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Lectotype designation for *Orbitolinopsis flandrini* MOULLADE, 1960 (Foraminifera): The missing piece of a taxonomic puzzle

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Abstract: *Orbitolinopsis flandrini* MOULLADE, 1960, was described from Lower Cretaceous Urgonian limestones of southeastern France without the designation of a holotype. It represents a valid taxon since the selection of a holotype is only obligatory for taxa established after 1999 (ICZN, 4th edition, article 72.3). Today the original description is considered to be a mixture of several taxa belonging to *Orbitolinopsis* HENSON, 1948/*Cribellopsis* ARNAUD-VANNEAU, 1980 (transverse sections with cupules/septules in the central zone) and *Drevennia* ARNAUD-VANNEAU, 1980 (axial sections with an axial "columella-like" column). The short and in any case insufficient original description of *O. flandrini*, however, stressed the presence of a columellar-like central test as the main characteristic feature. In fact, the majority of the (sub)axial sections showing an axial column (lacking in *Orbitolinopsis*) are considered to belong to *Drevennia* (Family Pfenderinidae). Therefore, the new combination *Drevennia flandrini* (MOULLADE, 1960) is proposed and a lectotype herein designated from the original illustrations. *Drevennia ecougensis*, the type-species of the genus, is found to be a subjective junior synonym of the latter. New finds from Serbia and Spain extend the stratigraphic range of *D. flandrini*, from the upper Berriasian to the lowermost upper Aptian. The first occurrences of *Drevennia*, *Dobrogelina* NEAGU, 1979, *Pfenderina* HENSON, 1948, and *Moulladella* BUCUR & SCHLAGINTWEIT, 2018, in the upper Berriasian give evidence for an adaptive radiation of the Pfenderinidae during the time reported and from other, mostly complex larger benthic foraminifera (*e.g.*, Orbitolinidae).

Key-words:

- Foraminifera;
- Orbitolinidae;
- Pfenderinidae;
- taxonomy;
- ICZN;
- Lower Cretaceous

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Résumé : *Sélection du lectotype d'*Orbitolinopsis flandrini *MOULLADE, 1960 (Foraminifère) : La pièce manquante d'un puzzle taxinomique*.- *Orbitolinopsis flandrini* MOULLADE, 1960, a été décrit dans les calcaires urgoniens (Crétacé inférieur) du sud-est de la France. La validité de ce taxon n'est pas en question, la désignation d'un holotype n'étant obligatoire que pour les taxons décrits après 1989 (CINZ, 4e édition, article 72.3). Aujourd'hui, la description originale de cette espèce est considérée comme fondée sur un mélange de taxons rapportés aux genres *Orbitolinopsis* HENSON, 1948, *Cribellopsis* ARNAUD-VANNEAU, 1980 (sections transversales à cupules/septules dans la partie centrale) et

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Drevennia ARNAUD-VANNEAU, 1980 (sections axiales avec une colonne axiale "semblable à une columelle"). Toutefois cette description originale, courte et donc insuffisante, soulignait la présence d'une partie centrale du test semblable à une "columelle" comme étant la caractéristique distinctive de l'espèce. De fait, la majorité des sections (sub-) axiales montrant une colonne axiale (absente chez les *Orbitolinopsis*) sont considérées comme appartenant au genre *Drevennia* (Famille des Pfenderinidae). Par conséquent, la nouvelle combinaison *Drevennia flandrini* (MOULLADE, 1960) est proposée et un lectotype est sélectionné à partir des illustrations originales. *Drevennia ecougensis*, l'espèce-type du genre, est mise en synonymie avec *D. flandrini*, cette dernière espèce ayant priorité sur *D. ecougensis* (synonyme subjectif plus ancien). De nouvelles découvertes en Serbie permettent d'élargir la répartition stratigraphique de *D. flandrini* du Berriasien supérieur à l'Aptien inférieur. Les premières apparitions de *Drevennia*, *Dobrogelina* NEAGU, 1979, *Pfenderina* HENSON, 1948, et *Moulladella* BUCUR & SCHLAGINTWEIT, 2018, au Berriasien supérieur apportent la preuve d'une radiation adaptative des Pfenderinidae à cette époque, phénomène déjà noté pour d'autres types de foraminifères benthiques principalement chez les grands foraminifères complexes (*e.g.*, Orbitolinidae).

Mots-clefs :

- Foraminifères ;
- Orbitolinidae ;
- Pfenderinidae ;
- taxinomie ;
- CINZ ;
- Crétacé inférieur

Introduction

Urgonian (upper Hauterivian-lower Aptian) shallow-water carbonates of southeastern France display a high diversity of Orbitolinidae. CLAVEL (2014: Fig. 5) reported 38 species belonging to the subfamilies Orbitolininae (6), Dictyoconinae (21), and Praedictyorbitolininae (11). The genera with the most species are *Cribellopsis* ARNAUD-VANNEAU, 1980, *Orbitolinopsis* HENSON, 1948, and *Paracoskinolina* MOULLADE, 1965. Depending on the importance of structural elements for generic or specific rank among different workers (*e.g.*, MOULLADE, 1963; SCHROEDER, 1964), many of these taxa were, and are still insufficiently understood. One example refers to *Orbitolinopsis flandrini* MOULLADE, 1960, initially described from the Barremian of south-eastern France. It has not been included in the compilation of CLAVEL *et al.* (2014), because its assignment to *Orbitolinopsis* has been questioned by several authors since its original description. Based on a literature study and new finds from upper Berriasian shallow-water carbonates of Serbia, the problems related to understanding this taxon are presented herein.

