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The Barremian heteromorph ammonite *Dissimilites* from northern Italy: Taxonomy and evolutionary implications

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A new acrioceratid ammonite, *Dissimilites intermedius* sp. nov., from the Barremian (Lower Cretaceous) of the Puez area (Dolomites, northern Italy) is described. *Dissimilites intermedius* sp. nov. is an intermediate form between *D. dissimilis* and *D. trinodosum*. The new species combines the ribbing style of *D. dissimilis* (bifurcating with intercalating single ribs) with the tuberculation style of *D. trinodosum* (trituberculation on entire shell). The shallow-helical spire, entirely comprising single ribs intercalated by trituberculated main ribs, is similar to the one of the assumed ancestor *Acrioceras*, whereas the increasing curvature of the younger forms resembles similar patterns observed in the descendant *Toxoceratoides*. These characters support the hypothesis of a direct evolutionary lineage from *Acrioceras* via *Dissimilites* to *Toxoceratoides*. *D. intermedius* sp. nov. ranges from the upper Lower Barremian (*Moutoniceras moutonianum* Zone) to the lower Upper Barremian (*Toxancyloceras vandenheckii* Zone). The new species allows to better understand the evolution of the genus *Dissimilites*. The genus appears within the *Nicklesia pulchella* Zone represented by *D. duboise*, which most likely evolved into *D. dissimilis*. In the *Kotetishvilia compressissima* Zone, two morphological forms developed: smaller forms very similar to *Acrioceras* and forms with very long shaft and juvenile spire like in *D. intermedius* sp. nov. The latter most likely gave rise to *D. subalternatus* and *D. trinodosum* in the *M. moutonianum* Zone, forms which were probably ancestral to the genus *Toxoceratoides*.

Key words: Ammonoidea, Acrioceratidae, *Dissimilites*, Barremian, Cretaceous, Alps, Italy.

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Introduction

The ammonoids from the Lower Cretaceous sediments in the Puez area (Dolomites, South Tyrol, North Italy) have been mostly utilized so far for the stratigraphical purposes (Lukeneder and Aspmaier 2006; Lukeneder 2010, 2011, 2012b), a task that has been recently summarized by Lukeneder (2012b). The present paper provides a systematic revision of one of the stratigraphically important forms, the heteromorph acrioceratid ammonite *Dissimilites*. All known occurrences of *Dissimilites* are listed and discussed and a reconstruction of its evolution is proposed.

Institutional abbreviations.—NHMW, Natural History Museum Vienna, Austria; STMN, South Tyrol Museum of Nature Sciences (PZO and CP inventory numbers), Bozen, Italy.

Other abbreviations.—CP, Col Puez; Dsp, spire diameter; Hf, whorl height at flexus; Hp1, whorl height at start of

proversum; Hp2, whorl height at end of proversum; Hr, max. whorl height of retroversum; ir, intercalatory ribs; L, max. length; Lp, proversum length; Lr, retroversum length; min Hsp, minimal whorl height of spire; mr, main ribs; P, Puez; Pp1, proversum part 1; Pp2, proversum part 2; Pp1b, proversum part 1 breadth; Pp2b, proversum part 2 breadth; sp, spines; Spb, spire breadth; α , angle of retroversum; β , angle formed by pro- and retroversum; γ , open angle on inner side of proversum; δ , angle at end of proversum; -x- marks position of main tuberculated ribs on spire and proversum and bifurcating ribs on retroversum in given rib-formulae; 1 or 2 shows value of intercalatories.

Material

The ammonite specimens discussed herein originate from the Puez locality (Dolomites; Fig. 1). The material collected

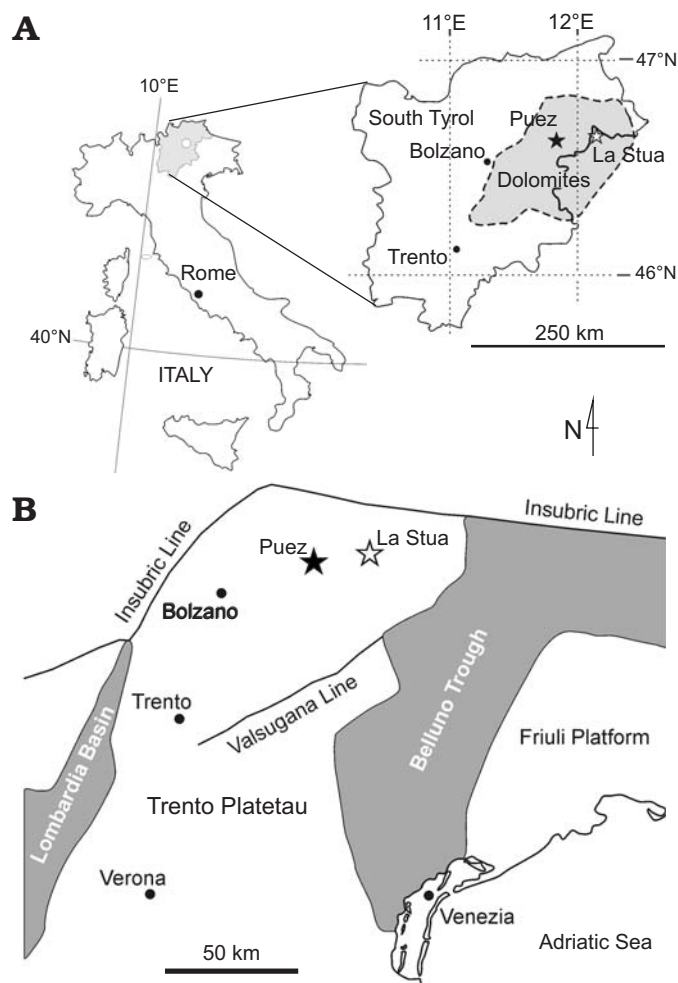


Fig. 1. Locality maps of the study area. **A.** Location of South Tyrol in northern Italy and Puez area (black star) and neighbouring La Stua section (white star) within the Dolomites. **B.** Position of the Puez and La Stua localities on the Trento Plateau.

by Christian Aspmair (Bozen, Italy) is stored in the STMN. The bed-by-bed collected material assembled by the authors is stored at the NHMW. Ammonites are moderately well preserved, mostly as compressed inner molds without shell. In total, fourteen specimens of *Dissimilites* have been examined (Figs. 2–4).

The entire Upper Hauterivian to Upper Barremian ammonite fauna from Puez consists of 44 genera in 17 families (Lukeneder 2012b). Acrioceratidae are represented by *Acrioceras* Hyatt, 1900 and *Dissimilites* Sarkar, 1954, Anycloceratidae by *Toxancyloceras* Delanoy, 2003 and *Audouliceras* Thomel, 1965, and Heteroceratidae by *Moutoniceras* Sarkar, 1954.

Geological setting and biostratigraphy

The ammonite-bearing outcrop at Puez is situated on the southern side of the Piz de Puez, Puez-Odle-Gardenaccia

Plateau in the Dolomites, northern Italy (Lukeneder 2010). During Early Cretaceous times the locality was situated in the northern part of the Trento Plateau. La Stua locality is located 20 km to the east of the Puez area (Stöhr 1993, 1994), in the eastern part of the Trento Plateau, geographically near the northern border of the Veneto district. During the Barremian, the Trento Plateau constituted a part of the so-called Adriatic Plate. The Adriatic Plate (also called Apulian Plate) of the South Alpine-Apennine Block was bordered by the Penninic Ocean (= Alpine Tethys) to the north and the Vardar Ocean to the south-east (Cecca 1998; Dercourt et al. 1993; Stampfli and Mosar 1999; Scotese 2001; Stampfli et al. 2002).

Lower Cretaceous sediments on the Trento Plateau are represented mostly by limestone, marly limestone, and marl. The Puez Formation in the Puez area comprises three members, i.e., from bottom to top, the Puez-Limestone, Puez-Redbed, and Puez-Marl Member (Lukeneder 2010). A detailed description of the geology and lithostratigraphy is given by Lukeneder (2010). Ammonites, including *Dissimilites*, derive from the lowermost part of the formation, the Puez-Limestone Member. An ammonite-based stratigraphical framework has recently been refined by Lukeneder (2012b).

During the late 19th and early 20th century, a rich cephalopod fauna was collected from Lower Cretaceous sediments from this area by Haug (1887, 1889), Hoernes (1876), Uhlig (1887), Rodighiero (1919), Reithofer (1928), and Pozzi (1993). Additionally, microfossils and ammonites were investigated from the “Alpe Puez” by Cita and Pasquaré (1959) and Cita (1965), who assumed a Hauterivian to Barremian age for the sediments outcropping in the Puez area. After these publications no further investigations were undertaken at the main locality of Puez, except for a few descriptive papers dealing with some small ammonoid faunas from different localities near Puez, most of all from La Stua (Baccelle and Lucchi-Garavello 1967; Stöhr 1993, 1994). The latter contributions compared the faunas from La Stua with the Puez ammonite faunas reported by Haug (1887, 1889) and Uhlig (1887). The most recent works on the Lower Cretaceous from this area were focused on stratigraphy (Lukeneder and Aspmair 2006), palaeoecology (Lukeneder 2008), lithostratigraphy (Lukeneder 2010, 2011), and ammonite biostratigraphy (Lukeneder 2012b).

In this paper we follow the ammonite zonation established by the Cretaceous Ammonite Working Group (Reboulet et al. 2009) which has been refined for the Puez area by Lukeneder (2012b). Assessing the evolutionary patterns of *Dissimilites* requires careful stratigraphic control. Therefore we found it necessary to add up-to-date definitions of the ammonite zones in order to indicate exact stratigraphic positions of occurrence and avoid confusion with former interpretations in earlier papers.

Nicklesia pulchella and *Kotetishvilia compressissima* zones.

