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Article

New and poorly known Aptian Acrioceratidae (Acrioceratidae, Ammonoidea) from Cassis - Roquefort-la-Bédoule (Bouches-du-Rhône, France)

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With 6 figures

Abstract: *Brainaella marcoulinense* gen. nov. et sp. nov. is described on the basis of new material from the Upper Aptian of the reference succession of Cassis - Roquefort-la-Bédoule (Bouches-du-Rhône, France). The morphological features of this new taxon suggest affinities with the late Early Aptian *Toxoceratoides rochi* Casey, a poorly understood species revised in the present contribution. The study of these two taxa sheds new light on the taxonomic status, content and evolution of the long-debated families Helicancylidae Hyatt and Acrioceratidae Vermeulen.

Key words: Acrioceratidae, Ammonite, Aptian, Systematic, Evolution, France.

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1. Introduction

The systematic of small-sized Aptian Ancyloceratoidea from the Mediterranean Tethys has received little attention in recent literature, despite the description of new genera in the past decade (Bert 2009; Delanoy et al. 2013). The great majority of the ammonite material is fragmentary and was included in the poorly-defined and highly debated families Helicancylidae Hyatt, 1894 or Acrioceratidae Vermeulen, 2004 (see discussions in Bert 2009; Vermeulen 2010; Delanoy et al. 2013). Recent investigation in the area of Cassis - Roquefort-la-Bédoule (Bouches-du-Rhône, France) led to the discovery of several well-preserved acrioceratid specimens in the upper Lower and Upper Aptian. The aim of this paper is to revise the poorly understood species *Toxoceratoides rochi* Casey, 1961 and to describe a new, small-sized Ancyloceratoidea *Brainaella marcoulinense* gen. et sp. nov. Our new material sheds new light on the taxonomy, evolution and content of the families Helicancylidae and Acrioceratidae.

2. Geological setting

The studied material was collected from the Aptian of the Cassis - Roquefort-la-Bédoule area (Bouches-du-Rhône, France; Fig. 1), known as the unit-stratotype of the former Bedoulian Substage (Moullade et al. 2000). This reference succession was deposited in the South Provençal Basin of the northern margin of the Tethys. A limestone-marl succession of late Early to Late Aptian age crops out in the Comte and La Marcouline quarries (Conte 1995; Moullade et al. 2004, 2005) near the Cassis railway station (N 43°14’12.35’’/E 5°33’49.73’’).

The Roch’s types of *T. rochi* originate from an unknown level of the Comte Quarry section (Moullade et al. 2000) that span the upper Lower Aptian. Additional topotypes collected by G. Conte originate from the upper part of the Comte Quarry section dated to the upper *D. furcata* Zone *sensu* Ropolo et al. (2006). Another topotype (MPP.B-EM.64) was collected *in situ* by one of us (C.F.) from bed 178 of this section in as-

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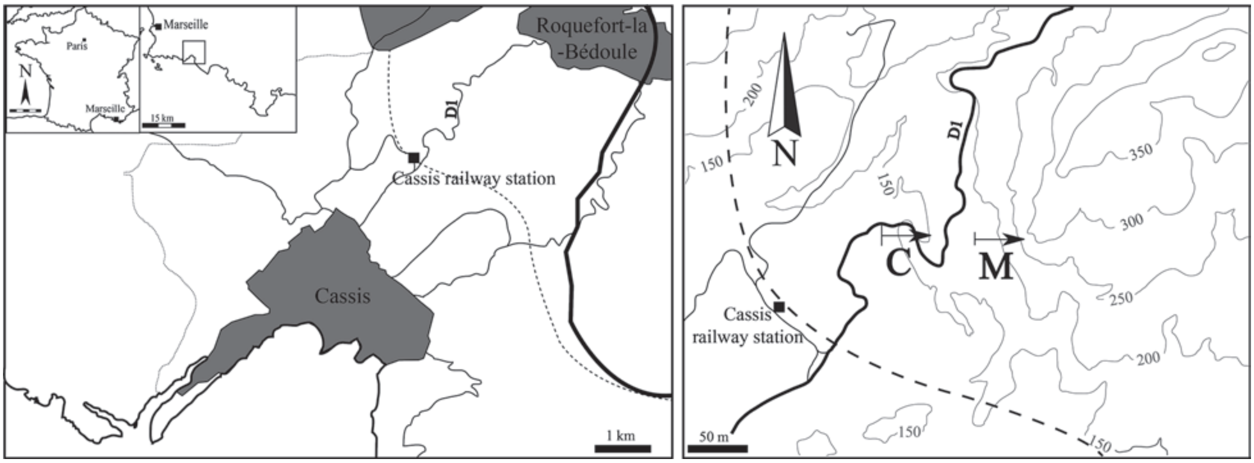

Fig. 1. Location of the Comte (C) and La Marcouline (M) Quarry sections (Cassis, Bouches-du-Rhône, France); modified after Moullade et al. (2004).

sociation with *Dufrenoyia* of the *dufrenoyi* (d’Orbigny, 1841) group.