Historical background and taxonomical problems

In 1960, MOULLADE described *Orbitolinopsis flandrini* n.sp. from the Barremian of the Drôme department in southeastern France. Based on the test morphology, MOULLADE (1960: p. 190) distinguished a cylindro-conical Form A (*op.cit.*: Pl. 2, figs. 8-20) and conical Form B (*op.cit.*: Pl. 2, figs. 21-28). In his rather short description, a reduced central zone similar to a columella (solid reticulum) was stressed as characteristic for the species. Neither a holotype nor a type-locality was indicated. This procedure was in line with the requirements of the International Code of Zoological Nomenclature (ICZN) at that time. It was only with the 4th edition published in the year 2000 that the nomination of a type (holotype or syntype) to be designated in the original publication (established after 1999) became obligatory (article 72.3). This means that *O. flandrini* was validly published and does not represent a *nomen nudum*. Two years later, BASSOULLET and MOULLADE (1962) differentiated the subspecies *Orbitolinopsis flandrini flandrini* for the Form A (mean ratio height/diameter = 2), and *Orbitolinopsis flandrini inflatus* for the Form B (mean ratio height/diameter 1.4) of MOULLADE (1960). In the monograph of MOULLADE (1966: p. 42), both subspecies were again mentioned but for *O. flandrini flandrini*, some of the original illustrations (Pl. 2, figs. 8, 14-17 in MOULLADE, 1960) were omitted. The specimen illustrated in figure 17 of Plate 2 of MOULLADE (1960) was assigned to *O. flandrini elongatus* DIENI *et al.*, 1963, which was subsequently revised by ARNAUD-VANNEAU (1980) as *Cribellopsis elongata*.

One of the first workers commenting on *O. flandrini* was HOFKER (1966). According to him (*op. cit.*: p. 900), *O. flandrini* Form B might represent juvenile specimens of *Orbitolinopsis kiliani* HENSON, 1948. Concerning Form A (= *O. flandrini flandrini*), HOFKER stated that the "structure is not quite clear", but the horizontal sections (MOULLADE, 1960: Pl. 2, figs. 18-20) "certainly show features of *Orbitolinopsis*". ARNAUD-VANNEAU (1980: p. 700) treated *O. flandrini* as an orbitolinid species and attributed it to an undetermined genus ("genres indéterminés d'Orbitolinidae"). In the monograph of the Urgonian microfauna of southeastern France, ARNAUD-VANNEAU (1980) also established the new genus *Drevennia* with the type-species *D. ecougensis*. It is worth mentioning that any resemblances with *O. flandrini* have not been envisaged or discussed by ARNAUD-VANNEAU (1980). The possible identity of both taxa was first suggested by BECKER (1999, p. 415), who noted also the lack of a holotype for *O. flandrini*. As already remarked above, this is not an argument for the invalidity of the species. According to BECKER (1999), the specimens illustrated by MOULLADE (1960) in figures 8-9, 11 and 14-16 of Plate 2 are seemingly morphologically identical to *D. ecougensis* (Fig. 1.E-F). On the other hand, those