—The *N. pulchella* Zone was defined by Lukeneder (2012a), ranging from the bottom of bed P1/105 up to the top of bed P1/111 (Fig. 5). New findings show that *M. moutonianum* goes down to bed P1/103, which means that the *N. pulchella*

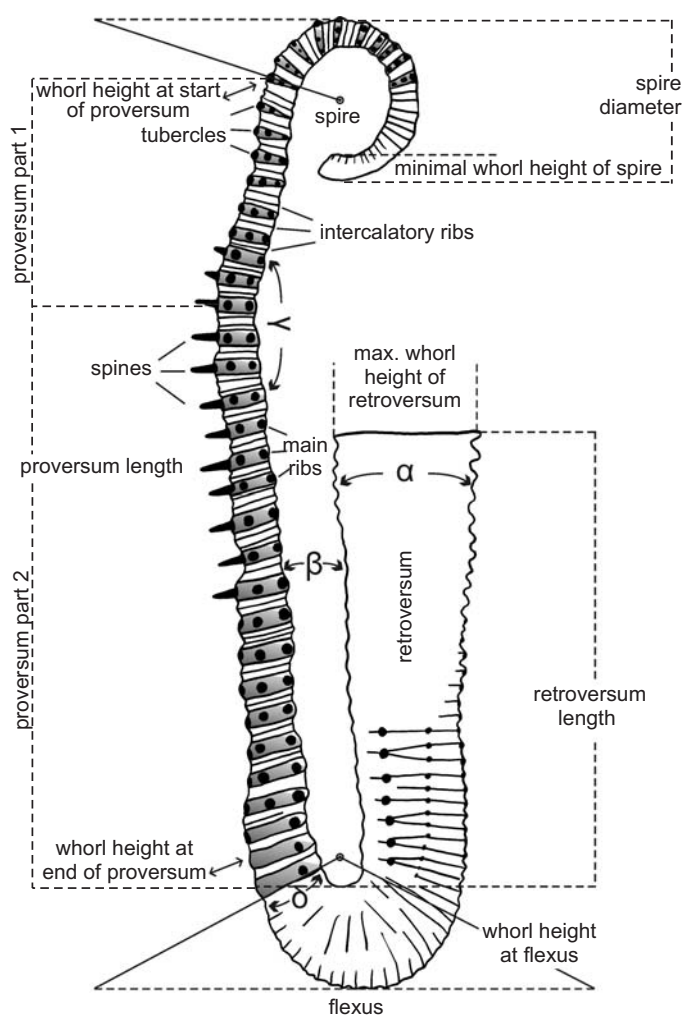


Fig. 2. Dimensions and terms used in *Dissimilites intermedius* sp. nov. from Puez, based on the holotype, the most entire specimen (NHMW 2012/0002/0001). α , angle of retroversum; β , angle formed by pro- and retroversum; γ , open angle on inner side of proversum; δ , angle at end of proversum.

and *K. compressissima* zones are even more condensed (i.e., 3.5 m) than it was interpreted so far. No members of Acrioceratidae (*Acrioceras*, *Dissimilites*) occur here. The *K. compressissima* Zone extends up to the top of bed P1/102.

***Moutoniceras moutonianum* Zone.**—The first occurrence of the index ammonite *M. moutonianum* has previously been thought to occur in bed P1/119 (Lukeneder 2012b). More recent findings show that *M. moutonianum* appears already in bed P1/103 associated with *Macroscaphites tirolensis*, extending therefore the *M. moutonianum* Zone into an interval from P1/103 up to P1/137. The Acrioceratidae occur with *Dissimilites intermedius* sp. nov. (bed P7/-3.4 m = bed P1/103, P7/-3.2 m = P1/105, P1 bed 110) and *Dissimilites trinodosum* (beds P1/130). Heteroceratidae are present at the base of the zone for the first time with the zonal index ammonite *M. moutonianum*. Macroscaphitidae occur with singletons of two species, i.e., *Costidiscus nodosostriatum* and *M. tirolensis*.

***Toxancyloceras vandenheckii* Zone.**—The *T. vandenheckii* Zone reaches from the bottom of bed P1/138 up to the top of bed P1/193 (Fig. 5). The appearance of the index ammonite *T. vandenheckii* in bed P1/138 marks the lower boundary of the *T. vandenheckii* Zone. The *T. vandenheckii* Zone is subdivided into the *T. vandenheckii* Subzone and the younger *B. barremense* Subzone. Acrioceratidae occur with *D. trinodosum* (beds P1/146, 169, 172). *Dissimilites* is accompanied by the family Ancyloceratidae with the zonal index species *T. vandenheckii* and *Toxancyloceras* sp. Within the family Leptoceratoididae, *Karsteniceras* sp. occurs in the lower part of the zone. Hamulinidae occur only in the lower part with *Hamulina* sp., *Anahamulina* cf. *uhligi* and *Anahamulina* sp., and with *Pychohamulina* cf. *acuaria* in both parts. The lower part yields members of *Duyeina* cf. *kleini* and *Duyeina* sp., whereas the upper part is characterized by the occurrence of the hamulinid member *Vasicekina* cf. *pernai*. Macroscaphitidae occur with a single specimen at the base, along with *Costidiscus* sp.

Systematic palaeontology

The authors follow the basic classification of Cretaceous Ammonoidea by Wright et al. (1996), Vermeulen (2004, 2006), and Klein et al. (2007).

Class Cephalopoda Cuvier, 1798

Order Ammonoidea Zittel, 1884

Suborder Ancyloceratina Wiedmann, 1966

Superfamily Ancyloceratoidea Gill, 1871

Family Acrioceratidae Vermeulen, 2004

Subfamily Helicancyclininae Hyatt, 1894

Genus *Dissimilites* Sarkar, 1954

Type species: *Hamites dissimilis* d'Orbigny, 1842 from Escragnoles, Lower Barremian, SE France; subsequent designation by Sarkar 1954: 619; lectotype designated by Busnardo in Gauthier 2006: pl. 20: 8.

Dissimilites intermedius sp. nov.

Figs. 3A–C, F, G, I, 4A–C, F, G, I.

1955 *Dissimilites* cf. *dissimilis* d'Orb. sp. (forme n° 1); Sarkar 1955: 138, pl. 4: 17.

1994 *Ancyloceras*; Costamoling and Costamoling 1994: text-fig. 93.

2006 *Acrioceras* (*Dissimilites*) *dissimilis* (d'Orbigny); Lukeneder and Aspmair 2006: pl. 6: 7.

2006 *Dissimilites* (*Dissimilites*) *trinodosum* (d'Orbigny); Lukeneder and Aspmair 2006: pl. 7: 1.

2012 *Dissimilites trinodosum*; Lukeneder 2012b: text-fig. 6B.

Etymology: After the intermediate morphology between *Dissimilites dissimilis* and *Dissimilites trinodosum*.

Type material: Holotype, the specimen NHMW 2012/0002/0001 (Figs. 3A, 4A), mainly flattened specimen, in partly limonitic sculpture mould, with perfectly preserved sculpture. Only one side of the holotype is available for observation and retains perfect conch outlines without any trace of fragmentation. The embryonal part of the shell and suture lines are not visible. The holotype is relatively large, which indicates the presence of the body chamber and thus an adult stage of

starting from the lateral to the ventro-lateral tubercles, instead of intercalatory ribs. The last main rib marks approximately the starting position of the body chamber.

Paratype NHMW 2011/0159/0027 (bed P1/110; Figs. 3G, 4G) shows the fibulation on the last 10–12 trituberculated main ribs on the proversum more precisely. Fibulation occurs between the lateral and ventro-lateral tubercles, instead of intercalatory ribbing. The same pattern is visible in paratypes NHMW 2012/0002/0002 (bed P7/ -3.2 m = P1/105; Figs. 3C, 4C) and NHMW 2012/0002/0003 (bed P7/ -3.2 m = P1/105; Figs. 3B, 4B).

The three paratypes are almost equal in size (65 mm, 82 mm, 83 mm) and adult (as indicated by the almost entire retroversum), but somewhat smaller than the holotype (131 mm); this size difference may reflect sexual dimorphism (e.g., micro- vs. macroconchs) or a decrease of elongation of the proversum in evolution, resulting in a shorter proversum shaft, since the holotype (bed P7/-3.4 m) was found approximately 20 cm below the paratypes (bed P7/-3.2 m). Paratypes show the typical curvature of the first part of the proversum and its shallow-helical whorl morphology, ornamented with trituberculated main ribs. All specimens exhibit this characteristic feature of the species: trituberculation from spire over flexus to final retroversum combined with irregular alternation of single and bifurcating ribs on retroversum, flat ventral side on flexus (Figs. 3I₃, 4I₃) and fibulation of main ribs on Pp2 of proversum. The paratypes show a comparable change in angle from the Pp1 to the Pp2, which starts from the flexus (most external point of flexus) in paratypes NHMW 2011/0159/0027 at 54 mm, in NHMW 2012/0002/0002 at 60 mm and in NHMW 2012/0002/0003 at 69 mm.

Flexus.—No thick main ribs occur. Ribbing is sharp and starts from 5–6 less pronounced, elongated tubercles to clavae from the umbilical region. Ribs bifurcate from the umbilical tubercles or at the mid flank from small, tiny tubercles. The ribs are still trituberculated at this point. Umbilical and ventro-lateral tubercles are bigger than lateral tubercles. Lateral tubercles occur on mid flank on every branch of the bifurcating ribs. A shallow, almost smooth area occurs on the venter throughout the flexus (Figs. 3I₃, 4I₃). The flexus shows a maximum whorl height of 13 mm. Fine ribs cross the dorsal area as described for the proversum. As noted above, all tubercles give rise to tiny spines, which has been proven by computer tomography (Lukeneder 2012a).

Retroversum.—The retroversum opens from the proversum at an angle β of approx. 4° and shows a maximum length of 78 mm (Fig. 2; see Table 1). The distance between pro- and retroversum is the same as the whorl height of the proversum or half the retroversum whorl-height. Shell height increases by α 14–15° up to the aperture, ending with a peristome. Ribbing is characteristic for the new species. Ribs are sharp and radial. Ribs bifurcate from umbilical tubercles and cross the venter without interruption. Bifurcating ribs are intercalated irregularly by straight single ribs also crossing the venter and showing the same thickness. All ribs on the retroversum

(body chamber) show trituberculation. The umbo-lateral tubercle is the most prominent one, followed by a smaller ventro-lateral tubercle and by the tiny lateral tuberculation. The lateral tuberculation is situated at approximately two-thirds of the flanks height. The position is the same as on the anterior flexus. The aperture (peristome) is marked by a collared last rib. The dorsal area shows the same ribbing as the proversum and flexus, with fine ribbing starting from dorso-lateral tubercles or at the umbilical region, crossing the dorsal area without interruption. A single dorsal rib starts from each tubercle and is intercalated by 2 single short ribs.

Remarks.—The newly described species, *Dissimilites intermedius* sp. nov., differs from all other descendant species of the genus by its unique combination of tuberculation and ribbing style, i.e., the trituberculation on bifurcate ribs and intercalatory ribs throughout the entire shell.

