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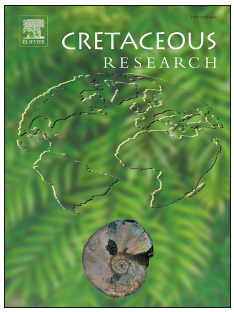

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The ammonites of the Les Ferres Aptian Basin (Lower Cretaceous, Southeast of France): the genus *Toxoceratoides* (Ancyloceratina, Helicancylidae)

Stéphane Bersac [a, *] and Didier Bert [a, b, c]

[a] Laboratoire du Groupe de recherche en paléobiologie et biostratigraphie des Ammonites (GPA), Bois-Mésanges, quartier Saint-Joseph, F-04170 La Mure-Argens, France

[b] Réserve naturelle nationale géologique de Haute-Provence, service Environnement, Conseil départemental des Alpes de Haute-Provence, 13, rue du Docteur-Romieu, CS 70216, F-04995 Digne-Les-Bains cedex 9, France

[c] Laboratoire Géosciences, UMR-CNRS 6118, université de Rennes-1, campus Beaulieu, bâtiment 15, F-35042 Rennes cedex, France

[*] Corresponding author: geosteber@yahoo.fr (S. Bersac)

Abstract:

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Toxoceratoides (Ancyloceratina, Helicancylidae) 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

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

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2. Material and method

2.1. Material

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

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

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2.2. Method

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

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

- Stage *i* (Bulot et al., 2018, p. 189) is adorned with uniform, simple and atuberculate ribs or ribs bearing a single ventrolateral tubercle.
- Stage *ii* presents an *'alternation of* (...) *primary ribs and atuberculate intercalatories'* (Bulot et al., 2018, p. 189). The main ribs are tuberculate and attenuated on the siphonal area. They are usually separated by one or more atuberculate intercalary ribs but can be more rarely contiguous. The intercalary ribs are generally not attenuated on the siphonal area. Stage *ii* can be subdivided in an early part named here 'stage *iia*' with bituberculate main ribs (lateral and lateroventral tubercles, see Bulot et al., 2018, fig. 2R) and a late part named here 'stage *iib*' with trituberculate main ribs (laterodorsal, lateral and lateroventral tubercles).

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

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

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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 Helicancylidae for the following reasons:

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

- (2) the family-group names Helicancylidae 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 Helicancylidae, Hyatt, 1894 has seniority on the name Acrioceratidae, Vermeulen, 2004.

Toxoceratoides sp.

Fig. 4A

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

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

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

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

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(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).

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188

189 *Material (see Supplementary Appendix)*. 1 specimen from Bed 405 of VAL
190 section (*D. multicostatus* 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. multicostatus *Subzone (*D. deshayesi *Zone)*.
196 The specimen No. SBC.06061-00003/VAL066 (Fig. 4B) is the only
197 Helicancylidae we collected in the *D. multicostatus* 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

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208 replaced by stage *iii*. Its ribs are simple and atuberculate (rochi ribs) or arise in
209 pairs from a laterodorsal tubercle (royerianus ribs). The peristome is not
210 preserved and the septal suture is not observable. The proportion of rochi ribs is
211 42.85% for this specimen (Table 1).

212

213 *Description of the material of the* D. grandis *Subzone (*D. deshayesi *Zone)*. The
214 10 specimens of the *D. grandis* Subzone (*D. deshayesi* Zone) are all fragments
215 but it is nevertheless possible to follow their ontogeny from a specimen to
216 another. H has been measured only on 5 specimens; it varies from 7.2 mm to
217 11.7 mm with a mean value of 10.04 mm (Table 1).