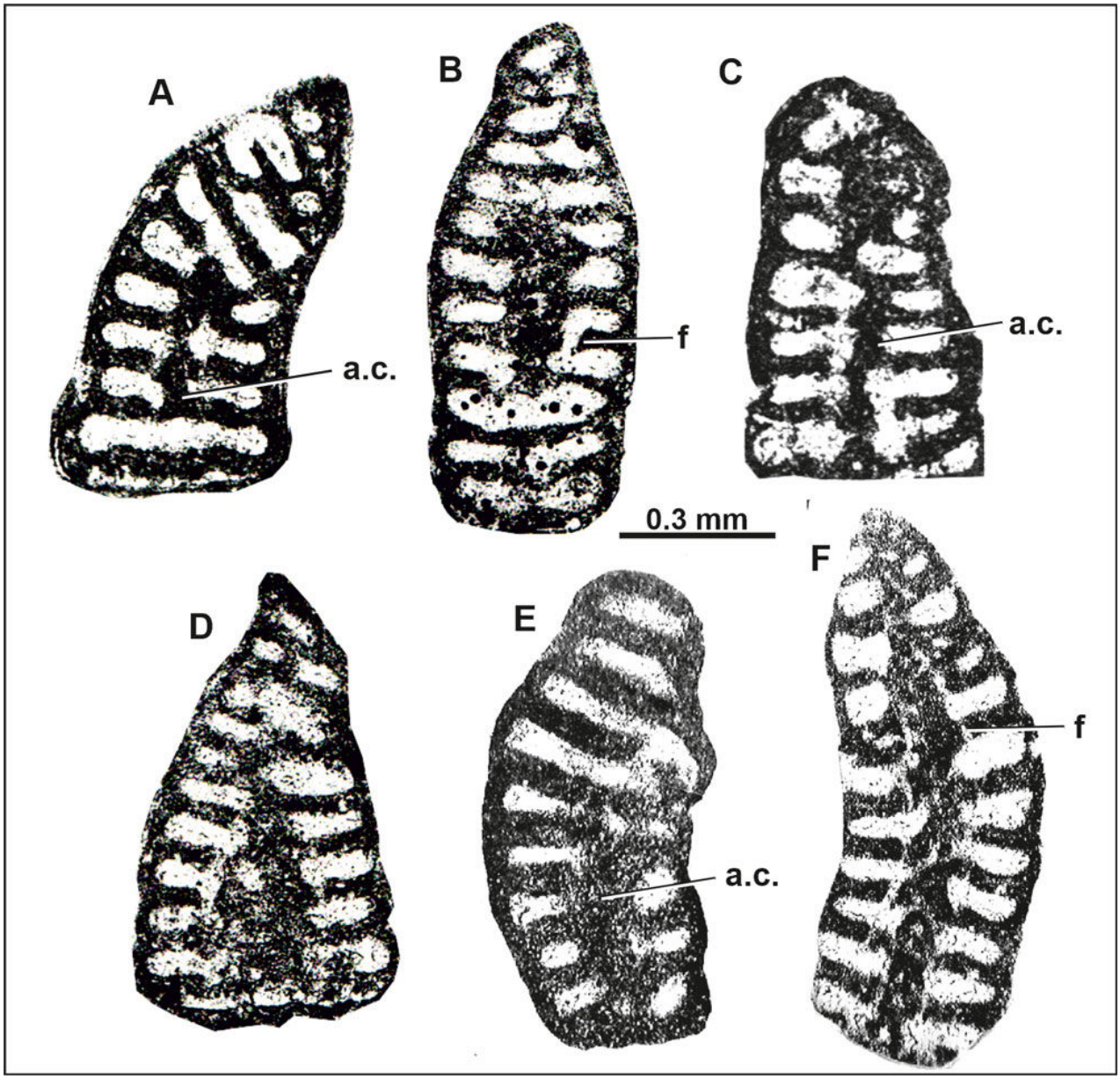

Figure 1: *Drevennia flandrini* (MOULLADE) comb. nov. (**A-D**: from MOULLADE, 1960: Pl. 2, fig. 16 = lectotype designated herein, figs. 8, 14-15 = paralectotypes, Barremian of southeastern France; **E-F**: *Drevennia ecougensis* from ARNAUD-VANNEAU, 1980: Pl. 84, figs. 10-11. Abbreviations: a.c. = axial column, f = foramen.

specimens illustrated in figures 12-13 and 17-20 of Plate 2 (*op.cit.*) were interpreted as *incertae sedis*. This conclusion is herein accepted. BECKER also correctly noted the lack of the typical central structure of *Orbitolinopsis* with cupules (see ARNAUD-VANNEAU, 1980) in *O.* ? *flandrini* raising doubts about its generic status. Furthermore, BECKER (1999) concluded that an exact definition of *O.* ? *flandrini* is only possible by re-analyzing the original material of MOULLADE (1960) and the designation of a lectotype. Independently from the correct conclusions of BECKER (1999), the specimens illustrated by that author as *O.* ? *flandrini*, do in our opinion not belong to the form described by MOULLADE (1960). The small forms are spirally coiled throughout, without showing uniserial adult chambers and an axial column, are considered to belong to another genus (neither *Drevennia* nor *Orbitolinopsis*). Finally, CLAVEL *et al.* (2010: p. 6) followed the opinion of ARNAUD-VANNEAU (1980) that the assignment of the species *flandrini* to the genus *Orbitolinopsis* was very doubtful ("très douteuse"). Concerning *O. inflatus* (former Form B of MOULLADE, 1960), CLAVEL *et al.* (2010) concluded that the specimens (here: transverse sections) belong to different species and genera, namely *Cribellopsis* sp. for the transverse sections illustrated in figures 26-28 of Plate 2 of MOULLADE (1960) due to the presence of radial partitions in the marginal zone. The axial/subaxial sections of MOULLADE (1960: Pl. 2, figs. 22-24) instead were interpreted as belonging to *Orbitolinopsis cuvillieri* due to the presence of cupules.

Table 1: Historical summary.