The type material (20 specimens) of *Dissimilites dissimilis* derives from the collection of d'Orbigny (1842). D'Orbigny's (1842: 529, pl. 130: 4–7) syntypes of *Hamites dissimilis* were collected from Lower Barremian of Escagnolles, SE France. Busnardo (2006) revised the species, including the specimens by d'Orbigny (1842), figured two of d'Orbigny's specimens of *D. dissimilis*, designated one of them as a lectotype (Busnardo 2006: pl. 20: 8) and figured one paralectotype (Busnardo 2006: pl. 20: 9). However, the original figure in d'Orbigny (1842: 529, pl. 130: 4) and the lectotype of Busnardo (2006: pl. 20: 8) differ markedly. Busnardo's (2006) lectotype shows three to sometimes four strong, branching ribs extending from one umbilical tubercle on the retroversum, in contrast to single or bifurcate ribbing in d'Orbigny's (1842: pl. 130: 4–7) original drawing. The discrepancy most probably results from subjective interpretation and drawings of d'Orbigny (1842). All in all *D. intermedius* sp. nov. differs both from the specimens figured by d'Orbigny (1842) as well as by Busnardo (2006) by its trituberculation on the entire shell.

D'Orbigny (1852) described a similar specimen of *Dissimilites dissimilis* (= *Hamulina dissimilis* in d'Orbigny 1852: 212) from Barremian beds near Escagnolles in southern France (Ravin de Saint-Martin). He (d'Orbigny 1842: 529) noted the specific features, 3–5 intercalatory ribs on the proversum “... ces côtes tuberculeuses se trouvent d'abord cinq petites côtes annulaires simples, réduites à quatre, puis à trois en approchant du coude.”, no trituberculation on hook and retroversum, and mostly 2–3 ribs branching on retroversum from an internal tubercle. Spines shown in d'Orbigny's specimens (1852: pl. 3: 2, 3) are all restored on plates (also noted by Busnardo 2006) and spines could be detected on the holotype herein (Fig. 3A). The Puez specimens differ by trituberculation of flexus and retroversum on the single and branching ribbing. Additionally, the specimens from Puez exhibit only 1 (dominant) or 2 (rare) intercalatory ribs on the proversum (see rib formulae). The proversum from d'Orbigny's (1852) specimen is straighter than in the Puez specimens, where an angle is observable in the middle part of the proversum.

Dissimilites subalternatus (Breskovski, 1966) and *Dissimilites brestakensis* (Dimitrova, 1967) (= *Hamulina brestak-*

ensis in Dimitrova 1967) show “looping” of trituberculate main ribs on proversum, only a single intercalatory rib on proversum and the disappearance of lateral tubercles on hook and retroversum. According to Avram (2001) and Klein et al. (2007), *D. brestakensis* (juvenile stage) is a junior synonym of *D. subalternatus*. *D. dissimilis* features “looping” primary ribs, different numbers of intercalatory ribs and the presence of lateral tubercles on the hook.

Following this synonymy, the specimen illustrated by Obata and Matsukawa (2007) from the Barremian of Japan as *Hamulina* aff. *brestakensis* has to be named *Dissimilites* aff. *subalternatus*. In Obata and Matsukawa (2007: fig. 2) the distribution of *D. aff. subalternatus* in Japan is indicated as Upper Barremian. *D. intermedius* sp. nov. from Puez differs from *D. aff. subalternatus* by trituberculation on the entire shell.

Avram (1976) described an “almost entire” specimen (i.e., without spire and early stages of proversum) of *Dissimilites dissimilis* from the Barremian of Romania (Comarniac, Outer Eastern Carpathians) showing 2–3 intercalatory ribs on the proversum, no lateral tubercles on hook and retroversum, and loss of internal tuberculation on adult shaft. The main differences to *D. intermedius* sp. nov. are the missing trituberculation on hook and retroversum, higher numbers of intercalatory ribs (2–3 vs. 1–2 in *D. intermedius* sp. nov.) and more rounded tubercles on the hook in Avram’s (1976) specimen.

The specimen of *Dissimilites* cf. *dissimilis* (“forme n° 1”: Trigance, SE France) illustrated in Sarkar (1955: pl. 4: 17) is morphologically equivalent (although fragmented) to the herein presented form, and thus regarded synonymous. It shows the typical, weak trituberculation from proversum, over the hook and on the retroversum. All other individuals presented by Sarkar (1955) as *D. cf. dissimilis* (“forme n° 2”) and *D. piveteaui* differ mainly in the missing trituberculation on hook and retroversum.

Major similarities exist with an individual from the Lower Barremian *Nicklesia pulchella* Zone of SE-France (Moriez, coupe Notre Dame) published as *D. dissimilis* by Ebbo et al. (2000), which is well comparable because of the fact that the specimen is almost complete. The specimen from Moriez shows the same buckle of the proversum as the specimen from Puez. Most probably, this feature relates to an ontogenetic change in growth direction. However, the new species also shows remarkable differences to the specimen from France, such as trituberculate ribs on the flexus and retroversal ribs, which are formed by irregularly alternating single and bifurcating ribs. In the Puez specimen, the distance between the pro- and retroversum, which are almost parallel, is half of the retroversum height. This contrasts with the specimen of Ebbo et al. (2000) showing an opening angle β of approx. 20° (vs. 4° in *D. intermedius* sp. nov.) and a distance between pro- and retroversum measuring 1 to 1.4 times the height of the retroversum. Similarly, the distance from the most juvenile part of the spire to the proversum is 18 mm in *D. aff. dissimilites* and only 5 mm in *D. intermedius* sp. nov. The spire in *D. intermedius* sp. nov. shows trituberculate ribbing, whereas Ebbo et al. (2000) reported no visible ornamentation on the spire, perhaps due to

bad preservation. The latter authors noted the onset of ribbing at a diameter of approximately 11.7 mm in shell height. Both species show the same number of intercalatory ribs (1–2) on the proversum. The periostome is not preserved in the French specimen but marked by a final thickened rib in *D. intermedius* sp. nov.. The suture line is not visible in either of the type specimens, but the last chamber is visible immediately before the hook. The suture line, showing a trifid lobus, is visible in specimen PZO-CP56.

Dissimilites intermedius sp. nov. differs from *D. duboise* Vermeulen, 2009 by its extended trituberculation on the retroversum and on the final part of the proversum, and the absence of a bituberculation phase. Additionally, the stratigraphic occurrence of the two species is different, with the *Kotetishvilia compressissima*–*Moutoniceras moutonianum* to lower *Toxancyloceras vandenheckii* Zone for *D. intermedius* sp. nov. and the lower *Nicklesia pulchella* Zone for *D. duboise*.

The specimen from the Pizes de Puez (i.e., the same locality) figured by Costamoling and Costamoling (1994: 94, fig. 93) and identified as *Ancyloceras* shows exactly the same features as our specimens, especially the tiny trituberculation on the hook and additionally on the bifurcating and singular intercalatory ribbing on the retroversum.

Geographic and stratigraphic range.—*Dissimilites intermedius* sp. nov. is so far known only from the type locality and from Trigance (SE France) where it occurs in *M. moutonianum* Zone of upper Lower Barremian to the lower Upper Barremian (*T. vandenheckii* Zone).

Dissimilites trinodosum (d’Orbigny, 1852)

Figs. 3D, E, H, J–N, 4D, E, H, J–N.

- *1852 *Hamulina trinodosa*; d’Orbigny 1852: 215, pl. 4: 1, 2, 3.
- 1889 *Crioceras trinodosum* (d’Orb) Uhl.; Haug 1889: 208, pl. 13: 3.
- 1966 *Hamulina trinodosa* d’Orbigny, 1851; Breskovski 1966: 83, pl. 4: 4.
- 1967 *Hamulina dissimile* d’Orbigny, 1851; Nagy 1967: 66, pl. 4: 2, 3.
- 1993 *Dissimilites trinodosum* (d’Orbigny); Stöhr 1993: 72, pl. 3:7.
- 1994 *Dissimilites trinodosus* (d’Orbigny); Avram 1994: pl. 15: 3, 4, 5.
- 2001 *Dissimilites trinodosus* (d’Orbigny); Avram 2001: pl. 1: 2, 3, 4.
- 2006 *Acrioceras (Dissimilites) trinodosum* (d’Orbigny); Lukeneder and Aspmaier 2006: pl. 6: 8.
- 2006 *Dissimilites (Dissimilites) trinodosum* (d’Orbigny); Lukeneder and Aspmaier 2006: pl. 6: 9.
- 2012 *Dissimilites trinodosum*; Lukeneder 2012b: text-fig. 6A.
- 2012 *Dissimilites trinodosum*; Lukeneder 2012b: text-fig. 8G.
- 2012 *Dissimilites trinodosum*; Lukeneder 2012b: text-fig. 8H.

Holotype: Specimen illustrated by d’Orbigny (1852: 215, pl. 4: 1, 2, 3); holotype by monotypy.

Material.—Two specimens derive from Puez, Early Barremian (top *Moutonianum moutonianum* Zone), log P1 bed 130 (NHMW 2011/0159/0026) and Late Barremian, P1 bed 146 (NHMW 2011/0159/0056). Two additional specimens derive from Late Barremian, P1 beds 169 and 172, top of the middle *T. vandenheckii* Zone (NHMW 2011/0159/0055 and NHMW 2005z0245/0036). Four additional specimens NHMW 2012/0003/0001–3, PZO-CP68) derive from La Stua, only regarded as Barremian in age because they were not collected bed-by-bed (Fig. 1).

without interruption. In NHMW 2011/0159/0026 (Fig. 3D, 4D), fibulation seems to appear also on the flexus between the first three ribs between lateral and ventro-lateral tubercles.

Retroversum.—The retroversum opens from the proversum almost subparallel with an angle β of approx. $2\text{--}3^\circ$ and shows a maximum length of 54 mm (NHMW 2005z0245/0036) and 42 mm (NHMW 2011/0159/0026). The distance between pro- and retroversum is half of the whorl height of the proversum or one third of the retroversum whorl height. Shell height increases slowly by $\alpha 6^\circ$ up to the aperture. The ribs are sharp and slightly retroradiate (NHMW 2005z0245/0036) to almost radial (NHMW 2011/0159/0026). Only the first trituberculated rib bifurcates from an umbilical tubercle (NHMW 2005z0245/0036; Figs. 3J, 4J), and the evolving branches cross the venter without interruption (Figs. 3D₃, J₃, 4D₂, J₃). After that bifurcating rib, only straight, single, trituberculated ribs occur (15 trituberculated ribs), which cross the venter and are of similar thickness (see rib formulae). Umbo-lateral tuberculation is virtually similar in size as the ventro-lateral tuberculation and the lateral tuberculation. The distance between the umbo and lateral tubercle is visibly larger than between lateral and ventro-lateral tubercles. Measured distances on the first single ribs are 5 mm vs. 3 mm. Lateral tuberculation is situated at approx. two thirds of the flank height. The position is similar as on the anterior flexus. The aperture seems to be marked by a collared last rib (NHMW 2011/0159/0026; Figs. 3D, 4D). The dorsal area shows the same ribbing pattern as proversum and flexus, with a single tiny rib starting from each dorso-lateral tubercle and crossing the dorsal area in a proversum bow. These bows are intercalated by parallel bows of tiny ribs, starting on the umbilical area and crossing the dorsal area without interruption (NHMW 2005z0245/0036).