The type specimen of *Brainaella marcoulinense* gen. nov. sp. nov. originates from bed M-52 of the La Marcouline Quarry section first described by Moullade et al. (2004, fig. 4), to which the reader is referred. The ammonite fauna of bed M-52 is dominated by the poorly understood *Ammonites flexisulcatus* d’Orbigny, 1841, now referred to as the desmoceratid *Caseyella* Cantú Chapa, 1976 by Moreno-Bedmar et al. (2013). Stratigraphically significant species that occur in the assemblage also include *Epicheloniceras waageni* (Anthula, 1900), *E. tschernyschewi* (Sinzow, 1906), *Pseudoaustraliceras ramososeptatum* (Anthula, 1900), and *Colombiceras tobleri* (Jacob & Tobler, 1906), which fall in the upper part of the *Epicheloniceras martini* Zone *sensu* Ropolo et al. (2008).

3. Systematic palaeontology

The nomenclature of the coiling and the naming of the parts of the heteromorphic shell follow the terminology of Vašíček (1972) and Aguirre-Urreta (1986).

Order Ammonoidea Zittel, 1884
Suborder Ancyloceratina Wiedmann, 1966
Superfamily Ancyloceratoidea Gill, 1871
Family Acrioceratidae Vermeulen, 2004

Remarks: Examination of the type specimen of *Ptychoceras aequicostatus* Gabb, 1864, kept in the collections of the Museum of Paleontology of the University of California at Berkeley (UCMP cat. n° 12090), shows that this species is based on a worn fragment of a flexus that lacks any valuable diagnostic features (Fig. 2a, b). It should be noted that additional material (fragments of a helix and a proversum) was subsequently reported in the type material of *P. aequicostatus* by Gabb (1869), for which the genus *Helicancylus* was introduced. According to the I.C.Z.N. rules, the subsequent emendation of Gabb (1869) is abusive. For the reasons given above and in agreement with Vermeulen (2010), albeit for different reasons, we consider that *P. aequicostatus* is a *nomen dubium,* and subsequently that the genus *Helicancylus* Gabb, 1869 and the family Helicancylidae that it typifies are *nomina nuda*. Therefore, we use Acrioceratidae as a substitute for Helicancylidae, since recent authors (Bert 2009; Vermeulen 2010; Bulot in Vincent et al. 2010) agree that these two families share the same content.

Genus *Toxoceratoides* Spath, 1924

Type species: *Toxoceras royerianum* d’Orbigny, 1842, by subsequent designation of Casey (1961: 77-78); ICZN opinion pending. In the original designation of Spath (1924: 78, footnote 6), reference was made to a specimen of *T. royeri* attributed with doubt by v. Koenen (1902, pl. 37, figs. 7-8) to d’Orbigny’s species. Identity of this specimen remains doubtful.

Discussion: Busnardo (in Gauthier et al. 2006: 143) stated that the designation of a neotype by Casey (1961: 80) is invalid since one of d’Orbigny’s syntypes survived. However, Busnardo (in Gauthier et al. 2006: 143) clearly stated that the pyritic type series of *T. royerianus* from the d’Orbigny collection were destroyed by oxidation and that their lectotype is based on a specimen from the Cornuel collection originally labelled *Ancyloceras matheroni* d’Orbigny.