MOULLADE, 1960	BASSOULLET & MOULLADE, 1962	MOULLADE, 1966	ARNAUD-VANNEAU, 1980	BECKER, 1999	CLAVEL *et al.*, 2010	This work
O. flandrini n.sp. Forme A: **Pl. 2, figs. 8-20**	*O. flandrini flandrini* n.subsp.	*O. flandrini flandrini*: **Pl. 2, figs. 9-13, 18-20** (non figs. 8, 14-16) of 1960 *O. flandrini elongatus* DIENI *et al.*: **Pl. 2, fig. 17** of 1960	*O.* ? *flandrini*: **Pl. 2, figs. 9-10, 12**, doubtful: **Pl. 2, figs. 18-20** not *flandrini*: **Pl. 2, figs. 8, 11, 13-17**	different taxa: **Pl. 2, figs. 8-9, 11, 14-16** might be *Drevennia*; not determinable: Pl. 2, figs. 12-13, 17-20	sharing opinion of ARNAUD-VANNEAU, 1980, as *O. flandrini* a doubtful orbitolinid	*Drevennia flandrini* nov. comb.: **Pl. 2, figs. 8-9, 11, 14-16** of 1960 Lectotype: **Pl. 2, fig. 16** in MOULLADE, 1960
O. flandrini n.sp. Forme B: **Pl. 2, figs. 21-28**	*O. flandrini inflatus* n.subsp.	*O. flandrini inflata*	*O.* ? *inflata*: **Pl. 2, figs. 21-24** of 1960	not mentioned *expressis verbis*	*Cribellopsis* sp.: **Pl. 2, figs. 25-28** *O. kiliani*: **Pl. 2, figs. 22-24**	sharing opinion of CLAVEL *et al.*, 2010 taxon *inquierendum*

In summary, in accordance with the observations of previous workers, we conclude that the initial description of *O. flandrini* MOULLADE represents a mixture of different species/genera. The axial sections displaying seemingly identical test morphologies, dimensions (see *Dimensions* in the chapter Systematic description), internal structure, namely the "columellaire central zone" (excluding its belonging to *Orbitolinopsis*), and are considered identical to the form described by ARNAUD-VANNEAU (1980) twenty years later as *Drevennia ecougensis* (see BECKER, 1999). The transverse sections are considered as belonging to *Cribellopsis* and *Orbitolinopsis* (see HOFKER, 1966; CLAVEL *et al.*, 2010) (Table 1).

Material studied

We recently studied a Lower Cretaceous section from eastern Serbia where specimens of "*O.* *flandrini* have been found (BUCUR *et al.*, 2019, 2020). The samples studied belong to a carbonate succession outcroping north-north-east of the city of Niš, in the vicinity of the village of Kamenica (Fig. 2). The coordinates of the section base are N 43°23'03.7" and E 21°56'41.6". The limestones from this area belong to the Kurilovo fold structure (or anticline) (KRSTIĆ *et al.*, 1978, 1980) that is part of the Gornjak-Stuva Planina Unit, the westernmost part of the Carpatho-Balkanids of eastern Serbia. North of the Danube River it continues with the Sasca Unit belonging to the Getic domain of the South Carpathians (SĂNDULESCU, 1975, as Sasca-Gornjak Unit). On the geological map 1:100,000, sheet Aleksinac (KRSTIĆ *et al.*, 1978, 1980), the Lower Cretaceous carbonate deposits of the Kamenica area are assigned to the Valanginian-Hauterivian and Barremian-Aptian. New investigations have provided a Berriasian-*pro parte* Valanginian age for the Cretaceous succession of the Kamenica section (BUCUR *et al.*, 2019, 2020). It is the type-locality of the giant sized *Bispiraloconulus serbicus* (SCHLAGINTWEIT *et al.*, 2019, for further information). The specimens of "*Orbitolinopsis*" *flandrini* have been observed in the part of the section containing a diverse assemblage of orbitolinids and other larger benthic foraminifera (*e.g.*, spirocyclinids, pfenderinids, coscinoconids). The late Berriasian age is based on the associated microfaunistic-microfloristic assemblage (see *Associated microfossils* in following chapter), and rare calpionellids, such as *Calpionellopsis oblonga* COLOM, *Lorenziella plicata* REMANE or *Lorenziella hungarica* KNAUER & NAGY. Among the numerous Dasycladales, we just want to mention the occurrence of *Falsolikanella campanensis* (AZÉMA & JAFFREZO) (see also RADOIČIĆ, 1978), that represents an upper Berriasian marker taxon according to GRANIER (2019). The orbitolinids will be the subject of a separate investigation. We just name a few: examples: *Cribellopsis neoelongata* (CHERCHI & SCHROEDER), *Urgonina alpillensis* (FOURY), *Orbitolinopsis buccifer* ARNAUD-VANNEAU & THIEULOY, or *O. debelmasi* MOULLADE & THIEULOY. The present study is based on 20 specimens (15 illustrated herein) of "*Orbitolinopsis*" *flandrini* observed in 10 thin sections. These are housed in the Geology Department of the Babeş-Bolyai University, Cluj-Napoca (Ioan I. BUCUR collection). One specimen (Fig. 4.O) is from the lower upper Aptian (Gargasian) of the Reocin Formation, Cantabria, northern Spain. For details on the geological setting the reader is referred to SCHLAGINTWEIT *et al.* (2016).

Systematic micropaleontology

The high-rank classification (Phylum-Class) follows PAWLOWSKI *et al.* (2013). For the low-rank classification see KAMINSKI (2014). For a glossary of terms, see HOTTINGER (2006).