The ribbing pattern varies, as observable in NHMW 2011/0159/0026 (Figs. 3D, 4D). From the umbilical tubercle, the last bifurcating rib gives rise to a branch of two ribs; the front rib crosses the venter and ends at the following umbilical tubercle of the opposite flank, forming the back rib of that branch.

Remarks.—The described specimens of *Dissimilites trinodosum* differ from all other descendant species of this genus by their trituberculation on the proversum, flexus, and retroversum. Intercalatories are more regular on the proversum, with only one intercalatory throughout. Ribbing on the retroversum is single and trituberculate, except at the start of the retroversum, where 1–2 bifurcating ribs may occur. Tuberculation

in *D. trinodosum* shows almost the same strength throughout. D'Orbigny (1852) first described *D. trinodosum* (= *Hamulina trinodosa* in d'Orbigny 1852) from Barremian beds near Escagnolles in southern France (e.g., Ravin de Saint-Martin). As specific features, d'Orbigny (1852) noted the fewer intercalatory ribs on the proversum (1–2 in contrast to *D. dissimilis* with 3–5), trituberculation also on hook and retroversum, "... par la moitié moins de petites côtes intermédiaires aux côtes tuberculeuses de la partie droite..." (d'Orbigny 1852: 216), and single ribbing on retroversum. At the same morphological stages (i.e., ribbing style), the specimens from Puez differ only in size. The Puez individuals reach a max. length of 70 mm, which is almost half of the length of the French specimen (e.g., 20 cm given by d'Orbigny 1852). The spines illustrated in d'Orbigny's specimens (1852: pl. 4: 2, 3) are all restored in the drawings. Such spines are observable on the holotype of *D. intermedius* sp. nov. (Figs. 3A, 4A)

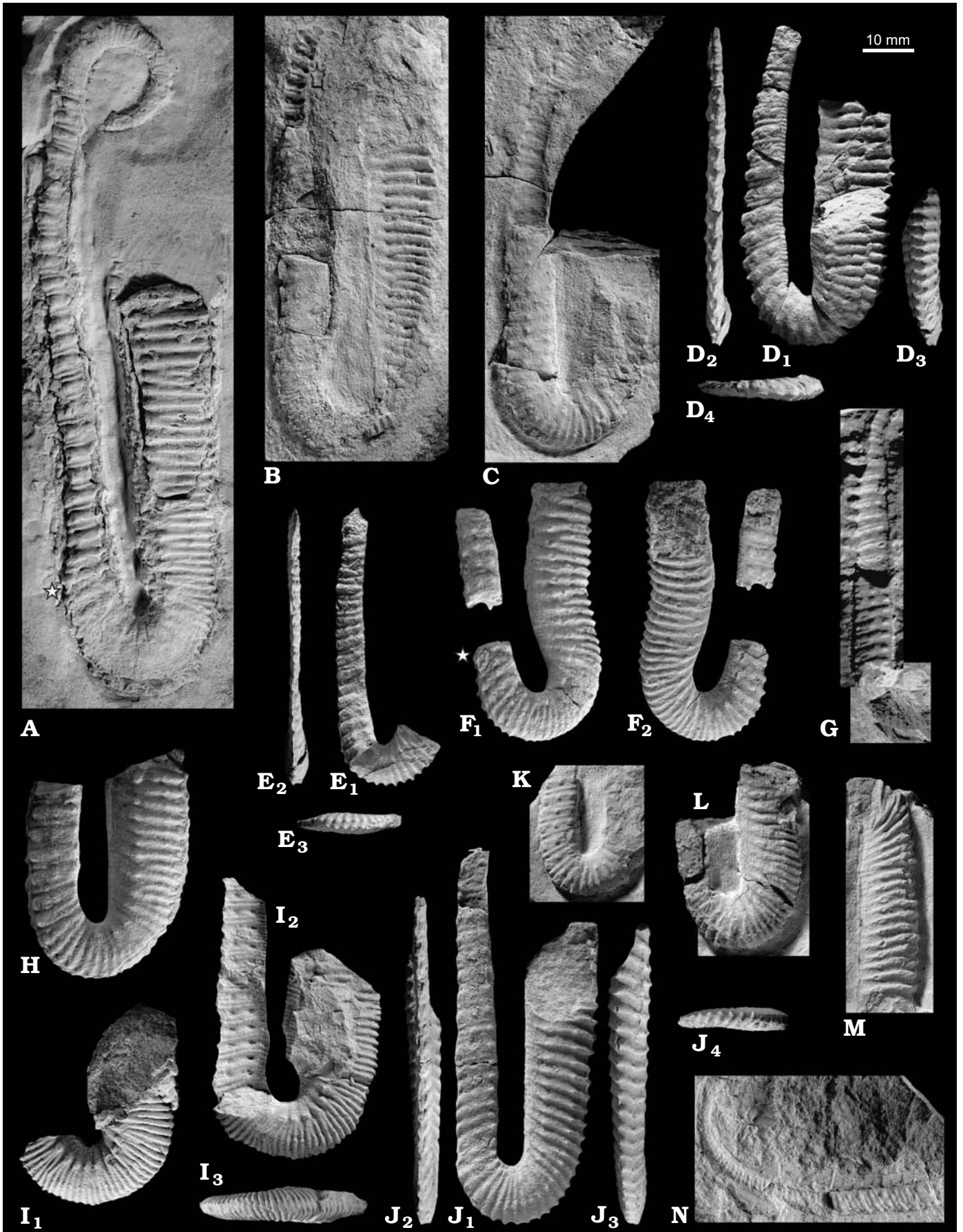
The specimens figured by Nagy (1967) from the Lower Barremian of the Gerecse Mountains (Hungary), named *Hamulina dissimile* (e.g., 1967: pl. 4: 2, 3), are here identified as *D. trinodosum*. A similar specimen was figured by Brezkovski (1966) from Upper Barremian beds of Romania as *Hamulina trinodosa* (1966: pl. 4: 4). Specimens illustrated herein are also comparable to specimens figured by Avram (1994: pl. 15: 3, 4, 5) and Avram (2001: pl. 1: 2, 3, 4.) as *D. trinodosus* from Lower and Upper Barremian outcrops in Romania. Moreover, the specimens we present herein are very similar taxonomically to the material from Puez locality figured by Haug (1889: pl. 13: 3) and to a single specimen from La Stua illustrated by Stöhr (1993: pl. 3: 7).

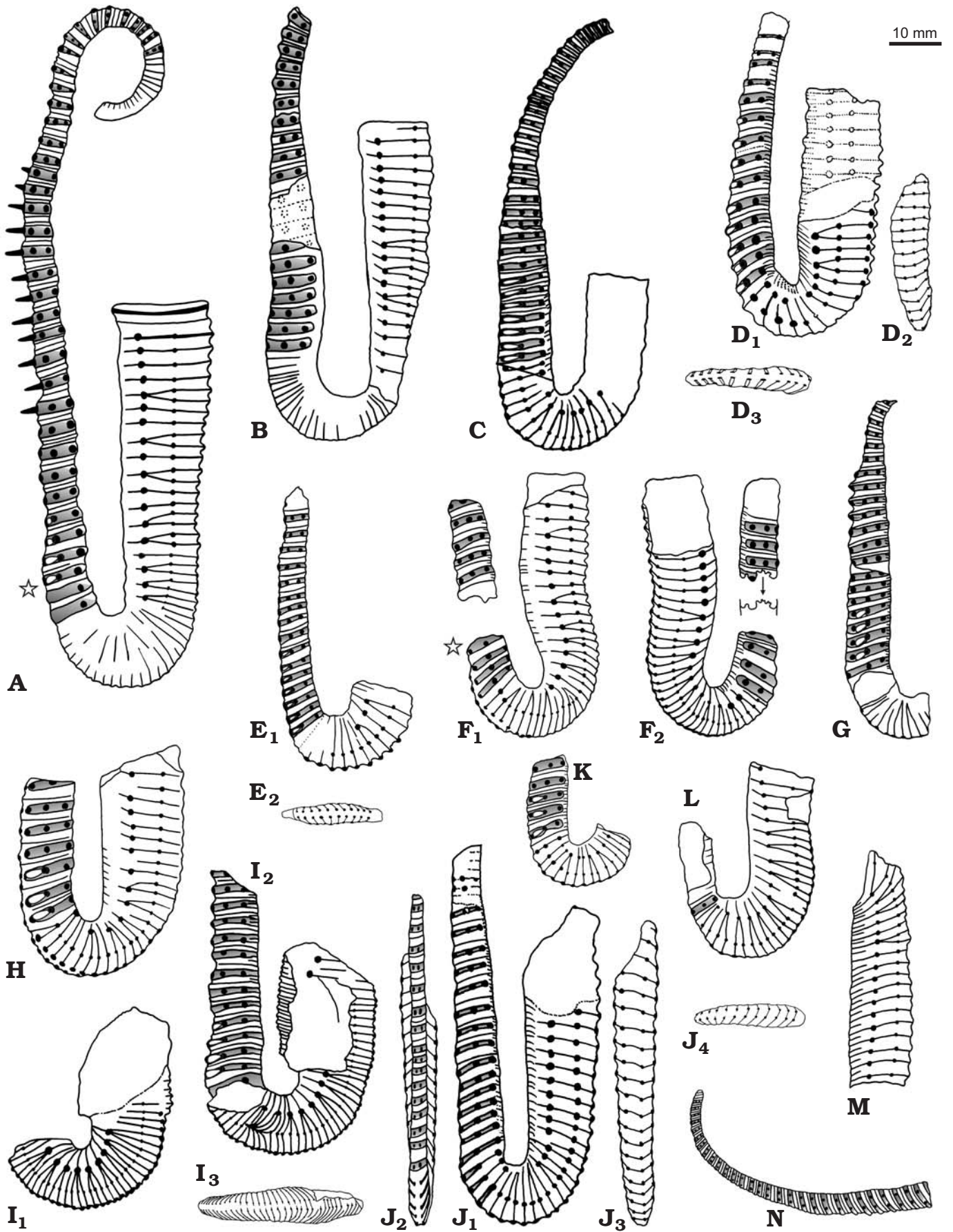
Geographic and stratigraphic range.—*Dissimilites trinodosum* is so far known from Europe (Italy, France, Bulgaria, Hungary, Romania) where it occurs from lowermost Lower Barremian (*Taveraidiscus hugii* Zone) to the upper Upper Barremian (*Toxancyloceras vandenheckii* and *Gerhardtia sartousiana* zones). *D. trinodosum* has been found in the Puez P1 section of the Trento Plateau (northern Italy, Southern Alps) from the top of the *Moutoniceras moutonianum* Zone up to the lower *Toxancyloceras vandenheckii* Zone.