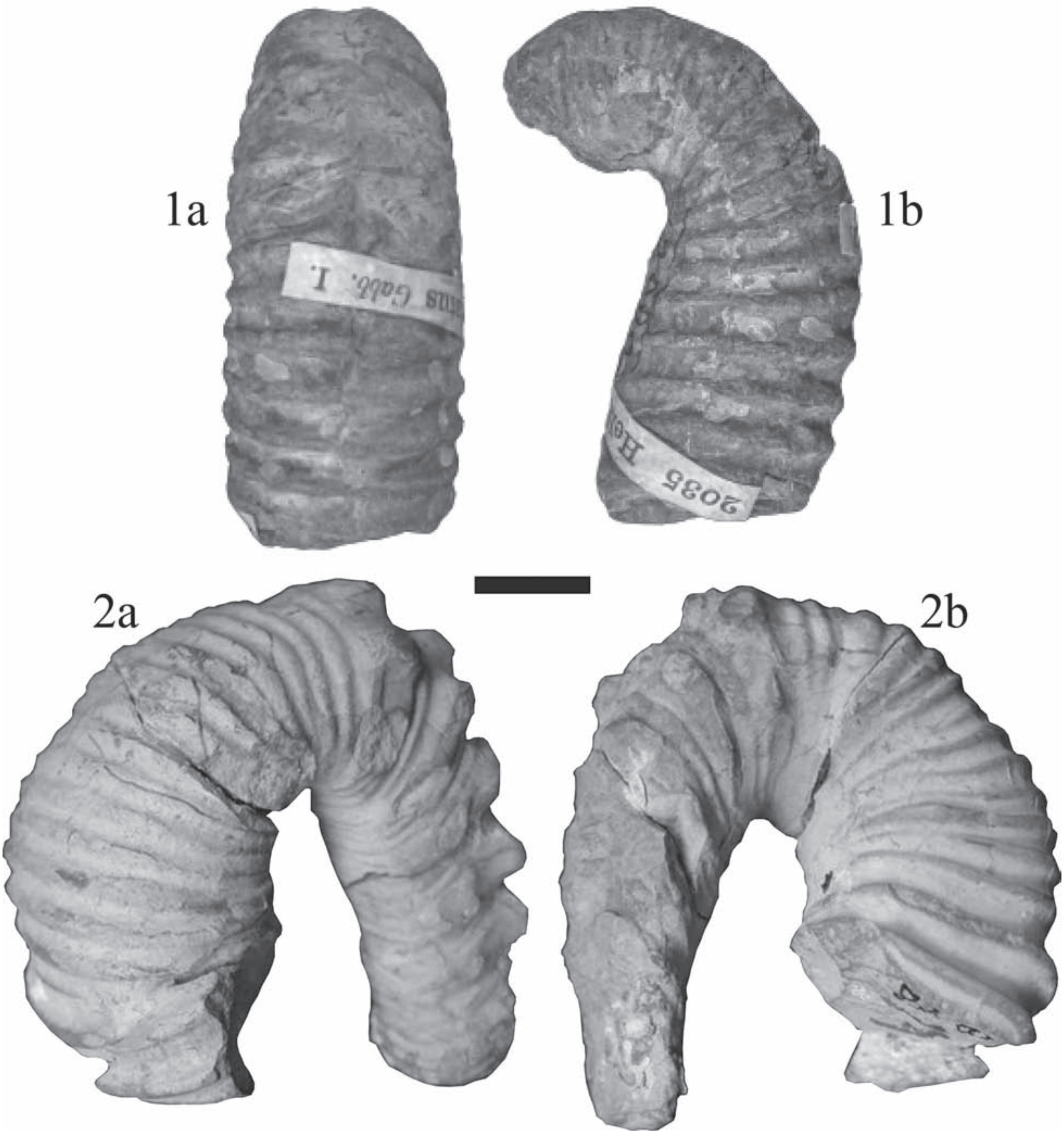

Fig. 2. a-b – Holotype of *Ptychoceras aequicostatus* Gabb, 1864 (UCMP cat. n° 12090) from an unknown Aptian horizon of the North fork of Cottonwood Creek, Alderson's Gulch (Shasta County, California, USA) (photograph by Dave Strauss, Berkeley). **c-d** – Lectotype of *Toxoceratoides rochi* Casey, 1961 (UJF-ID.78) from the Lower Aptian of Cassis (photograph by Emmanuel Robert, Lyon). Scale bar equals 10 mm.

Hence, according to Klein et al. (2007), the designation of the lectotype of *T. royerianus* is invalid according to article 74.1. of the ICZN, because the lectotype designated by Busnardo (in Gauthier et al. 2006) cannot be considered a syntype. In any case, the specimens illustrated by Casey (1961, text-fig. 30) and Busnardo (in Gauthier et al. 2006, pl. 27, figs. 3, 4) are conspecific.

Due to the taxonomic problems discussed above, *Toxoceratoides* has been applied in widely different ways (i.e. expanded genus conception, supposed worldwide distribution) in the literature (Klinger & Kennedy 1977; Aguirre-Urreta 1986). To address the problems of the specific content of the genus would be far beyond the scope of the present paper. In any case, there is a general agreement that the poorly known species *T. rochi* Casey, 1961 described below belongs to *Toxoceratoides* (see Klein et al. 2007).

Toxoceratoides rochi Casey, 1961
Figs. 2c, d, 3a-k, 4a-c

1927 *Ancyloceras royerianum* (d'Orbigny). – Roch, p. 30, pl. 1, fig. 4.
1933 *Ancyloceras Royerianus* (d'Orbigny). – Bončev, p. 246 (32), pl. 5, fig. 13.
1961 *Toxoceratoides rochi* Casey, p. 81.
1981 *Toxoceratoides* cf. *rochi* Casey. – Kakabadze, pl. 13, fig. 2.
1989 *Toxoceratoides* cf. *royerianus* (d'Orbigny). – Conte, p. 49, fig. 7 on p. 50.
1990 *Toxoceratoides royerianus* (d'Orbigny). – Thieuloy, pl. 1, fig. 1.
1999 *Toxoceratoides* aff. *royerianus* (d'Orbigny). – Conte, p. 13, fig. 3a, b.
2001 *Toxoceratoides stefanescui* n. sp. Avram in Avram et al., p. 18, pl. 1, figs. 6a, b, 7.
2002 *Toxoceratoides stefanescui* Avram. – Avram, p. 26, pl. 1, figs. 16a, b, 17 (= Avram et al. 2001, pl. 1, figs. 6a, b, 7).
2005 *Toxoceratoides* cf. *rochi* Casey. – Kakabadze in Kotetishvili et al., p. 364, pl. 80, fig. 2.
2006 *Ancyloceras mantelli* Casey. – Aly, p. 114, pl. 6, fig. 3a, b.
2007 *Toxoceratoides royerianus* (d'Orbigny). – Lebrun, p. 168, fig. 6.66.
2012 *Toxoceratoides royerianus* (d'Orbigny). – Moreno-Bedmar et al., figs. 4H, 7M.
2013 *Toxoceratoides royerianus* (d'Orbigny). – Delanoy et al., pl. 4, figs. P, R.

Type: Casey (1961) introduced *Toxoceratoides rochi*, without formal diagnosis and holotype designation, for two specimens from the upper Lower Aptian of Roquefort-la-Bédoule, originally described by Roch (1927) and identified as *T. royerianus*. The lectotype, herein designated, is the specimen of *Ancyloceras royerianum* (d'Orbigny), illustrated by Roch (1927, pl. 1, fig. 4). It is deposited in the Grenoble University collection (UJF-ID.78) and here refigured (Fig. 2c, d).

