



The late Berriasian early evolutionary burst of the Orbitolinidae: New insights into taxonomy, origin, diversification and phylogeny of the family based on data from eastern Serbia

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This work is dedicated to the memory of Rolf SCHROEDER, an outstanding micropalaeontologist who recently passed away. His numerous works on the Orbitolinidae are basic literature for their taxonomy and his name will always be linked to this group of larger benthic foraminifera.

Abstract: New data from the Carpatho-Balkanides of eastern Serbia evidence the more or less near-simultaneous "explosive" first appearances of several genera of the Orbitolinidae in the late Berriasian. Most of the observed taxa were previously recorded from strata not older than the Late Hauterivian (= classical Urgonian of southeastern France), evidence that these ages refer to local first appearance data. The diversified assemblage from Serbia includes representatives of the subfamilies Dictyocoeninae: genera *Cribellopsis* ARNAUD-VANNEAU, *Montseciella* CHERCHI & SCHROEDER, *Orbitolinopsis* HENSON, *Urgonina* FOURY & MOULLADE, *Valserina* SCHROEDER & CONRAD, *Vanneauina* SCHLAGINTWEIT, and Dictyorbitolininae: genus *Paracoskinolina* MOULLADE. Representatives of the Orbitolininae (with complex embryo) have not been observed. They appeared later in the fossil record seemingly during the Late Hauterivian-early Barremian. All together 17 taxa are reported, of which three in open nomenclature. A new species is described as *Cribellopsis sudari* n. sp. The majority of the observed species display medium-to high-conical tests and a rather simple exoskeleton lacking horizontal partitions (rafters). The new data contradict a phylogenetic evolution of distinct genera displaying different internal test structures one after the other in time (= ancestor-descendant relationships) as postulated by some authors. The explosive radiation ("early burst") of the Orbitolinidae in the late Berriasian is accompanied by the first appearance date of several other large benthic foraminifera including mostly agglutinating (e.g., *Ammocycloculina*, *Choffatella*, *Drevennia*, *Eclusia*, *Moulladella*, *Pfenderina*, *Pseudotextulariella*) but also complex porcelaneous taxa (*Pavlovcevina*) providing evidence for a bioevent in this time period that exceeds the number of taxa originating in the previous (Tithonian) and the following stage (Valanginian). The early evolutionary history of the Orbitolinidae can be considered a classical example of adaptive radiation within the clade's history.

Key-words:

- Foraminifera;
- Orbitolinidae;
- taxonomy;
- phylogeny;
- biostratigraphy

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Résumé : La diversification précoce des Orbitolinidae au Berriasien supérieur : Nouvelles perspectives sur la taxonomie, l'origine, la diversification et la phylogénie de la famille basée sur des données de Serbie orientale.- De nouvelles données provenant des Carpatho-Balkanides de Serbie orientale témoignent de premières apparitions "explosives" plus ou moins simultanées de plusieurs genres d'Orbitolinidae dans le Berriasien supérieur. Précédemment la plupart des taxons observés étaient répertoriés dans des couches guère plus anciennes que l'Hauterivien supérieur (= Urgonien classique du sud-est de la France), démontrant que ces âges de première apparition n'ont de signification que localement. L'assemblage diversifié de Serbie comporte des représentants des sous-familles Dictyococoninae avec les genres *Cribellopsis* ARNAUD-VANNEAU, *Montseciella* CHERCHI & SCHROEDER, *Orbitolinopsis* HENSON, *Urgonina* FOURY & MOULLADE, *Valserina* SCHROEDER & CONRAD et *Vanneauina* SCHLAGINTWEIT, et Dictyorbitolininae avec le genre *Paracoskinolina* MOULLADE. Aucun représentant des Orbitolininae (à embryon complexe) n'a été observé, cette sous-famille apparaissant plus tardivement dans le registre fossile, apparemment durant l'Hauterivien supérieur-Barrémien inférieur. Au total, 17 taxons sont reconnus, parmi lesquels trois sont laissés en nomenclature ouverte. Une nouvelle espèce est décrite : *Cribellopsis sudari* n. sp. La majorité des espèces observées montre des tests coniques moyens à hauts et un exosquelette plutôt simple dépourvu de cloisonnettes horizontales ("rafters"). Les nouvelles données contredisent une évolution phylogénétique des différents genres montrant différentes structures internes de test se succédant dans le temps (= relations ancêtre-descendant) comme certains auteurs le postulent. L'explosion radiative ("diversification précoce") des Orbitolinidae au Berriasien supérieur s'accompagne de l'événement de première apparition (FAD) de plusieurs autres grands foraminifères benthiques comprenant des taxons essentiellement agglutinants (e.g., *Ammocycloloculina*, *Choffatella*, *Drevennia*, *Eclusia*, *Moulladella*, *Pfenderina* et *Pseudotextulariella*) mais aussi porcelanés complexes (*Pavlovcevina*), constituant la preuve d'un bio-événement majeur à cette époque qui dépasse le nombre de taxons apparaissant dans les étages précédents (Tithonien) et suivant (Valanginien). L'histoire évolutive initiale des Orbitolinidae peut être considérée comme un exemple classique de radiation adaptative au sein de l'histoire d'un clade.