Taxonomic implications

The genus *Dissimilites* was first introduced by Sarkar (1954) in his revision of the Crioceratidae, unfortunately without figures of specimens. In his subsequent paper on heteromor-

Fig. 3. Upper Lower Barremian–lower Upper Barremian acrioceratid ammonoids *Dissimilites intermedius* sp. nov. (A–C, F, G, I) and *Dissimilites trinodosum* (d'Orbigny, 1852) (D, E, H, J–N) from Dolomites (Southern Alps, Italy), Puez locality (*Moutoniceras moutonianum* Zone [A–D, G], *Toxancyloceras vandenheckii* Zone [E, N], unknown zone [F, H, I, J]), and La Stua locality (L–N). A–C. Holotype NHMW 2012/0002/0001 (A), paratypes NHMW 2012/0002/0003 (B), and NHMW 2012/0002/0002 (C); bed P7/-3.4 m (= bed P1/103) and bed P7/-3.2 m (= P1/105). D. NHMW 2011/0159/0026, bed P1/130, lateral view (D₁), external views of proversum (D₂), retroversum (D₃), and flexus (D₄). E. NHMW 2011/0159/0056, bed P1/146, lateral view (E₁), external views of proversum (E₂) and flexus (E₃). F. PZO-CP56, lateral views (F₁, F₂); white star indicates the start of body chamber. G. Paratype NHMW 2011/0159/0027, bed P1/110. H. PZO-CP68, lateral view. I. NHMW 1886/0008/0017, lateral view (I₁, I₂), external view of flexus (I₃). J. NHMW 2005z0245/0036, lateral view (J₁), external views of proversum (J₂), retroversum (J₃), and flexus (J₄). K. NHMW 2012/0003/0002, lateral view. L. NHMW 2012/0003/0003, lateral view. M. NHMW 2012/0003/0001, lateral view. N. NHMW 2011/0159/0055, bed P1/169, lateral view. All specimens in natural size, coated with ammonium chloride before photographing.





phic forms from south-east France, Sarkar (1955) reported different variations of *D. dissimilis* (“forme n° 1” and “forme n° 2”), *D. trinodosum*, and a new species, *D. piveteaui*.

Dissimilites is herein included in the subfamily Helicancyclinae Hyatt, 1894 (nom. transl. Casey 1961: 76. ex Helicancyclidae Hyatt, 1894: 565) within the recently defined family Acrioceratidae Vermeulen, 2004; this concept was also followed by Klein et al. (2007).

The problem of integrating the small heteromorph ammonite morphologies from the Barremian (e.g., *Acrioceras*, *Dissimilites*, *Artareites*) and the Aptian (e.g., *Helicancylus*, *Toxoceratoides*, *Tonohamites*) was discussed in detail by Casey (1961) and Aguirre Urreta (1986). Wright et al. (1996) proposed a scheme that incorporated the subfamily Helicancyclinae Hyatt, 1894 in the family Ancyloceratidae Gill, 1871. Casey (1961), Aguirre Urreta (1986), Ebbo et al. (2000), and Vařiřek (2006) followed the expanded concept of the family Ancyloceratidae Gill, 1871, whereas Vermeulen (2004, 2006) and Klein et al. (2007) favoured the concept of the family Acrioceratidae Vermeulen, 2004. Bert (2009) included the genus *Dissimilites* into the family Helicancyclidae Hyatt, 1894 (Acrioceratidae Vermeulen, 2004). The evolutionary lineage from *Acrioceras* over *Dissimilites* to *Toxoceratoides* with a speculative position of the connective genera *Artareites* and *Argvethites* with indicated stratigraphy (Reboulet et al. 2009) is given in Fig. 6.

Vermeulen (2004) includes the genera *Acrioceras* Hyatt, 1900, *Dissimilites* Sarkar, 1955 and *Toxoceratoides* Spath, 1924 into one family, Acrioceratidae. The latter author notes that *Dissimilites* is most probably a descendant of *Acrioceras* and appears within the *Nicklesia pulchella* Zone. Starting from the *Kotetishvilia compressissima* Zone, two morphological forms develop: (i) shortened forms which are very similar to *Acrioceras* and (ii) forms with very long shaft and juvenile spire. Concerning the maximal size (e.g., shaft length), the open juvenile spire of the specimen presented herein as *D. intermedius* sp. nov. is similar to that seen in the second morphotype group of Vermeulen (2004). *Toxoceratoides* Spath, 1924 seems to be a descendant of the genus *Dissimilites* Sarkar, 1955 (Vermeulen 2004).

In his phylogenetic paper on heteromorphes Vermeulen (2006) strengthens the arguments for the monophyly of the family Acrioceratidae Vermeulen, 2004. Within this paper, he supports once again ranges given in Vermeulen (2004, 2005) and the evolutionary trend from *Acrioceras* Hyatt, 1900 to *Dissimilites* Sarkar, 1955, followed by *Toxoceratoides* Spath, 1924, and *Argvethites* Rouchadze, 1933.

Klein et al. (2007) placed *Dissimilites* Sarkar, 1954 within the family Acrioceratidae Vermeulen, 2004, whereas Wright

et al. (1996) regarded *Dissimilites* as a subgenus of *Acrioceras* and additionally placed the subfamily Ancyloceratinae in the family Ancyloceratidae Gill, 1871. For a detailed discussion of the genus *Acrioceras* see also Delanoy and Bulot (1990) and Thomel et al. (1987, 1990).

Bert (2009) placed the genus *Dissimilites* within the family Helicancyclidae Hyatt, 1894 with its type genus *Helicancylus* Gabb, 1869. Bert (2009) discusses the members of Helicancyclidae in detail. Within this family, he proposes two lineages, i.e., *Acrioceras*–*Dissimilites* (see also Sarasin and Schöndelmayer 1902) and their possible descendant *Artareites* Bert, 2009 and *Toxoceratoides*–*Helicancylus*. Bert (2009) reported *Dissimilites trinodosum* from the *Toxancyloceras vandenheckei* Biozone (= *T. vandenheckii* Zone; subzone of *Barrancyloceras barremense*) from south-eastern France (e.g., Majastre section). Both species, *D. dissimilis* and *D. trinodosum*, differ from members of *Artareites* Bert, 2009 in having stronger and constant trituberculation on at least the proversum. *Artareites* exhibits only the fibulating rib type on the main ribs (e.g., ventral), but lacks trituberculation. *Artareites* first appears within the *T. vandenheckii* Zone (*B. barremense* Subzone). In contrast to *Artareites*, the initial spire can be shallowly helical in *Acrioceras*, *Helicancylus*, and *Toxoceratoides*. In the new species *D. intermedius* the initial spire apparently shows a shallow-helical morphology with trituberculation on the initial spire. Bert (2009) proposed *Artareites* as an intermediate form between *Dissimilites* and *Toxoceratoides*, and therefore *Artareites* as a descendant of *Dissimilites*. He strengthens his arguments by noting that in southern France the appearance of *Artareites* is coeval to the vanishing of *Dissimilites*. Bert (2009) described the insecurity in determining, from which form or ancestor *Artareites* derives: from *D. trinodosum* or from an unknown, earlier non-trituberculate form in the *Toxancyloceras vandenheckii* Zone (e.g., *Barrancyloceras barremense* Subzone).

The possible existence of dimorphic pairs is not discussed herein due the weakness of the fossil record with regard to that feature. Delanoy et al. (1995) and Bert (2009) discussed the possibility of a sexual dimorphic pair of *Emericiceras* (?macroconch) and *Dissimilites* or *Acrioceras* (?microconchs). Bert (2009) noted that, proposing an evolutionary lineage of *Acrioceras*–*Dissimilites*, no macroconch (e.g., *Emericiceras*) would show the transition from *K. compressissima* Zone up to *M. moutonianum* Zone. Vermeulen (2008) disagrees with the idea of dimorphic pairs in *Acrioceras* and *Emericiceras*, mostly due to different stratigraphic occurrences and absence of *Acrioceras* macroconchs in the Hauterivian and *Dissimilites* macroconchs in the Lower Barremian, and likewise for uppermost Barremian to Aptian descendants, such as *Toxoceratoides*

← Fig. 4. Drawings of acrioceratid ammonoids *Dissimilites intermedius* sp. nov. (A–C, F, G, I) and *Dissimilites trinodosum* (d’Orbigny, 1852) (D, E, H, J–N) figured in Fig. 3. A–C. Holotype NHMW 2012/0002/0001 (A), paratypes NHMW 2012/0002/0003 (B), and NHMW 2012/0002/0002 (C); note spines. D. NHMW 2011/0159/0026, lateral view (D₁), external views of retroversum (D₂), and flexus (D₃). E. NHMW 2011/0159/0056, lateral view (E₁), external view of flexus (E₂). F. PZO-CP56, lateral views (F₁, F₂); white star indicates the start of body chamber, note suture line in F₂. G. Paratype NHMW 2011/0159/0027, lateral view. H. PZO-CP68; lateral view. I. NHMW 1886/0008/0017, lateral view (I₁, I₂), external view of flexus (I₃). J. NHMW 2005z0245/0036, lateral view (J₁), external views of proversum (J₂), retroversum (J₃), and flexus (J₄). K. NHMW 2012/0003/0002, lateral view. L. NHMW 2012/0003/0003, lateral view. M. NHMW 2012/0003/0001, lateral view. N. NHMW 2011/0159/0055, lateral view. All drawings in natural size.