Diagnosis: Medium-sized *Toxoceratoides* with gracile spire, weakly curved proversum and a short retroversum. Early ontogeny unknown. Whorl cross section suboval with flattened flanks on the proversum. Coarse ornamentation with typical stout primary trituberculate ribs. One or two secondary ribs between primaries. Prominent flattened ventral tubercles on the upper part of the proversum that take the form of elongated clavi. Ribs simple and smooth on the retroversum, rarely bifurcated at the dorsal margin. Suture line is unknown.

Material: Besides the lectotype, the studied material includes eight topotypes (MPP-CT66.B14A, MPP-CT66.B14B, MPP-CT.TN41, MPP-B150.66t, MPP-B15.1, MPP-B224) from the Conte collection and MPP.B-EM.64 from the Frau collection). Specimens MPP-CF03/03.1, MPP-CF03/03.2 and MPP-CF03/03.3 were collected by one of us (L.G.B.) from bed CF-03/03 of the Col de Flachères section (Hautes-Alpes, France) described in the seminal work of Dauphin (2002). All the specimens discussed above are housed in the Musée de Paléontologie de Provence (Aix-Marseille University).

Description: Among the material at our disposal, the following specimens illustrate the ontogeny and variability of the species:

Specimen MPP-CT66.B14B (Fig. 3a-c) is a complete body chamber with the upper part of the proversum. On the proversum, the ornamentation is typical of *Toxoceratoides* with main trituberculate ribs, and single intercalatories that cross the venter. The dorsal and lateral tubercles are punctiform, while the ventral ones are stout and flattened along the axis of the coil. The ornamentation is composed of dense, simple, smooth ribs that cross the venter and extend from the base of the flexus to the end of the body chamber. Some ribs bifurcate at the dorsal margin on the flexus. The whorl cross section of the retroversum is suboval.

Specimen MPP-B150.66t (Fig. 3g) exhibits the ornamentation of the lower part of the proversum. At this growth stage, tubercles are always slender, and there are two intercalatories between the trituberculate primaries.

Specimen MPP-B15.1 (Fig. 3j, k) differs by its larger size. The stout ornamental stage appears at an earlier growth stage than in the previous specimen, and ends in the middle part of the flexus. The ribs on the retroversum are coarser and more widely spaced; the flanks are flattened, producing a slightly subrectangular whorl cross section that matches the lectotype.

Specimen MPP.B-EM.64 (Fig. 3f) exhibits the general toxoceratid morphology of the shell. The innermost whorl of the spire is not preserved. The ornamentation of the phragmocone is not visible due to its limonitic preservation. The ornamentation of the upper part of the proversum matches that of the other studied specimens with prominent flattened ventral tubercles.

The three specimens from Col de Flachères illustrated on Fig. 4 match well the topotype specimens described above.

Fig. 3. *Toxoceratoides rochi* Casey, 1961 from the upper Lower Aptian of the Comte Quarry (Cassis, Bouches-du-Rhône, France): **a-c** – MPP-CT66.B14B, incomplete body chamber; **d-e** – MPP-CT66.B14A, incomplete body chamber; **f** – MPP-B-EM.64, incomplete phragmocone; **g** – MPP-B150.66t, incomplete proversum; **h** – MPP-B224, incomplete body chamber; **i** – MPP-CT.TN41, incomplete body chamber; **j-k** – MPP-B15.1, incomplete proversum and body chamber. All specimens are plaster casts of Conte's specimens except MPP-B-EM.64. Scale bar equals 10 mm.