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

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

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228 At the beginning of the flexus, stage *iib* is abruptly replaced by stage *iii* (Bersac
229 and Bert, 2019, pl. 3, figs. 13, 14). Its ornamentation is represented by slightly
230 rursiradiate ribs that can be of royerianus, rochi or intermediate type. Most of
231 the specimens exhibit a mixture of each type of ribs (Fig. 4C1-D2, Bersac and
232 Bert, 2019, pl. 3, figs. 15, 16). One specimen (SBC.06061-00006/CHP038, Fig.
233 4E1, E2) exhibits some ribs bearing a discrete lateroventral tubercle. The
234 royerianus ribs seem to predominate on the flexus and the beginning of the
235 retroversum whereas the rochi ribs seem to be more frequent on the distal part of
236 the retroversum (Fig. 4C1, C2). On the proversum, the flexus and the
237 retroversum, the dorsal area is adorned with dense and thin ribs concave towards
238 the peristome. No specimen has its peristome preserved. The septal suture is not
239 observable. The proportion of rochi ribs has been measured on 4 specimens: it
240 ranges from 30% to 61.53% and is 47.88% on average (Table 1).

241

242 *Remarks on the biostratigraphic position of* T. royerianus *in its type-stratum. T.*
243 *royerianus* was recently revised by Bulot et al. (2018) on the basis of topotype
244 material from the *Argiles à Plicatules* (a lower Aptian formation of the Paris
245 Basin, see Corroy, 1925; Amédro and Matrion, 2004; Bersac and Bert, 2015,
246 2018, 2020). Bulot et al (2018, fig. 3) argued that this formation ranges from the
247 *D. forbesi* Zone to the *Epicheloniceras martini* Zone and that *T. royerianus*

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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).

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- 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, personnal 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 *Cheloniceras parinodum* Subzone (= *D. multicostatus* 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

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

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

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

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

344

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

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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 *Toxoceratoides* 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 *Toxoceratoides* 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 *Toxoceratoides* 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.

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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).

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

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

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

deformation. Transition between stages *iia* and *iib* 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

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

448

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

459

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

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

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

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

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

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

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485 concerns in addition the proportion of rochi ribs. This proportion continuously
486 varies from a specimen to another (Fig. 8). Its strongly negatively skewed
487 distribution (which thus significantly departs from normality) can be due to the
488 fact that the proportion of rochi ribs in this sample tends toward the value of
489 100%, without, naturally, exceeding it.

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

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

500 - The variation of coiling (more or less curved proversum, variable angle
501 between proversum and retroversum). This kind of variability among
502 heteromorph ammonites has already been described (Kakabadze, 2004; Bert,
503 2013; Delanoy et al., 2013; Bersac and Bert, 2020), especially in other
504 representatives of the family Helicancylidae (*Helicancylus bonarellii* (Leanza,

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505 1970) in Aguirre-Urreta, 1986, p. 292, fig. 13A-F; *Toxoceratoides nagerai*
506 (Leanza, 1970) in Aguirre-Urreta, 1986, p. 298, fig. 16A-D, 17A-D).

507 The variability of the sample of the *D. furcata* Subzone appears to be continuous
508 and involves processes already observed in other ammonite monospecific
509 samples. Consequently, we interpret this sample as being monospecific. Such
510 continuous variability is not involved by sexual dimorphism (see Bert, 2013,
511 2019 for a description of the various rules of ammonoid intraspecific
512 variability).

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

515

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

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

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

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

547

548 3.2. Evolutionary patterns of the *Toxoceratoides* of the LFAB (Fig. 10)

549

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

554

555 3.2.1. From the *D. forbesi* Zone to the *D. grandis* Subzone

556

557 In this interval, the *Toxoceratoides*:

558 - belong to the species *T. royerianus*;

559 - have a small population. In the *D. forbesi* Zone and the *D. multicostatus*
560 Subzone, the population size of *Toxoceratoides* could have been small, as
561 suggested by the very small number of specimens collected (2 specimens, see

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

564 - have a low proportion of rochi ribs that may slowly increase over time (Table
565 1);

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

570

571 3.2.2. From the *D. grandis* Subzone to the *D. furcata* Zone

572

573 - The population size of *Toxoceratoides* sharply increases (Bersac and Bert,
574 2019, fig. 18).