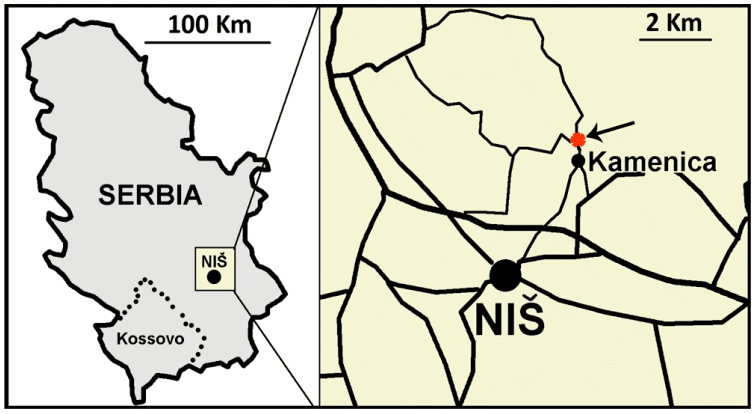

Figure 2: Location of the Kamenica section near the city of Niš in eastern Serbia.

Phylum FORAMINIFERA ORBIGNY, 1826

Class Globothalamea PAWLOWSKI *et al.*, 2013

Order Loftusiida KAMINSKI & MIKHALEVICH in KAMINSKI, 2004

Suborder Orbitolinina KAMINSKI, 2004

Superfamily Pfenderinoidea SMOUT & SUGDEN, 1962, nom. correct. KAMINSKI, 2014 (pro Pfenderinacea)

Family Pfenderinidae SMOUT & SUGDEN, 1962

Subfamily Pfenderininae SMOUT & SUGDEN, 1962, nom. transl. LOEBLICH & TAPPAN, 1964

Remarks: Among the four genera comprising the Pfenderininae (see SEPTFONTAINE, 1988; KAMINSKI, 2014), *Pfenderella* REDMOND, 1964, is reported from the Middle Jurassic, while the other three have their first appearances in the (upper) Berriasian: *Dobrogelina* NEAGU, 1979, *Pfenderina* HENSON, 1948 (see GRANIER, 2019), and *Drevennia* ARNAUD-VANNEAU, 1980 (this work). The paleopfenderinid *Moulladella* BUCUR & SCHLAGINTWEIT, 2019, also has its first appearance in the upper Berriasian documenting a radiation-diversification of this group, and other complex larger benthic foraminifera (*e.g.*, Orbitolinidae) during this time.

Genus *Drevennia* ARNAUD-VANNEAU, 1980, emend. herein

Type species: *Drevennia ecougensis* ARNAUD-VANNEAU, 1980 = *D. flandrini* (MOULLADE, 1960), comb. nov.

Lectotype designation: From the original illustrations of *Orbitolinopsis flandrini* by MOULLADE (1960), the specimen illustrated in figure 16 of Plate 2 is selected herein as lectotype. It represents an oblique axial section of a bent test showing the solid column in the central test part of some chambers. The lectotype is illustrated herein in Figure 1.A. From the further specimens illustrated by MOULLADE (1960), only figures 8-9 and 14-15 of Plate 2 belong to the same species as the lectotype herein designated and are designated as paralectotypes (ICZN, Recommendation 74 F). The collection of MOULLADE's specimens is deposited at the Muséum d'Histoire Naturelle de Nice and still awaits curation (GRANIER, 2020, pers. comm.).

Diagnosis: Test elongate, cylindrical to cylindro-conical, may be slightly bent at the transition from the trochospiral to uniserial stages. Initial part trochospirally coiled about a central columella. Later uncoiled, with uniserial chambers broader than high and of almost constant height throughout ontogeny. The central part of the uniserial chambers is occupied by an axial column formed by stacked inverted cones protruding slightly into the basal part of the subsequent chamber. Few multiple foramina surround the axial column, and are straight to obliquely arranged. The central column may be transjected by a central canal. The thick wall is homogeneous microgranular to finely agglutinated.

Remarks: In the original description, *D. ecougensis* was poorly illustrated with three illustrations/specimens: one isolated specimen (ARNAUD-VANNEAU, 1980: Pl. 55, fig. 8), and two from thin-sections (*op.cit.*: Pl. 84, figs. 10-11, axial and axial-oblique sections). The latter two are re-illustrated herein Fig. 1.E-F. Transverse sections were not provided. Additionally, at least one specimen of *Pseudolituonella* sp. (*op.cit.*: Pl. 84, fig. 9) is herein interpreted as a section of *D. ecougensis* evidently not passing through the median test plane and therefore not cutting the axial central column throughout. It is partly sectioned in the latest chamber, showing also the surrounding cribrate foramina. The dimensions (chamber height, thickness of wall, septa) also appear to be equal. The genus diagnosis includes the presence of a more or less opaque columellar mass in the central part of the chambers ("masse columellaire plus ou moins opaque ... dans la partie central des loges", ARNAUD-VANNEAU, 1980: p. 569). Let us remember that the term columella is typically reported from trochospirally coiled forms as a "solid, trochospiral structure formed by the basal walls of spiral chambers coalescing around the coiling axis" (HOTTINGER, 2006: p. 11). Conse-