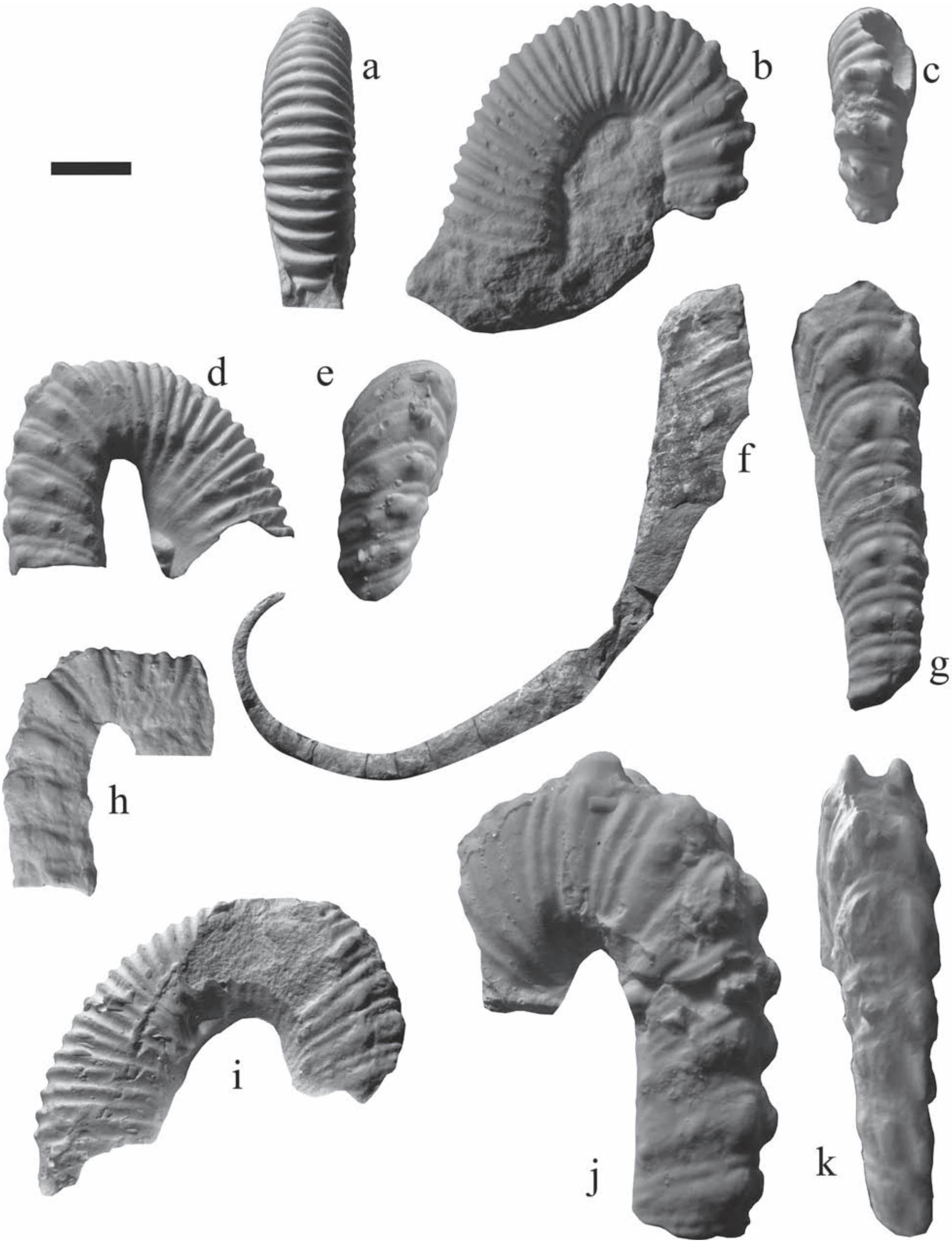

Fig. 3.

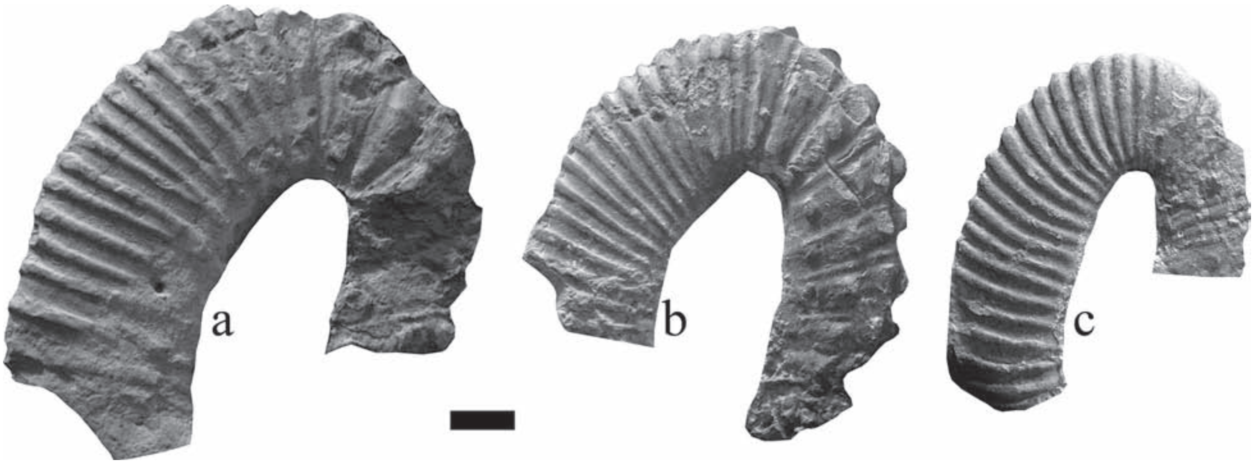

Fig. 4. *Toxoceratoides rochi* Casey, 1961 from the upper Lower Aptian of Col de Flachères (Hautes-Alpes, France): three incomplete body chamber **a** – MPP-CF03/03.1; **b** – MPP- CF03/03.2; **c** – MPP-CF03/03.3. Scale bar equals 10 mm.

These specimens also exhibit three types of ornamentation on the retroversum with (Fig. 4a) thick straight ribs that bifurcate on the dorsal margin, (Fig. 4b) thick, straight and simple ribs and (Fig. 4c) smooth, slightly rectiradiate simple ribs.

Discussion: All the specimens listed in the synonymy fall within the range of variability of the species as described above. The specimen illustrated by Moreno-Bedmar et al. (2012, fig. 7m), characterized by a slender morphology and ornamentation, represent a gracile morphology of the species.

The type material of *Toxoceratoides stefanescui* is almost identical to the stouter and more robust specimens of *T. rochi*, including the lectotype, from Cassis - Roquefort-la-Bédoule and Col de Flachères. According to art. 23 of the ICZN, *T. stefanescui* is considered a junior synonym of *T. rochi*.