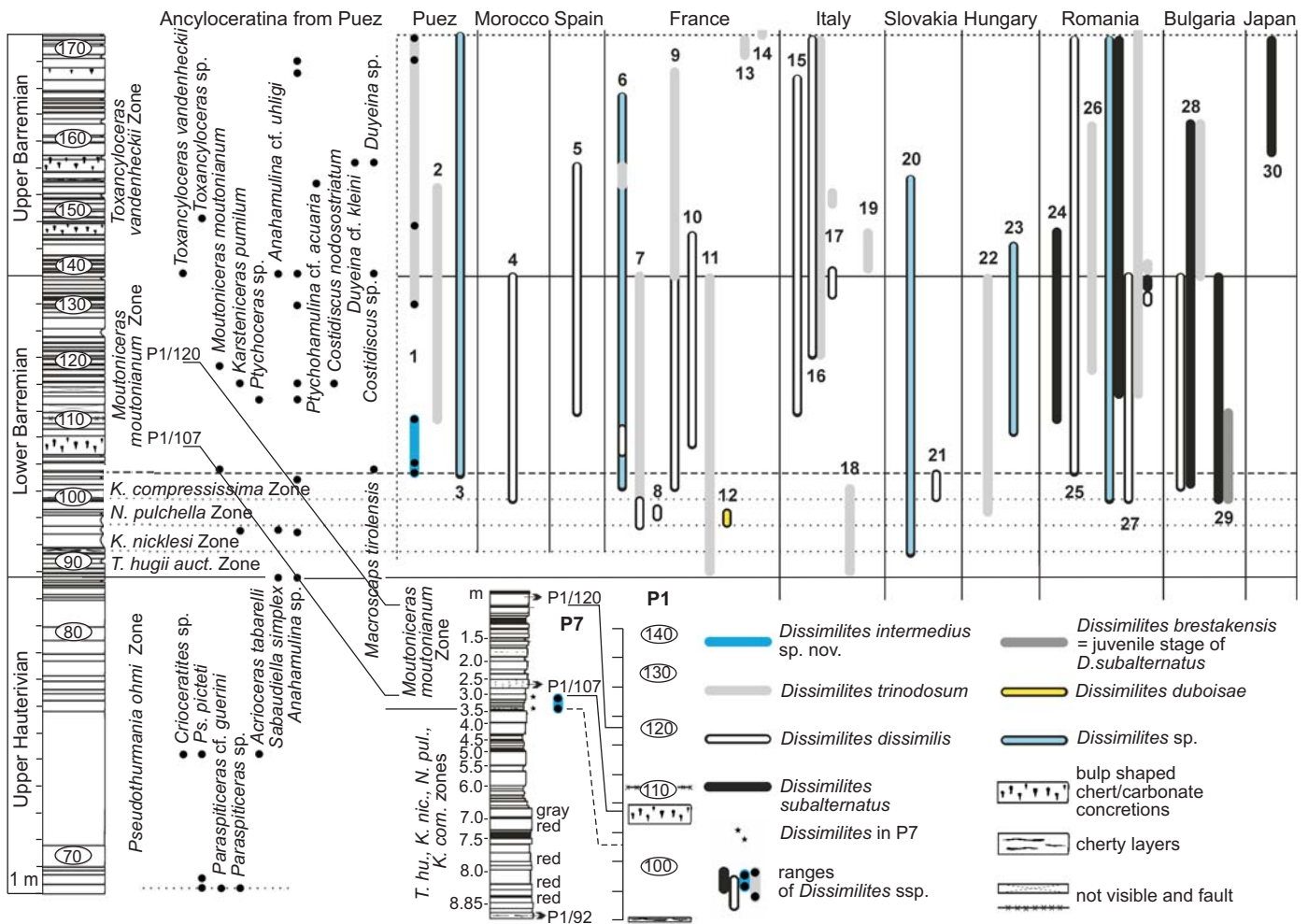


Fig. 5. Ranges of ancyloceratid ammonoids occurring in the Pueze sections (P1 and P7) with indicated biostratigraphic ammonite zonation from Upper Hauterivian and Barremian. Distribution and range of *Dissimilites* species from Pueze and all known occurrences worldwide. 1, this paper; 2, Lukeneder 2012; 3, Lukeneder and Aspmair 2006; 4, Company et al. 2008; 5, Company et al. 1995; 6, Vermeulen, 2005; 2006; 7, Vermeulen 1995, 1998; Ebbo et al. 2000; 8, Ebbo et al. 2000; 9, Busnardo 1963; 10, d'Orbigny 1842, 1852; Busnardo 2006; 11, Kilian 1910; 12, Vermeulen 2009; 13, Bert 2009; 14, Bert et al. 2010; 15, Uhlig 1887; 16, Haug 1887; 17, Haug 1889; 18, Stöhr 1993; 19, Cecca and Pallini 1994; 20, Uhlig 1883; 21, Vašíček 2006; 22, Nagy 1967; 23, Fülöp 1960; Fözy and Janssen 2009; 24, Simionescu 1998; 25, Avram 1976; 26, Avram 1994; 27, Avram 2001; 28, Breskovski 1966, 1975; 29, Dimitrova 1967; 30, Obata and Matsukawa 2007. Note indicated biostratigraphic ammonite zonation. Ammonite occurrences and ranges are marked by solid black circles. Bold horizontal line, stage boundary; dashed horizontal lines, zonal boundaries; dotted horizontal lines, subzonal boundaries. Taxonomic abbreviations: *Ps.*, *Pseudothurmanina*; *T.*, *Taveraidiscus*; *K.*, *Kotetishvilia*; *N.*, *Nicklesia*; *hu.*, *hugii*; *nic.*, *nicklesi*; *pul.*, *pulchella*; *com.*, *compressissima*.

des (see also Vermeulen and Bulot 2007). Notably, in most entirely preserved specimens of *Acrioceras* a helical spire stage is present. In *Dissimilites intermedius* sp. nov. this character is visible in very few specimens, which are entirely preserved. Nevertheless, this character demonstrates that *Dissimilites* is a member of the family Acrioceratidae Vermeulen, 2004 and the subfamily Helicancyclininae Hyatt, 1894.

This is of importance if we consider *Dissimilites* as a possible ancestor of *Toxoceratoides*, which, to the opinion of numerous authors such as Casey (1959, 1961), shows a shallow helical juvenile spire, similar to *Acrioceras* (Hyatt 1894; Wright et al. 1996), *Helicancyclus* (Gabb 1869; Kakabadze 1981; Aguirre Urreta 1986), and *Argvethites* (Rouchadze 1933). These phylogenetic aspects were also discussed by Vermeulen (2005), who suggested an evolutionary lineage from Upper Hauterivian–Lower Barremian *Acrioceras* over

Lower–Upper Barremian *Dissimilites* to uppermost Barremian–Aptian *Toxoceratoides*, giving rise to Aptian *Argvethites* (Fig. 6). Vermeulen's (2008) *Dissimilites duboise* co-occurs with the last members of the genus *Acrioceras*, i.e., *Acrioceras terveri* Astier, 1851.

Vermeulen (2005) points out the known ranges as Upper Hauterivian (*Plesiodiscus ligatus* Zone) up to Lower Barremian (*Nicklesia pulchella* Zone) for *Acrioceras* and *N. pulchella* Zone to *T. vandenheckii* Zone (e.g., = lower *Heinzia sayni* Zone of Vermeulen, 2005; see Reboulet et al. 2009) for *Dissimilites*. Vermeulen (2005) gave a range for *Argvethites*, spanning from *Gerhardtia sartousiana* Zone into the Aptian and *Imerites giraudi* Zone (e.g., *I. giraudi* to *Martelites sarasini* Zone of Vermeulen 2005; see Reboulet et al. 2009). Reboulet et al. (2009) incorporated the *M. sarasini* Zone as the middle subzone into the *I. giraudi* Zone. Vermeulen

(2005) noted and figured (e.g., by dashed range lines) that several first or last occurrences of these genera are still uncertain, making the phylogenetic junction points arguable.

It seems that there was a trend in general shell elongation within the *Dissimilites*; from *D. dissimilites* towards *D. trinodosum*. This was accompanied by increasing tuberculation of the hook and retroversum. A second lineage shows a reduction of size concurrently with an increasing curvation of the proversum; the latter developed towards *Toxoceratoides* (Fig. 6). There is agreement that *D. trinodosum* is the descendant of *D. dissimilites* (Vermeulen 2004; Bert 2009). Possible implication of ontogenetic heterochronies can not be considered due to the scarcity of material (14 specimens from Puez), which prevents from any reliable performance of statistics to clarify intraspecific variability.

Geographic and stratigraphic occurrences of *Dissimilites*

In the following paragraphs, the occurrences of the species of the genus *Dissimilites* are discussed according to geographical regions, from East (Morocco) to West (Japan). A biostratigraphic and palaeogeographic synopsis is given in Figs. 5–7. Within each geographic area, occurrences and references are arranged in the order of their publication dates. For those localities described by several authors interrelationships are established.

Africa.—Company et al. (2008) reported *Dissimilites dissimilis* from the upper Lower Barremian of the western High Atlas of Morocco (Sidi M'Bark section, Imsoune section, Adrar section, Tamri section).

In summary, *D. dissimilis* occurs from the lowermost *K. compressissima* Zone up to the top of the *M. moutonianum* Zone (= middle *Coronites darsi* Zone in Company et al. 2008; see Reboulet et al. 2009) in this region (Fig. 7).

Walchendorf et al. (1967) reported *Acrioceras dissimilis* from the Lower Aptian of South Mozambique (e.g., Chalala) and stated that *Acrioceras* Hyatt, 1900 is the senior synonym of *Dissimilites* Sarkar, 1955, an opinion that was followed by Arkell (1957), but is rejected herein. In contrast to Walchendorf et al. (1967) the African specimens were included in *Toxoceratoides krenkeli* by Klein et al. (2007), which is followed herein.

Europe.—Occurrences of *D. dissimilis* from southeastern Spain (e.g., Subbetic Domain) were reported from the *K. compressissima* Zone up to the *T. vandenheckii* Zone (up to lower *Barrancyloceras barremense* Subzone) by Company et al. (1995).

D'Orbigny (1852) described two species: *D. dissimilis* (= *Hamulina dissimilis* in d'Orbigny 1852) and *D. trinodosum* (= *Hamulina trinodosa* in d'Orbigny 1852), from Barremian beds near Escagnolles in southern France (Ravin de Saint-Martin). From Ravin de Saint-Martin (section 062), Vermeulen

(1996) described Barremian faunas with *D. trinodosum* and *D. dissimilis* (e.g., both bed 18), which he included to the *M. moutonianum* Zone (lowermost *Coronites darsi* Zone in Vermeulen 1995, 1996, 1998; *M. moutonianum* Zone in Reboulet et al. 2009). Busnardo (2006) revised d'Orbigny's (1852) type material of *Hamites dissimilis* from Escagnolles (Lower Barremian; SE France). Busnardo (2006: pl. 20: 8, 9) figured two specimens as *D. dissimilis*, which was followed by Klein et al. (2007). We herein do not follow this assignment, due to the enormous difference in the ribbing pattern of the two specimens. The lectotype designated by Busnardo (2006: pl. 20: 8) shows 2–3 intercalatories between main trituberculate ribbing and strong bi-, tri- and sometimes even quadrifurcating ribbing on the retroversum, while the paralectotype (Busnardo 2006: pl. 20: 9) shows no or only a single intercalatory rib between strongly looping primaries on the proversum and only single to bifurcating ribbing on the retroversum. D'Orbigny (1852) figured a somewhat idealized specimen from his collection of Escagnolles, but, as noted by Busnardo (2006), shows looping primary ribs on the retroversum.