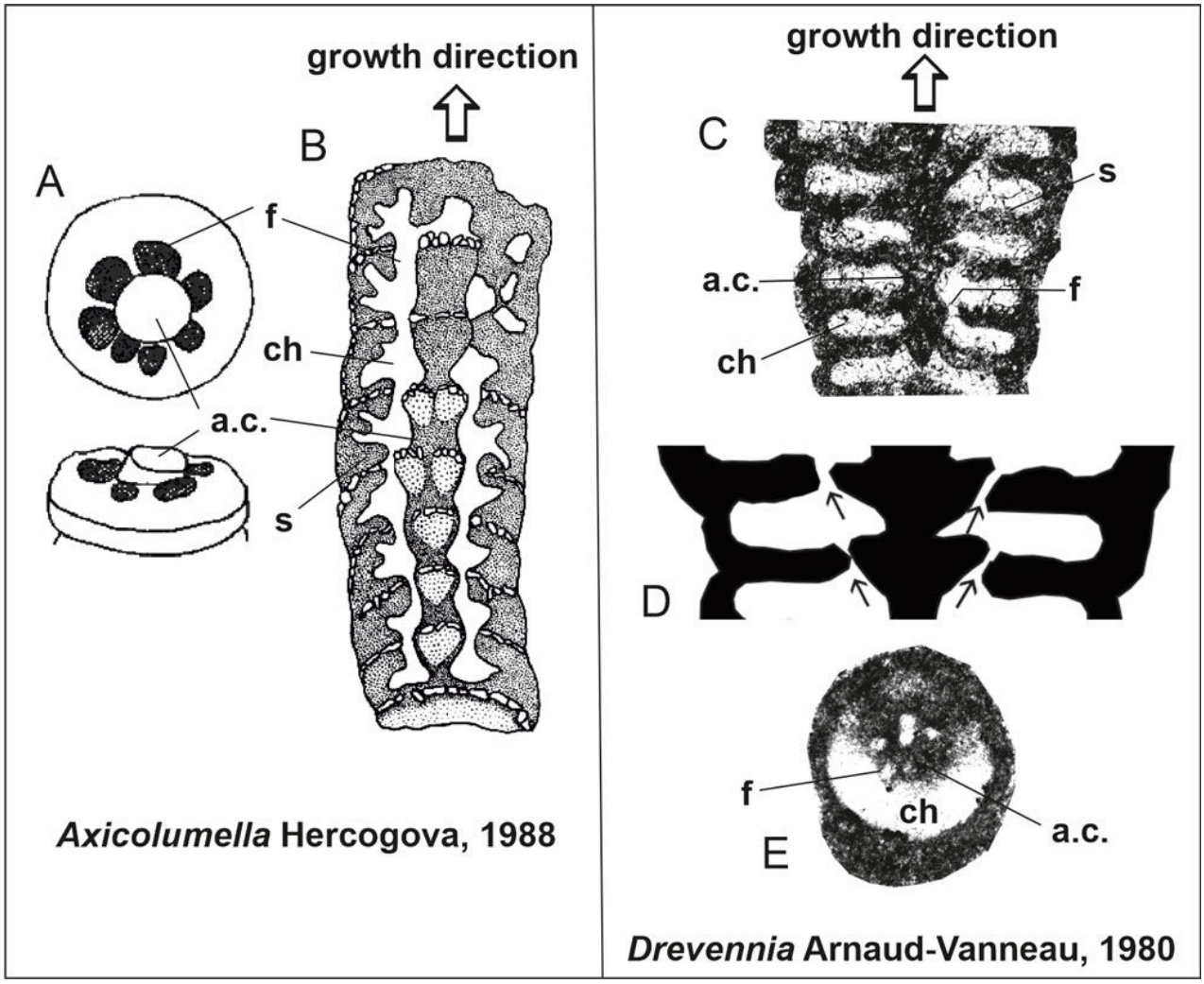

Figure 3: Comparison of *Axicolumella* HERCOGOVÁ (lower Turonian) (**A-B**) and *Drevennia* ARNAUD-VANNEAU (Barremian) (**C-E**). **A** *Axicolumella cylindrica* (PERNER), broken specimen showing open chamber with central axial column and attaching cribrate foramina. **B** *ibidem*; schematic drawing of longitudinal section showing internal structure (from HERCOGOVÁ, 1988, Fig. 11, pars, and Fig. 12, pars, modified). **C** *Drevennia flandrini* (ARNAUD-VANNEAU) comb. nov., excerpt from Fig. 4.E showing internal structure. **D** *ibidem*; schematic drawing from two chambers showing cone-in-cone structure of axial column, and oblique arrangement of foramina. **E** *ibidem*; oblique transverse section showing axial column and multiple foramina. Abbreviations: a.c. = axial column, ch = chamber lumen, f = foramen, s = septum.

quently, the term columella can only be applied to the early stage of *Drevennia* with trochospirally coiled chambers. In the uniserial stage this central (or axial) element occurs inside the chambers and is comparable to the structure reported from upper Cretaceous (lower Turonian) *Axicolumella* HERCOGOVÁ, 1988. This genus has uniserial chambers with "an axial column composed of segments, which are components of individual chambers" (HERCOGOVÁ, 1988: p. 173), and "these segments have the shape of truncated cones standing on the base with the smaller diameter" (remark: = widening in growth direction). A comparable structure with constrictions is also present in *Drevennia* and is visible in the holotype shown in figure 11 of Plate 84 of ARNAUD-VANNEAU (1980) (Fig. 1.F). *Axicolumella* belongs to the family Thomasinellidae (see KAMINSKI, 2014) displaying a distinctly agglutinated test with bifurcations. We state also some similarities to the Maastrichtian-Paleocene trochospirally coiled *Pachycolumella* SEPTFONTAINE *et al.*, 2019. It possesses a conspicuous central columella appearing as a helicoidal succession of inverted half-cones.

