been small, as suggested by the very small number of specimens collected (2 specimens, see

Supplementary Appendix). In the *D. grandis* Subzone, the population size slightly increases (Bersac and Bert, 2019, fig. 18);

- have a low proportion of rochi ribs that may slowly increase over time (Table 1);

- have a globally robust shape in the *D. grandis* Subzone (stage *ii* with strong tuberculate ribs separated by one atuberculate rib and stage *iii* bearing bifid and monotuberculate royerianus ribs). Note that in the earlier levels of the LFAB, the specimens are too fragmentary to determine their robustness.

3.2.2. From the *D. grandis* Subzone to the *D. furcata* Zone

- The population size of *Toxoceratoides* sharply increases (Bersac and Bert, 2019, fig. 18).

- The proportion of rochi ribs sharply increases at the same time, rising from about 50% to 92% (Table 1).

- The specimens are more slender on average, due to a significant intraspecific variability.

These abrupt evolutionary changes compared to the precedent interval represent a speciation event that determines the transition from *T. royerianus* to *T. rochi*. This event could occur during the late *D. grandis* Subzone (see Chapter 3.1, ‘discussion’ of the systematic palaeontology of *T. royerianus*).

It is to note that we could not highlight in the LFAB the evolution of the lateroventral tubercles of stage *ii* described by Bulot et al. (2018), due to *post mortem* deformation of the specimens.

3.2.3. During the *D. furcata* Zone

- The proportion of *rochi* ribs continues to increase, but slower than before (from about 92% to 96%, see Table 1).

- The adult size of the specimens seems to slowly increase (see H in Table 1).

4. Conclusion

T. sp., *T. royerianus* and *T. rochi* have been recognized within our sample of *Toxoceratoides* from the *D. forbesi* Zone - *D. furcata* Zone interval of the LFAB.

The large size of our sample of *Toxoceratoides rochi* (133 specimens) allowed highlighting the unprecedented range of morphological disparity of this species. This disparity is so significant that it encompasses the morphology of several species of *Toxoceratoides* and even of some genera of Helicancyllidae (*Tonohamites*, *Helicancyllus*). Nevertheless, additional data are necessary to decide if some of these taxa can be synonymized or not with *T. rochi* and *Toxoceratoides* respectively. If we had applied a typological concept of the species to the sample studied, we would probably have recognized dozens of species and several genera of Helicancyllidae.

Concerning the evolutionary patterns, the proportion of rochi ribs seems to be characterized by periods of slow increase separated by a sudden significant increase between the *D. grandis* Subzone and the *D. furcata* Subzone. This sudden increase, that occurs in a transgressive context (Bersac and Bert, 2019), is contemporaneous with the sharp increase ('bloom') of the population size of *Toxoceratoides*, which constitutes a speciation event determining the transition from *T. royerianus* to *T. rochi*. These elements suggest that the evolution of

Toxoceratoides could correspond to a punctuated equilibrium model (Eldredge and Gould, 1972) rather than a gradualist model.

The increasing trend in H highlighted in our samples is based on the study of frequently deformed specimens. As a consequence, this trend has to be confirmed by studying contemporaneous populations of non-deformed *Toxoceratoides* from other paleogeographic areas.

The proportion of rochi ribs in *Toxoceratoides* may be used as a complementary biostratigraphic tool. However, it would be necessary to study this parameter in larger samples from the *D. grandis* Subzone and from earlier biostratigraphic units to confirm this proposition. It would also be interesting to determine if this parameter could be modulated or not by paleogeography.

Disclosure of interest

The authors declare that they have no competing interest.

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Figures, table and plates

Fig. 1. Map of the Les Ferres area with location of the sections that provided the studied material. Geographic coordinates of the sections: GRS1 (lat.: 43.842177°, long.: 7.076508°), VAL (lat.: 43.842256°, long.: 7.09677°), GRO

(lat: 43.843379°, long: 7.1°), CHP (lat.: 43.845193°, long.: 7.102648°), CLE
(lat.: 43.845193°, long.: 7.102648°). See online version for colours.