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

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

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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

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

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

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

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

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

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

625

626 Disclosure of interest

627

628 The authors declare that they have no competing interest.

629

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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

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

822

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

825

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

828

829 Fig. 4. The arrow indicates the beginning of the body chamber. All specimens:
830 Bersac's collection. A: *Toxoceratoides* sp., SBC.06061-00007/CLE036, CLE
831 section, Bed 400, *Deshayesites forbesi* Zone. B: *Toxoceratoides royerianus*
832 (d'Orbigny, 1842), SBC.06061-00003/VAL066, VAL section, Bed 405,
833 *Deshayesites multicostatus* Subzone (*Deshayesites deshayesi* Zone). C-G:
834 *Toxoceratoides royerianus* (d'Orbigny, 1842), *Deshayesites grandis* Subzone
835 (*Deshayesites deshayesi* Zone). C: SBC.06061-00006/CHP359, CHP section,
836 Bed 416. D: SBC.06061-00006/CHP041, CHP section, Bed 416. E: SBC.06061-
837 00006/CHP038, CHP section, Bed 416. F: SBC.06061-00007/CLE004, CLE
838 section, Bed 416. G: SBC.06061-00001/GRS510, GRS1 section, Bed 97. H-P:

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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.

847

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

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

860

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

866

867 Fig. 7. The arrow indicates the beginning of the body chamber. All specimens:
868 Bersac's collection. A-N: *Toxoceratoides rochi* Casey, 1961, *Dufrenoyia furcata*
869 Subzone (*Dufrenoyia furcata* Zone). A: SBC.06061-00001/GRS224, GRS1
870 section, Bed 102. B: SBC.06061-00001/GRS644, GRS1 section, Bed 102. C:
871 SBC.06061-00001/GRS649, GRS1 section, Bed 106. D: SBC.06061-
872 00001/GRS582, GRS1 section, Bed 102. E: SBC.06061-00006/CHP201, CHP
873 section, Bed 421. F: SBC.06061-00001/GRS022, GRS1 section, Bed 102. G:
874 SBC.06061-00001/GRS616, GRS1 section, Bed 99. H: SBC.06061-
875 00001/GRS323, GRS1 section, Bed 99. I: SBC.06061-00001/GRS182, GRS1
876 section, Bed 100. J: SBC.06061-00001/GRS046, GRS1 section, Bed 102. K:
877 SBC.06061-00001/GRS522, GRS1 section, Bed 104. L: SBC.06061-

878 00001/GRS717, GRS1 section, Bed 102. M: SBC.06061-00001/GRS523, GRS1
879 section, Bed 104. N: SBC.06061-00001/GRS127, GRS1 section, Bed 102. O:
880 *Toxoceratoides rochi* Casey, 1961, SBC.06061-00001/GRS731, GRS1 section,
881 Bed 113. *Dufrenoyia dufrenoyi* Subzone (*Dufrenoyia furcata* Zone).

882

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

888

889 Fig. 9. Patterns of intraspecific variability of *Toxoceratoides rochi* Casey, 1961.
890 A: slightly curved proversum, intermediate angle between proversum and
891 retroversum. B: substraight proversum, open angle. C: substraight proversum,
892 narrow angle. D: stage *ii* with rare intercalary ribs, stage *iii* with rare royerianus
893 ribs. E: stage *ii* with one intercalary rib between main ones on a regular basis,
894 stage *iii* with only rochi ribs. F: stage *ii* with several intercalated ribs between
895 primary ones, stage *iii* with rare royerianus ribs. G: early onset of stage *ii*, late
896 onset of stage *iii*. H: later onset of stage *ii*, early onset of stage *iii*. I: very late
897 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.

901

			Proportion of rochi ribs	H (mm)
Toxoceratoides rochi	GRS 1 section (les Graous Member, *Dufrenoyia furcata* 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)
Toxoceratoides royerianus	*Toxoceratoides* Bed (*Deshayesites grandis* Subzone)		47.88 % (N=4)	10.04 (N=5)
	Ammonitoceras Level ? (*Deshayesites multicostatus* Subzone)		42.85 %(N=1)	13.9 (N=1)
Toxoceratoides sp.	Top of HAL (*Deshayesites forbesi* Zone)		0 % (N=1)	9 (N=1)

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

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Declaration of interests

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

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Stéphane Bersac

Didier Bert

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