Lory and Sayn (1895) mentioned a specimen as *Crioceras trinodosum* from SE France (Châtillon-en-Diois), which is based on the accompanying fauna, most probably Late Barremian in age. Kilian (1910) and Paquier (1900) mentioned *Crioceratites trinodosum* from the Lower Barremian of SE France (Drôme and Basses Alpes, Diois, and Baronies area). The specimen from the Lower Aptian of south-east France (Homme-d'Armes) that was figured by Kilian and Reboul (1915: 75, pl. 1: 4) as *Crioceras dissimile* (sub. *Hamulina*), was interpreted as a misclassification by Klein et al. (2007), a standpoint followed herein. It may rather be incorporated into the genera *Anahamulina* Hyatt, 1900, *Amorina* Vermeulen, 2005, or *Duyeina* Vermeulen, 2005.

Sarkar (1955) reported several specimens from south-east France: *D. cf. dissimilis* ("forme n° 1" and "forme n° 2"), *D. trinodosum* and a new species *Dissimilites piveteaui*. He suggests *D. cf. dissimilis* ("forme n° 1") to be of Barremian age, *D. cf. dissimilis* ("forme n° 2") of Late Barremian, and *D. piveteaui* of Barremian and Early Barremian age.

The first individual of *D. cf. trinodosum* from the Barremian stratotype in Angles (SE France) was reported by Busnardo (1963) from the Upper Barremian interval (beds 152–161; in Busnardo 1963: 106–107). Additionally, a find of *D. dissimilis* was reported as Lower Barremian from a nearby, more western section (Busnardo 1963: 108, cote 981, niveau 5). Considering recent literature (Vermeulen 2005), the bed numbers given by Busnardo (1963: beds 152–161), would correspond to the *Hainzia sayni* Zone (Vermeulen 2005) and thus to the adequate lower *T. vandenheckii* Zone (Reboulet et al. 2009). Bed 152 corresponds to the last finding of *Dissimilites* at Angles by Vermeulen (2005: 154, bed 152) identified as *Dissimilites* sp.

Vermeulen (2005) reported the occurrence of *Dissimilites* from the Barremian stratotype over an interval of approx. 20 m from the upper *K. compressissima* Zone (e.g., bed 120 with *Dissimilites* sp.) up to the middle *T. vandenheckii* Zone (e.g.,

= lower *Heinzia sayni* Zone of Vermeulen, 2005; see Reboulet et al. 2009). He noted *D. cf. dissimilites* from the lower part of the *M. moutonianum* Zone (e.g., bed 126, lower *Coronites darsi* Zone of Vermeulen 2005; see Reboulet et al. 2009) and *D. cf. trinodosum* from up to the lower *T. vandenheckii* Zone (e.g., bed 144, *Holcodiscus uhligi* Zone of Vermeulen 2005; see Reboulet et al. 2009). Vermeulen (2008) erected the most recent species of the genus *Dissimilites* from south-east France (Clos de Barral), namely *Dissimilites duboise* Vermeulen, 2009. It occurs in the lower parts of the *N. pulchella* Zone, representing the oldest known species of *Dissimilites* so far. From the Nauvin section (SE France, Moustiers Sainte-Marie area), Bert et al. (2010) described *D. trinodosum* from his *Gassendiceras alpinum* Subzone (= equivalent to the *Barrancyloceras barremense* Subzone; after Reboulet et al. 2009), corresponding to the *T. vandenheckii* Zone.

Uhlig (1887: 100) described a specimen of *Crioceras dissimile* in his paper on Neocomian fossils of the Gardnazza Plateau, northern Italy, which includes also the Puez area. Haug (1887: 260) listed only in his synopsis the occurrence of *Crioceras trinodosum* and *Crioceras dissimile* from the “Upper Neocomian” of the Puez area in northern Italy (= “Oberneokom von der Puezalpe”). More detailed descriptions of *Crioceras trinodosum* and *Crioceras dissimile* were given by Haug (1889) from the same locality (Puez area) and attributed to the same age, Upper Neocomian (e.g., Hauterivian–Barremian). The figured specimen of *C. trinodosum* (Haug 1889: pl. 13: 3) shows clear trituberculation on the prosum, hook, and retrosum. It also shows only a single intercalatory rib on the prosum, and only single, straight, sharp ribs between the main ribs shortly after the hook. The latter specimens are all “rock-fall samples” which cannot be assigned to any particular horizon.

Rodighiero (1919: 306) published a list in which he included *Crioceras mojsisovicsi* n. sp. from the Barremian of Colle Muntiella (= Col de la Muntejela; Dolomites, N. Italy), which is located on the Gardenaccia Plateau near Puez. This specimen is as attributed to *D. dissimilis* herein. Reithofer (1928) summarized the faunistic knowledge at that time from Puez, including *Crioceras dissimile* and *Crioceras trinodosum*, which correspond to findings of Uhlig (1887) and Haug (1887).

Stöhr (1993) reported three specimens from the Lower Barremian of northern Italy (La Stua) and figured a single *D. trinodosum* (Stöhr 1993: pl. 3: 7; his nr. 91.1). The latter author gives a range from the Hauterivian–Barremian boundary up to the Upper Lower Barremian for *D. trinodosum* at La Stua (Stöhr 1993: fig. 1). The first occurrence of *D. trinodosum* at the Hauterivian–Barremian boundary proposed by Stöhr (1993) is most probably based on a species misidentification. The short range at the top is probably due to poor outcrop situation or unsuccessful sampling. Stöhr (1993) described and figured a specimen showing trituberculate ribbing on both pro- and retrosum, suggesting assignment to *D. trinodosum*. Additional specimens are preserved only as internal molds with trituberculated prosum (Stöhr 1993);

this is insufficient for species determination and therefore for stratigraphic implications.

Cecca and Pallini (1994) reported *D. cf. trinodosus* from the Gorgo a Cerbare section within the Umbria-Marche Apennines of Italy. The latter authors do not figure the specimen but refer it to the lowermost upper Barremian, the *T. vandenheckii* Zone.

Lukeneder and Aspmaier (2006) identified several specimens from the Puez area as *Acrioceras (Dissimilites) dissimilis* (pl. 6: 7), *Acrioceras (Dissimilites) trinodosum* (pl. 6: 8), and *D. (Dissimilites) trinodosum* (pls. 6: 9, 7: 1). All were suggested to be typical Barremian forms (Lukeneder and Aspmaier 2006).

Lukeneder (2012b) described specimens of *D. trinodosum* from northern Italy with precise stratigraphical positions (?*N. pulchella*, *M. moutonianum*, and *T. vandenheckii* zones; Lukeneder 2012b: figs. 6A, B, 8H, respectively). All these specimens have been reevaluated and incorporated in the synonymy lists herein (see above). As discussed above, the biostratigraphic zonation has changed due to new findings. No members of *Dissimilites* have been found in strata older than the *M. moutonianum* Zone at Puez.

Uhlig (1883: pls. 25: 2, 3, 25: 4a–d, respectively) figured *D. dissimile* (= *Crioceras dissimile* in Uhlig 1883) from Niedek, Slovakia and from Escagnolles, France, and mentioned *D. trinodosum* (i.e., *Crioceras trinodosum* in Uhlig 1883: 270) from Kozy in Poland. Klein et al. (2007) agreed with the classification of the Slovakian specimens but incorporated Uhlig’s (1883) specimen from France into the synonymy of *D. subalternatus* without providing any reasons. This was probably because it showed only a single intercalatory rib on the retrosum and no lateral tubercle on the hook and retrosum, and is therefore plausible. No precise stratigraphic range can be given for Uhlig’s (1883) specimens due to the sampling method (not bed-by-bed) and lack of knowledge of the exact localities. Based on the accompanying fauna, however, the stratigraphic range of *Dissimilites* in Uhlig’s (1883) material from Slovakia can be estimated with upper Lower Barremian to lower Upper Barremian.

Vašíček (2006) reported a single *D. dissimilis* specimen from the Lower Barremian *K. compressissima* Zone of the Central Western Carpathians (Slovakia, Butkov Quarry). The specimen more closely resembles *D. subalternatus* according to looping, tuberculation style, and intercalatories.

In his synopsis on the Lower Cretaceous of the Bakony Mountains Fülöp (1960) noted Barremian specimens of “*Hamulina dissimilis* ORB.” from several drill cores (e.g., Sümeg, Városlöd, and Szenta). Nagy (1967: 66, pl. 4: 2, 3) reported specimens of *Hamulina dissimile* from the Lower Barremian of the Gerecse Mountains (Hungary). Fözy and Janssen (2009) reported *Dissimilites* sp. from the Lower Barremian of the Gerecse Mountains, ranging from the upper *N. pulchella* Zone to the *T. vandenheckii* Zone in the Bersek Quarry (sections A–E).

Simionescu (1898: pl. 4: 8a, b) figured a Barremian (“unknown horizon” in Avram 1976) specimen as *Crioceras dis-*

simile from the Murierii Valley, Romania and reported two specimens of *Crioceras trinodosum* (not figured; same locality). The first specimen was refigured by Avram (2001: pl. 2: 21a, b), who noted that this specimen is most probably a *D.* aff. *subalternatus*, an opinion followed by Klein et al. (2007) by incorporating it in the synonymy of *D. subalternatus*. That concept is followed herein, due to strong zigzagging between umbilical and ventro-lateral tubercles, looping of ribbing on the proversum and the fewer intercalatories compared with *D. dissimilis*. In his synopsis of Lower Cretaceous ammonite faunas, Simionescu (1900: 133, 136 respectively) also mentioned *Crioceras dissimile* from France, Spain, Italy, the Czech Republic, and Romania, and *Crioceras trinodosum* from Italy, France, the Czech Republic, and Romania.

Avram (1976) described an “almost entire” specimen (e.g., without spire and early stages of proversum) of *D. dissimilis* from the Barremian of Romania (Comarniac, Outer Eastern Carpathians). Avram figured three specimens of *D. trinodosum* (1994: pl. 15: 3–5) from the Lower Barremian (Temeneacia valley) and lower Upper Barremian (Orsova-Moldova Noua and Tiganski valley) outcrops near Svinita in the South Carpathians of Romania.