Other species: *Drevennia* is a monospecific genus.

Occurrences: Spain: Barremian and lower Aptian of Sierra de Montsec, Province Lerida-Huesca (BASSOULLET and MOULLADE, 1962; SCHROEDER *et al.*, 1982). Upper Barremian of Organyà Basin, Pre-Pyrenees, NE Spain (BERNAUS, 2000). Upper Aptian Reocin Formation of northern Spain, previously unrecorded (SCHLAGINTWEIT *et al.*, 2016: Cuchia quarry section). France: Barremian and Lower Aptian? of southeastern France (MOULLADE, 1960; ARNAUD-VANNEAU, 1980).

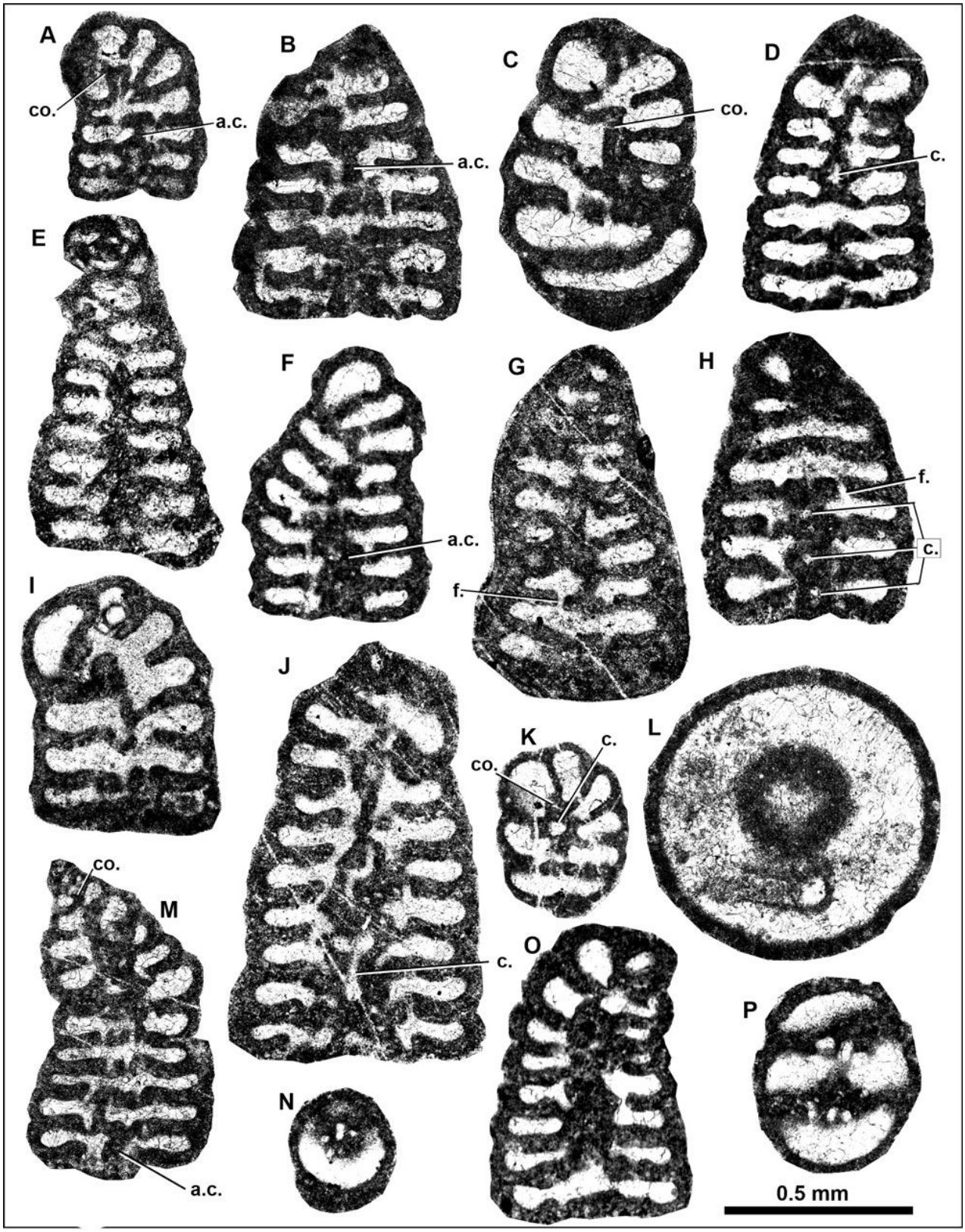

Figure 4: *Drevennia flandrini* (MOULLADE) comb. nov. from the upper Berriasian of the Kamenica section, eastern Serbia (A-N, P), and upper Aptian of the Cuchia quarry section, northern Spain (O). **A, C, I** Oblique axial sections of juvenile specimens. **B** Oblique section of the uncoiled adult part. **C, K** Oblique sections, including trochospirally coiled part. **D, F, G-H** Oblique axial sections only partly transjecting the trochospirally coiled part. **E** Axial section (detail shown in Fig. 3.C). **J** Subaxial section, not affecting the initial part. **L** Slightly oblique transverse section showing indistinct hollow axial column. **M** Axial section showing acute apex, test bent at the transition from trochospiral to uniserial parts. **N** Oblique transverse sections showing cribrate foramina. **O** Oblique axial section. **P** Oblique section of the uniserial part passing three chambers. Abbreviatons: a.c. = axial column, c. = canal, f. = foramen, co. = columella.