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Fig. 2. Bio-chronostratigraphic charts used in the present work. SZS: Standard
Mediterranean Zonal Scheme. St.: stages.

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Fig. 3. *Toxoceratoides* shell morphological terminology and measured
parameter. H: whorl height at the middle of the flexus.

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Fig. 4. The arrow indicates the beginning of the body chamber. All specimens:
Bersac's collection. A: *Toxoceratoides* sp., SBC.06061-00007/CLE036, CLE
section, Bed 400, *Deshayesites forbesi* Zone. B: *Toxoceratoides royerianus*
(d'Orbigny, 1842), SBC.06061-00003/VAL066, VAL section, Bed 405,
Deshayesites multicostatus Subzone (*Deshayesites deshayesi* Zone). C-G:
Toxoceratoides royerianus (d'Orbigny, 1842), *Deshayesites grandis* Subzone
(*Deshayesites deshayesi* Zone). C: SBC.06061-00006/CHP359, CHP section,
Bed 416. D: SBC.06061-00006/CHP041, CHP section, Bed 416. E: SBC.06061-
00006/CHP038, CHP section, Bed 416. F: SBC.06061-00007/CLE004, CLE
section, Bed 416. G: SBC.06061-00001/GRS510, GRS1 section, Bed 97. H-P:

839 *Toxoceratoides rochi* Casey, 1961, *Dufrenoyia furcata* Subzone (*Dufrenoyia*
840 *furcata* Zone). H: SBC.06061-00001/GRS284, GRS1 section, Bed 102. I:
841 SBC.06061-00001/GRS222, GRS1 section, Bed 102. J: SBC.06061-
842 00001/GRS358, GRS1 section, Bed 100. K: SBC.06061-00005/GRO076, GRO
843 section, Bed 418. L: SBC.06061-00001/GRS287, GRS1 section, Bed 102. M:
844 SBC.06061-00001/GRS159, GRS1 section, Bed 100. N: SBC.06061-
845 00001/GRS414, GRS1 section, Bed 104. O: SBC.06061-00001/GRS186, GRS1
846 section, Bed 100. P: SBC.06061-00001/GRS398, GRS1 section, Bed 104.

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848 Fig. 5: *Toxoceratoides rochi* Casey, 1961, GRS1 section, *Dufrenoyia furcata*
849 Subzone (*Dufrenoyia furcata* Zone), Bersac's collection. The arrow indicates
850 the beginning of the body chamber. A: SBC.06061-00001/GRS206, Bed 102. B:
851 SBC.06061-00001/GRS238, Bed 102. C: SBC.06061-00001/GRS585, Bed 102.
852 D: SBC.06061-00001/GRS527, Bed 104. E: SBC.06061-00001/GRS607, Bed
853 102. F: SBC.06061-00001/GRS367, Bed 99. G: SBC.06061-00001/GRS366,
854 Bed 99. H: SBC.06061-00001/GRS221, Bed 102. I: SBC.06061-
855 00001/GRS591, Bed 102. J: SBC.06061-00001/GRS383, Bed 102. K:
856 SBC.06061-00001/GRS579, Bed 102. L: SBC.06061-00001/GRS524, Bed 104.
857 M: SBC.06061-00001/GRS289, Bed 102. N: SBC.06061-00001/GRS321, Bed

99. O: SBC.06061-00001/GRS580, Bed 102. P: SBC.06061-00001/GRS034,
Bed 102. Q: SBC.06061-00001/GRS198, Bed 100.

Fig 6. Histogram of H (whorl height at the middle of the flexus in mm) of 57
specimens of *Toxoceratoides rochi* Casey, 1961 from the *Dufrenoyia furcata*
Subzone (*Dufrenoyia furcata* Zone, lower Aptian) of the Les Ferres Aptian
Basin and result of the Shapiro-Wilk normality test. Black curve: fitted normal
curve. Dark red curve: kernel density estimator. See online version for colours.