Toxoceratoides rochi is easily distinguishable from *T. royerianus* because of its peculiar ornamentation on the proversum with prominent and flattened tubercles. *T. royerianus* also differs by the regular bifurcation of the ribs along the dorsal margin of the retroversum. With the exception of Kakabadze (1981), these differences were overlooked in the literature as shown by the synonymy. On the basis of the morphological features and respective stratigraphic position (see Bulot et al., in press), we assume a direct ancestry of *T. rochi* from *T. royerianus.*

Occurrence: According to Roch (1927), G. Conte's manuscript notes and our own sampling, *T. rochi* occurs in the latest Early Aptian *Dufrenoyia furcata* Zone at its type locality. This age is also consistent with the record from the Col de Flachères, where the specimens co-occur with numerous *Dufrenoyia dufrenoyi* (d'Orbigny, 1841) a few centimetres above the NC2 marker bed *sensu* Dauphin (2002). The specimens from Spain are derived from the *D. deshayesi* and *D. furcata* zones (Moreno-Bedmar et al. 2012; Delanoy et al. 2013). Occurrence of *T. rochi* in the *D. deshayesi* Zone of southeast France is also supported by the specimen of Conte (1999). The material from the "Gargas marls" of southeast France (Conte 1989; Thieuloy 1999; Lebrun 2007), Caucasus (Kakabadze 1981, 2005), Romania (Avram 2002) and Egypt (Aly 2006) were also reported from the upper Lower Aptian. This confirms the increasing dispersal of Aptian ammonite faunas through the Mediterran-Caucasian Subrealm *sensu* Westermann (2000) (see discussion in Lehmann et al. 2015).

Genus *Brainaella* nov.

Etymology: Named in honour of the Braina family, and especially in honour of Hélène Braina, who has so often supported her son (C.F.) during his fieldtrips.

Type species: *Brainaella marcoulinense* nov. sp., by monotypy.

Diagnosis: Small heteromorph ammonite with initial whorls helically coiled, followed by a short straight proversum and recurved retroversum. Helix is large in proportion to the diameter. Whorl section of proversum and retroversum compressed, suboval, wider than high. Ornamentation of the proversum composed of irregular simple, bi- or trituberculated ribs. Increase in thickening of lateral and ventro-lateral tubercles on the upper part of the proversum. Tuberculated ribs disappear abruptly on the flexus of the retroversum, replaced by coarse, non-tuberculate, straight ribs that cross the venter. Suture line is unknown.

Discussion: As pointed out by Kakabadze (2004), Vermeulen (2006), and Bert et al. (2009), helicoidally initial whorls appear in various Barremian and Aptian families, such as the Heteroceratidae Spath, 1922, Ancyloceratidae Gill, 1871, and Hemihoplitidae Spath, 1924.

Fig. 5. Holotype of *Brainaella marcoulinense* gen. et sp. nov. (MPP-B-LM.36 – Frau collection), from the lower Upper Aptian of La Marcouline Quarry (Cassis, Bouches-du-Rhône, France). The specimen was coated with ammonium chloride prior to photography. Scale bar equals 10 mm.

Small-sized *Heteroceras* d'Orbigny, 1850 of Late Barremian age, such as *H. baylei* (Reynès, 1876), differ from *Brainaella* gen. nov. in their non-tuberculate and straight ribs.

Some species of *Kutatissites* Kakabadzé, 1970 share with *Brainaella* n. gen. a tripartite coiling with an initial helix, but the former genus differs in its much larger adult size, helicoidal coiling, and presence of strong tubercles throughout its ontogeny.

Mikhailova & Baraboshkin (2002) erected *Koeneniceras* for miniature heteromorphs with a short, initial helix from the Lower Aptian of the Russian Platform and North Germany. This taxon is easily distinguishable by its very small adult size and crioconic coiling.

Among the Hemihoplitidae, *Imerites* Rouchadzé, 1933 is easily distinguishable by its crioheterocone to imericone coiling, with fibulate and bituberculate ribs (Bert et al. 2009; Vermeulen & Lepinay 2010).

Finally, *Brainaella* gen. nov. is included in the Acrioceratidae since it shares the tripartite coiling and small adult size combined with simplified ornamentation on the retroversum that characterizes this family of heteromorphic ammonites.