Avram (2001) reported several specimens of the Barremian genus *Dissimilites* and Aptian genus *Toxoceratoides* from Romania. The latter author proposed a stratigraphic range from the *K. compressissima* Zone to *Gerhardtia sartousiana* Zone for *Dissimilites*. Avram (2001) reported *D. dissimilis* (d’Orbigny, 1842) as characteristic for the top of the Lower Barremian, whereas *D. trinodosum* and *D. subalternatus* were found at the top of the Lower Barremian and in the lower Upper Barremian. Avram (2001) stated that the spire of *Dissimilites* is not trituberculate as it is in *Acrioceras*. This is incorrect as seen in our holotype, which shows spire trituberculation.

Breskovski (1966, 1975) in his paper on zonal and subzonal subdivisions of the Barremian in Bulgaria provided also ranges of species belonging to *Dissimilites*: upper Lower Barremian (e.g., *Holcodiscus perezianus* Subzone after Breskovski 1975) for *D. dissimilis* (= *Hamulina dissimilis* in Breskovski 1975), upper Lower Barremian to lower Upper Barremian (e.g., *Holcodiscus perezianus*–*Melchiorites cassidoides* Subzones after Breskovski 1975) for *D. subalternatus* (= *Hamulina subalternata* in Breskovski 1975), lower Upper Barremian (e.g., *M. cassidoides* Subzone after Breskovski 1975) for *D. brestakensis* (= *Hamulina brestakensis* in Breskovski 1975), and lower Upper Barremian (e.g., *M. cassidoides* Subzone according to Breskovski 1975) for *D. trinodosum* (= *Hamulina trinodosa*, Breskovski 1966). To the opinion of Avram (2001), *D. brestakensis* represents a juvenile stage of *D. subalternatus*, an opinion which has also been adopted by Klein et al. (2007). Accordingly, the material of *D. subalternatus* from Bulgaria (Breskovski 1975) ranges from upper Lower Barremian to lower Upper Barremian. Dimitrova (1967) noted the occurrence of *Dissimilites brestakensis* (= *D. subalternatus*) in the Upper Barremian of Bulgaria (e.g., Brestag near Varna). Dimitrova (1967) described the co-occurrence with “*Pulchellia*” *compressissima* (= *Kotetishvilia armenica*

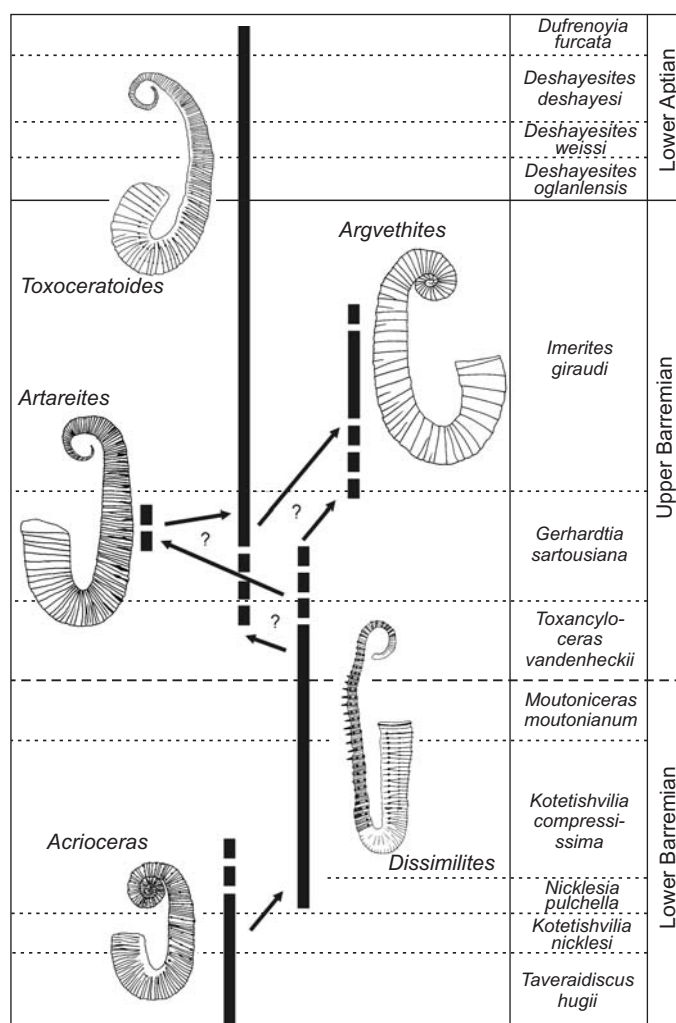


Fig. 6. Evolutionary line from *Acrioceras* over *Dissimilites* to *Toxoceratoides* with speculative position of the connective forms *Artareites* and *Argvethites*. Indicated stratigraphy to the right is in accordance with Reboulet et al. (2009). Bold horizontal line, stage boundary; dashed horizontal lines, substage boundaries; dotted horizontal lines, zonal boundaries.

after Vermeulen and Klein 2006), which most probably shows a stratigraphic range of upper Lower Barremian (e.g., base of *M. moutonianum* Zone; see Reboulet et al. 2009).

The specimen described and figured as *Crioceratites* aff. *dissimile* by Kazansky (1914: 42, pl. 1: 12, 13) from Lower Aptian beds (N 4b; beds with *Hoplites deshayesi* in Kazansky 1914; = *D. deshayesi* Zone after Reboulet et al. 2009) of Daghestan in the Northern Caucasus (e.g., Zoudakar; southern Russia) does not belong to *D. dissimilis*. As noted by Klein et al. (2007: 104) the Caucasian specimen is most probably a member of *Toxoceratoides* Spath, 1924. Reasonable doubts are with the identification of *Dissimilites* from the Aptian of Transcaucasia and the Caucasus to the north, reported by Kotetichvili (1983). The material probably also corresponds to the genus *Toxoceratoides*.

Asia.— The specimen published by Obata and Matsukawa (2007: figs. 5, 7) from the Barremian of Japan as *Hamulina*

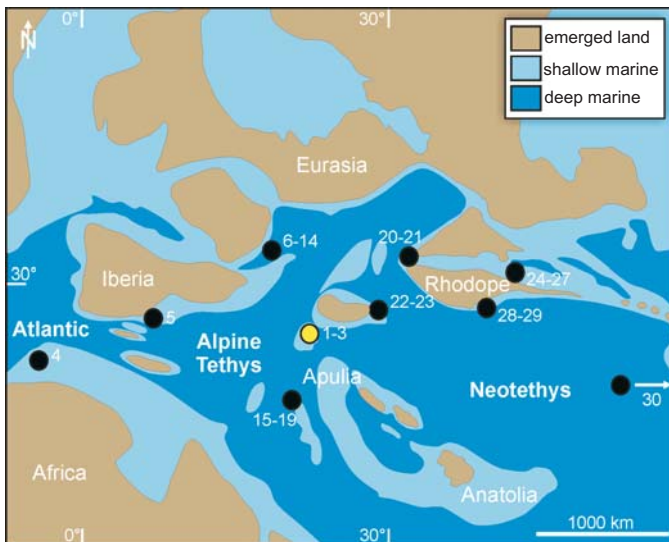


Fig. 7. Paleogeographical map of the Mediterranean area during the Early Barremian based on Dercourt et al. (1993) and Barrier and Vrielynck (2008). Numbers correspond to Fig. 5 and indicate localities of *Dissimilites* occurrences. Yellow spot shows locality of Puez, other localities are in black. 1–3, Puez; 4, Morocco; 5, Spain; 6–14, France; 15–19, Italy; 20, 21, Slovakia; 22, 23, Hungary; 24–27 Romania; 28, 29, Bulgaria; 30, Japan.

aff. brestackensis is more likely *D. aff. subalternatus*. The distribution of ammonites provided by Obata and Matsukawa (2007: fig. 2), points to an Upper Barremian occurrence of their *D. aff. subalternatus*.

Conclusions

A new species within the heteromorph genus *Dissimilites* Sarkar, 1954 is proposed, based on comprehensive material, including the most complete specimen known so far (spire, proversum, flexus, retroversum, peristome). *Dissimilites intermedius* sp. nov. (upper Lower Barremian, *Moutoniceras moutonianum* Zone) shows intermediate morphological features of the ancestral *Dissimilites dissimilis* and its descendant *Dissimilites trinodosum*. The new species combines the ribbing style of *D. dissimilis* (bifurcating ribs intercalated with simple ribs) with the tuberculation style of *D. trinodosum* (trituberculation on entire shell). We could also confirm the previously observed trend in shell length decrease in *Dissimilites* from the upper Lower Barremian (*M. moutonianum* Zone) to lower Upper Barremian (*Toxancyloceras vandenheckii* Zone). This size reduction is accompanied by a simultaneous increase of shell curvature during the same time interval. The shallow-helical spire with its consistent ornamentation with trituberculated main ribs shows a close relationship to the assumed ancestor *Acrioceras*, whereas the increasing curvature of the younger forms transfers to the descendant *Toxoceratoides*. Thus, the presented data support the concept of a direct evolutionary lineage from *Acrioceras* over *Dissimilites* to *Toxoceratoides*. The evolutionary trend in *Acrioceras*, *Dissimilites*, and *Toxoceratoides* in the Upper Barremian (e.g., *Gerhardtia sartousi-*

ana and *Imerites giraudi* zones) is strongly supported by the connective genera *Artareites* and *Argvethites*.

Additional ammonite findings show that the *M. moutonianum* Zone has a longer range than expected and that the *Taveraidiscus hugii*, *Kotetishvilia nicklesi*, *Nicklesia pulchella*, and *Kotetishvilia compressissima* zones are more condensed than previously thought. The fauna from the Puez locality comprises only two genera of the family Acrioceratidae: *Acrioceras* and *Dissimilites*. The genus *Dissimilites* starts at Puez with *D. intermedius* within the *M. moutonianum* Zone. The survey of the literature data revealed that *Dissimilites* appeared during the *N. pulchella* Zone, represented by *D. du-boise*, and later replaced by *D. dissimilis*. Two morphological forms develop in the *Kotetishvilia compressissima* Zone—the first one with a shortened spire, very similar to *Acrioceras*, and the second one with a very long shaft and juvenile spire, as seen in the new species *D. intermedius*. Later on, in the *M. moutonianum* Zone, *D. intermedius* sp. nov. is replaced by *D. subalternatus*. Besides, *D. trinodosum* occurs, which seems to be ancestral to the genus *Toxoceratoides*.

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