Fig. 7. The arrow indicates the beginning of the body chamber. All specimens:
Bersac's collection. A-N: *Toxoceratoides rochi* Casey, 1961, *Dufrenoyia furcata*
Subzone (*Dufrenoyia furcata* Zone). A: SBC.06061-00001/GRS224, GRS1
section, Bed 102. B: SBC.06061-00001/GRS644, GRS1 section, Bed 102. C:
SBC.06061-00001/GRS649, GRS1 section, Bed 106. D: SBC.06061-
00001/GRS582, GRS1 section, Bed 102. E: SBC.06061-00006/CHP201, CHP
section, Bed 421. F: SBC.06061-00001/GRS022, GRS1 section, Bed 102. G:
SBC.06061-00001/GRS616, GRS1 section, Bed 99. H: SBC.06061-
00001/GRS323, GRS1 section, Bed 99. I: SBC.06061-00001/GRS182, GRS1
section, Bed 100. J: SBC.06061-00001/GRS046, GRS1 section, Bed 102. K:
SBC.06061-00001/GRS522, GRS1 section, Bed 104. L: SBC.06061-

00001/GRS717, GRS1 section, Bed 102. M: SBC.06061-00001/GRS523, GRS1
 section, Bed 104. N: SBC.06061-00001/GRS127, GRS1 section, Bed 102. O:
Toxoceratoides rochi Casey, 1961, SBC.06061-00001/GRS731, GRS1 section,
 Bed 113. *Dufrenoyia dufrenoyi* Subzone (*Dufrenoyia furcata* Zone).

Fig 8. Histogram of rochi ribs proportion of 52 specimens of *Toxoceratoides*
rochi Casey, 1961 from the *Dufrenoyia furcata* Subzone (*Dufrenoyia furcata*
 Zone, lower Aptian) of the Les Ferres Aptian Basin section and result of the
 Shapiro-Wilk normality test.. Black curve: fitted normal curve. Dark red curve:
 kernel density estimator. See online version for colours.

Fig. 9. Patterns of intraspecific variability of *Toxoceratoides rochi* Casey, 1961.
 A: slightly curved proversum, intermediate angle between proversum and
 retroversum. B: substraight proversum, open angle. C: substraight proversum,
 narrow angle. D: stage *ii* with rare intercalary ribs, stage *iii* with rare royerianus
 ribs. E: stage *ii* with one intercalary rib between main ones on a regular basis,
 stage *iii* with only rochi ribs. F: stage *ii* with several intercalated ribs between
 primary ones, stage *iii* with rare royerianus ribs. G: early onset of stage *ii*, late
 onset of stage *iii*. H: later onset of stage *ii*, early onset of stage *iii*. I: very late
 ending of stage *i*, no stage *ii*. J: large size. K: intermediate size. L: small size.

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899 Fig. 10. Evolutionary patterns of the genus *Toxoceratoides* Spath, 1924
 900 according to Bulot et al. (2018) and this work. Biostratigraphic chart: see Fig. 2.

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			Proportion of rochi ribs	H (mm)
<i>Toxoceratoides rochi</i>	GRS 1 section (les Graous Member, <i>Dufrenoyia furcata</i> Subzone)	Bed 106	94.11 % (N=1)	18.8 (N=1)
		Bed 104	94.7 % (N=5)	13.88 (N=5)
		Bed 102	96.17 % (N=28)	13.47 (N=32)
		Bed 100	91.91 % (N=9)	12.95 (N=10)
		Bed 99	91.59 % (N=8)	11.97 (N=9)
<i>Toxoceratoides royerianus</i>	<i>Toxoceratoides</i> Bed (<i>Deshayesites grandis</i> Subzone)		47.88 % (N=4)	10.04 (N=5)
	<i>Ammonitoceras</i> Level ? (<i>Deshayesites multicostratus</i> Subzone)		42.85 % (N=1)	13.9 (N=1)
<i>Toxoceratoides sp.</i>	Top of HAL (<i>Deshayesites forbesi</i> Zone)		0 % (N=1)	9 (N=1)

902

903 Table 1. Mean values of the proportion of rochi ribs and whorl height at the
904 middle of the flexus (H) of the taxa recognized in the present article. N =
905 number of studied specimens. HAL = Hauterivian-Aptian limestones. Litho- and
906 biostratigraphic charts after Bersac and Bert (2019) and Fig. 2.

Declaration of interests

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

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