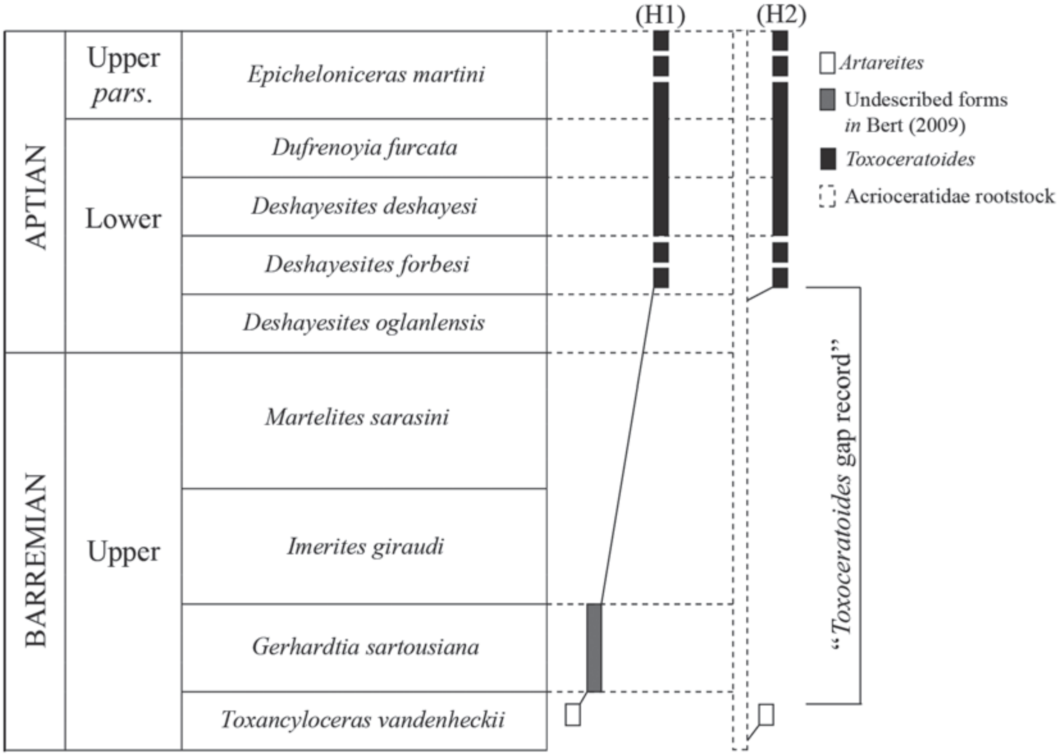

Fig. 6. Biostratigraphic subdivisions of the Late Barremian and Aptian (*pars*) interval and phyletic hypothesis of the origin of the Acrioceratidae *Toxoceratoides* Spath. Ammonite zones after Reboulet et al. (2014).

Brainaella marcoulinense gen. nov. et sp. nov.
Fig. 5

Etymology: Name refers to the La Marcouline Quarry (Cassis, Bouches-du-Rhône, France), the type locality.

Holotype: The specimen MPP-B-LM.36 from La Marcouline Quarry (Cassis, France), deposited in the Frau collection at the Musée de Paléontologie de Provence (Aix-Marseille Université). It is illustrated here (Fig. 5).

Diagnosis: As for the genus.

Description: The holotype is a small-sized adult (total length ~58 mm) with a complete tripartite shell (helix, proversum and retroversum). The helix is tightly in contact and proportionally large compared to the size of the shell (about 32% of the total diameter). The proversum is short and its width gradually increases towards the flexus of the retroversum. The retroversum is open with a relatively short and marked return that gives a general labeceratid aspect to the coiling. The adult body chamber comprises the retroversum and the upper part of the proversum. Throughout the adult ontogeny, the whorl cross section is rounded, suboval, much higher than wide, with convex flanks.

At least three growth stages can be recognized based on ornamentation:

(*i*) the first stage identified is composed of single, widely spaced, non-tuberculate ribs. The ventral area of the helix is worn and the ornamentation cannot be observed in this region;

(*ii*) at the end of the helix and on the proversum, the ornamentation becomes progressively irregular with bi- and trituberculate ribs. All ribs are equal, remain widely spaced, and tend to bend forward and weaken on the upper part of the flank. If present, the dorsal and lateral tubercles are weaker than the prominent ventral tubercles. The latter are pinched in the direction of coiling;

(*iii*) the adult stage begins at the flexus of the retroversum, and the ornamentation is composed of single, equal and straight non-tuberculate ribs. The suture line could not be studied but the last suture seems to end at the upper part of the proversum.

Discussion: *B. marcoulinense* sp. nov. has unique characters among the Aptian Acrioceratidae. The closest morphological similarities are with species that are commonly included in *Toxoceratoides*. The general ornamental features, especially the ribbing of the proversum of *Brainaella marcoulinense* sp. nov., are very similar to those of *T. rochi*. The latter differs in its higher rib density with intercalatories, and a more opened and slender toxoceratid coiling. *T. royerianus* is easily distinguishable from *Brainaella marcoulinense* nov. sp. by the regular ornament of narrow and sharps ribs branching in two or three from dorsal tubercles, with intercalatories. The rib density is higher throughout ontogeny and even more pronounced on the retroversum.

Among the upper Aptian Acrioceratidae, *Toxoceratoides*? *haughtoni* Klinger & Kennedy, 1977 and *T. nagerai* Aguirre-Urreta, 1986 show superficial similarities with *Brainaella marcoulinense* sp. nov. Whereas *T.*? *haughtoni* is easily distinguishable by its peculiar proversum and retroversum ornamentation that consists of alternation of fine, non-tuberculate, and strong looped ribs with massive ventrolateral and ventral tubercles, *T. nagerai* is marked by a feebly curved proversum and recurved retroversum, similar to those of *Brainaella marcoulinense* sp. nov., but its ornamentation of dense and fine intercalatories is highly distinctive.

The origin of *Brainaella marcoulinense* sp. nov. remains problematic due to the fragmented material of most acrioceratid species. *Brainaella marcoulinense* sp. nov. shares superficial ornamental and morphological features with *T. rochi*. In this regard, Casey (1960) previously suggested that the genus *Toxoceratoides* could possess a helix in the innermost whorl, but until now this character has still not been illustrated in the literature yet. It should be noted that the specimen MPP.B-EM.64 of *T. rochi* shows a very opened spire, suggesting that the innermost whorl is certainly reduced and not helicoidally coiled. Thus, due to its toxoceratid-like features, *Brainaella marcoulinense* sp. nov. can be considered an offshoot of the *Toxoceratoides* rootstock, but a direct link between *Brainaella marcoulinense* sp. nov. and *T. rochi* is hard to establish.

Occurrence: Bed M-52 of the La Marcouline Quarry section (Moullade et al. 2004), Upper Aptian, upper part of the *E. martini* Zone *sensu* Ropolo et al. (2008). It is currently known only from the South Provençal Basin of southern France.