***Drevennia flandrini* (MOULLADE, 1960), comb. nov.**

(Figs. 1, 3.C-E, 4)

pars 1960 *Orbitolinopsis flandrini* n.sp. Forme A - MOULLADE, p. 190, Pl. 2, figs. 8-9, 14-16.

1980 *Drevennia ecougensis* n.sp. - ARNAUD-VANNEAU, p. 569, Pl. 55, fig. 8; Pl. 84, figs. 10-11.

1980 *Pseudolituonella* sp. - ARNAUD-VANNEAU, Pl. 84, fig. 9.

1982 *Drevennia* cf. *ecougensis* ARNAUD-VANNEAU - SCHROEDER *et al.*, Pl. 3, fig. 6.

non 1999 *Orbitolinopsis*? *flandrini* MOULLADE - BECKER, p. 415, Pl. 16, figs. 9-13.

2005 *Pseudolituonella gavonensis* FOURY - POLAVDER and RADULOVIĆ, Pl. 1, fig. 7.

Description: Test free, elongate, high conical to cylindroconical with acute apex, sometimes bent (Figs. 1.F, 4.M). The initial part shows a high trochospiral coiling (~4 to ~6 whorls; Fig. 4.M) about a central columella (Fig. 4.A-C) that may display a central canal (Fig. 4.K). Details on the embryonic chambers are not known. The transition to the following uniserial stage may be marked by a change in growth direction (Figs. 1.A, 1.F, 4.M). The main test part consists of up to 10 discoidal chambers distinctly broader than high, almost rectangular in axial sections. Transverse sections of this part of the test are circular. The central part of the chambers is occupied by an axial column (calcitic mass). Both, chambers and axial column slightly increase in width during ontogeny. Depending on the plane of the section, the column may appear massive (Figs. 1.D, 4.E, 4.G), display an indistinct central hollow (Fig. 4.D, 4.L), or is pierced by an undulating (spirally coiled?) canal (Figs. 1.F, 4.H, 4.J). The column consists of stacked cones (cone-in-cone structure) widening in the growth direction and slightly extending into the base of the succeeding chamber (Figs. 1.F, 3.C-D, 4.D-E). Multiple foramina are arranged straight or with an oblique axis closely around the axial column (Fig. 3.D). Wall thick, microgranular to finely agglutinating, appearing homogeneous.

Dimensions:

- test diameter: 0.4-0.6 mm (ARNAUD-VANNEAU, 1980: up to 0.42 mm)
- test height: 0.7-1.1 mm (MOULLADE, 1960: always > 1.0 mm; ARNAUD-VANNEAU, 1980: up to 1.125 mm)
- thickness septa: 0.030-0.045 mm
- chamber height (adult): 0.11-0.14 mm
- diameter foramina: 0.020-0.025 mm
- wall thickness: 0.04-0.05 mm
- number of chambers last 0.5 mm: 5 (rarely 6) (MOULLADE, 1960: 4-6*; ARNAUD-VANNEAU, 1980: 5-6* = measured from illustrations)

Stratigraphy: The specimens illustrated herein from eastern Serbia are of late Berriasian age. The Barremian age of the sections (platform-basin transitions) from southeastern France studied by MOULLADE (1960, 1966) and containing *D. flandrini* is based on ammonites. BASSOULLET and MOULLADE (1962) mention the species from the "Barremian" of Spain associated with orbitolinids that SCHROEDER *et al.* (1982: p. 916) recognized as *O. praesimplex*. According to SCHROEDER (1972), the latter species indicates an early Aptian age. The Reocin Formation of Cantabria, N-Spain is late Aptian in age (SCHLAGINTWEIT *et al.*, 2016, for details). Summarizing, the stratigraphic range of *D. flandrini* can be indicated as late Berriasian-earliest late Aptian (Gargasian).

Microfacies and palaeoenvironment of the Serbian material: The samples with *D. flandrini* are orbitolinid-bearing packstones/grainstones/wackestones with common remains of bivalves, gastropods, echinoids, and rare corals. The palaeoenvironment corresponds to an inner platform facies, which also includes oolithic shoals (see also SCHLAGINTWEIT *et al.*, 2019). The samples are characterized by a highly diverse assemblage of small and large-sized agglutinated and calcareous benthic foraminifers. Calcareous algae (dasycladalean and rarely also gymnocodiacean algae) may be present (BUCUR *et al.*, 2020, for details).

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