4. Comments on the evolution of Acrioceratidae

Our extensive collecting in the Barremian-Aptian succession of the Cassis - Roquefort-la-Bédoule unit-stratotype area reveals the absence of Acrioceratidae between the *Martelites sarasini* Zone (uppermost Barremian) to the lower part of the *Deshayesites forbesi* Zone (Lower Aptian) *sensu* Frau et al. (2015). In comparison, the late Early Aptian *Dufrenoyia furcata* Zone to the early Late Aptian *Epicheloniceras martini* Zone is a period of pronounced diversification among the Acrioceratidae, already suggested by Conte (1995) and supported by the occurrence of *Brainaella marcoulinense* gen. et sp. nov. in association with new and poorly known forms of *Toxoceratoides* Spath, 1924 and *Tonohamites* Spath, 1924, which will be described elsewhere.

This observation challenges the linear evolution of the Acrioceratidae, as accepted in the literature. Detailed analysis of all available data shows that the Acrioceratidae include two stratigraphically distinct groups of taxa. From the Late Hauterivian to the early Late Barremian, *Acrioceras* Hyatt, 1894 – *Dissimilites* Sarkar, 1955 – *Artareites* Bert, 2009 form a fairly well-documented phyletic lineage (Bert 2009 with references therein). The late Early Aptian *Toxo-*

ceratoides is assumed to be the rootstock of all other Aptian acrioceratids, such as *Tonohamites* Spath, 1924 and *Hamiticeras* Anderson, 1938 (Bert 2009; Vermeulen 2010). A remarkable morphological convergence is observed between *Artareites* and *Toxoceratoides*, but potential forms that could link both lineages are not documented. In this respect, Bert (2009: 162) reported *Toxoceratoides* from the Late Barremian *T. vandenheckeii* and *G. sartousiana* zones of southeast France, but the relevant specimens are still to be described. Similarly, there is no record of acrioceratids in the uppermost Barremian and lowermost Aptian of Spain (Moreno-Bedmar et al. 2010), Italy (Lukeneder & Lukeneder 2014), England (Casey 1960), and Russia (Mikhailova & Baraboshkin 2002). Occurrences reported from Romania by Avram (2002) are based on fragmentary and poorly dated specimens. As already pointed out by Company et al. (2008: 21), the specimens from Morocco described by Witam (1998, pl. 5, figs. 2-6, pl. 6, figs. 1-4) as *Toxoceratoides* sp. belong to *Ancylezeiceras* of the *breistrofferi* (Sarkar, 1955) group. It is now established that the age of these specimens is of Late Barremian and not Early Aptian as originally stated by Witam (1998). This view is supported by a new collection made by one of us (L.G.B.) at Assaka and Tamanar (Morocco).

It is worth noting that the Late Barremian to Early Aptian interval is marked by severe trophic modifications, illustrated by widely distributed organic-rich deposits, platform drownings and the microfaunas crisis in the Tethyan Realm and adjacent parts of the Boreal Realm (Föllmi 2012). In this regard, recurrent and widespread anoxia is frequently invoked as a primary driver of moderate mass extinctions in the mid-Cretaceous (Elder 1989; Batt 1993; Kauffman & Hart 1995). In southern France, the Late Barremian platform drowning occurs at the boundary between the *G. sartousiana* and *I. giraudi* zones, and is overlain by organic-rich deposits reported in the *M. sarasini* Zone (Masse & Fenerci-Masse 2011; Frau et al. 2016). According to Machhour et al. (1998), this drowning succession is marked by pronounced dysaerobic bottom-water conditions. The lack of acrioceratid forms across the Barremian/Aptian boundary interval may be connected to severe anoxia. In any case, the gap in the record of Acrioceratidae exemplifies the concept of a "ghost lineage" well. It is actually impossible to determine if the ancestry of *Toxoceratoides* lies directly in the Late Barremian *Artareites* and/or its closely allied undescribed forms (hypothesis 1 = H1 on Fig. 6), or if there is no phyletic link with the *Dissimilites*-*Artareites* lineage and that *Toxoceratoides* resulted from iterative evolution among the acrioceratids stock (hypothesis 2 = H2 on Fig. 6).

Hypothesis 1 was accepted by Lukeneder & Lukeneder (2014, fig. 6), who assumed an evolution that took place in the Mediterranean-Caucasian Subrealm of the Tethyan Realm *sensu* Westermann (2000). On the contrary, in hypothesis 2, the early evolution of *Toxoceratoides* could have taken place outside the Mediterranean-Caucasian Subrealm as suggested by Bert (2009: 152). According to the author, *Toxoceratoides saulae* Murphy, 1975, from the uppermost Barremian of the Pacific Coast of Northern America would be the oldest representative of the genus that derivates from endemic species of *Artareites* of the *greeni* (Murphy, 1975) group. In our view, the Pacific Coast group of species differs from the Mediterranean-Caucasian *Artareites*, i.e. *A. landiorum* Bert, 2009 and its allied species (see discussion in Vermeulen 2010), in their medium size, subrectangular to subptrapezoidal whorl section, flat venter on the upper proversum, more or less marked ventral furrow on the flexus, smaller number of lateral tubercles on the proversum, and more prominent and rounded peri-ventral tubercles covering two to four ribs. It should also be noted that the general morphology and inner whorls of the Pacific Coast species are unknown and their age is still poorly constrained. Thus, a direct link between *Artareites* and *Toxoceratoides* is still not supported by palaeontological evidence. As a consequence, the phyletic relationship between the Late Barremian and Early Aptian Acrioceratidae is far less clear than currently assumed in the literature.

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