Mots-clés :

- foraminifères ;
- Orbitolinidae ;
- taxinomie ;
- phylogénie ;
- biostratigraphie

1. Introduction

Lower Cretaceous shallow-water carbonates of the Carpatho-Balkanides (e.g., HAAS *et al.*, 2011, Fig. 1) are outcropping in a wide area south of the Danube River extending from Southern Romania to Eastern Serbia and to Western Bulgaria. Studies of these Urgonian-type limestones were made by JANKIČEVIĆ (1978, 1996) who focused on the rudist assemblages. Micropalaeontological associations (calcareous algae, benthic foraminifera) have been investigated by RADOIČIĆ (1978), BUCUR *et al.* (1995, 2020), SUDAR *et al.* (2008), POLAVDER and RADULOVIĆ (2005), POLAVDER (2014) and SCHLAGINTWEIT *et al.* (2019a, 2019b). The stratigraphy of these shallow-water carbonates was a matter of discussion in the literature. Part of the limestones was considered to be Barremian-Aptian in the Geological map sheet Aleksinac (KRSTIĆ *et al.*, 1978, 1980). In contrast here-to, RADOIČIĆ (1978) described calcareous algae from this area highlighting a "Neocomian" age (see also BUCUR *et al.*, 1995). POLAVDER (2014) studied the rich orbitolinid assemblages from the Kamenica section of the Kurilovo anticline. As some of the identified species were previously known with their "first appearance dates" from the Upper Hauterivian-lower Barremian strata of southeastern France (CLAVEL *et al.*, 2014), POLAVDER (2014) concluded that the upper part of the studied carbonate sequence belongs to the Upper Hauterivian (Fig. 1). The most contradictionary fact is the coexistence of typically Berriasian-Va-

langinian algal and benthic foraminiferal assemblages together with these "Upper Hauterivian-lower Barremian" orbitolinids. Starting from these contradictions, the study of some geological sections from the western part of the Carpatho-Balkanides (Eastern Serbia) was continued in order to clarify the age of these deposits through detailed sampling and micropalaeontological investigations. BUCUR *et al.* (2020) documented a well diversified assemblage of calcareous algae, benthic foraminifera, associated with rare calpionellids that indicate a late Berriasian age. In the framework of this study, rich material of orbitolinids was obtained from the thin-sections studied but lacking systematic description. Belonging to the oldest known records of the Orbitolinidae, they provide many new data and insights on the taxonomy, biostratigraphy, and phylogeny of the whole group. These results are presented herein.

2. Geological overview

The Lower Cretaceous deposits of the Getic domain which outcrop in the Southern Carpathians (Romania) in the Reșița-Moldova Nouă zone also continues within the Carpatho-Balkanides (Eastern Serbia) between the Danube and Western Bulgaria (Fig. 1.A). The westernmost part of this zone comprises the folded geological structures Kurilovo and Ozren made of Paleozoic and Mesozoic rocks. According to the geological map 1:100.000 (sheet Aleksinac, KRSTIĆ *et al.*, 1978, 1980) this area belongs to the NNW-SSE oriented Gornjak-Stuva Planina Unit.

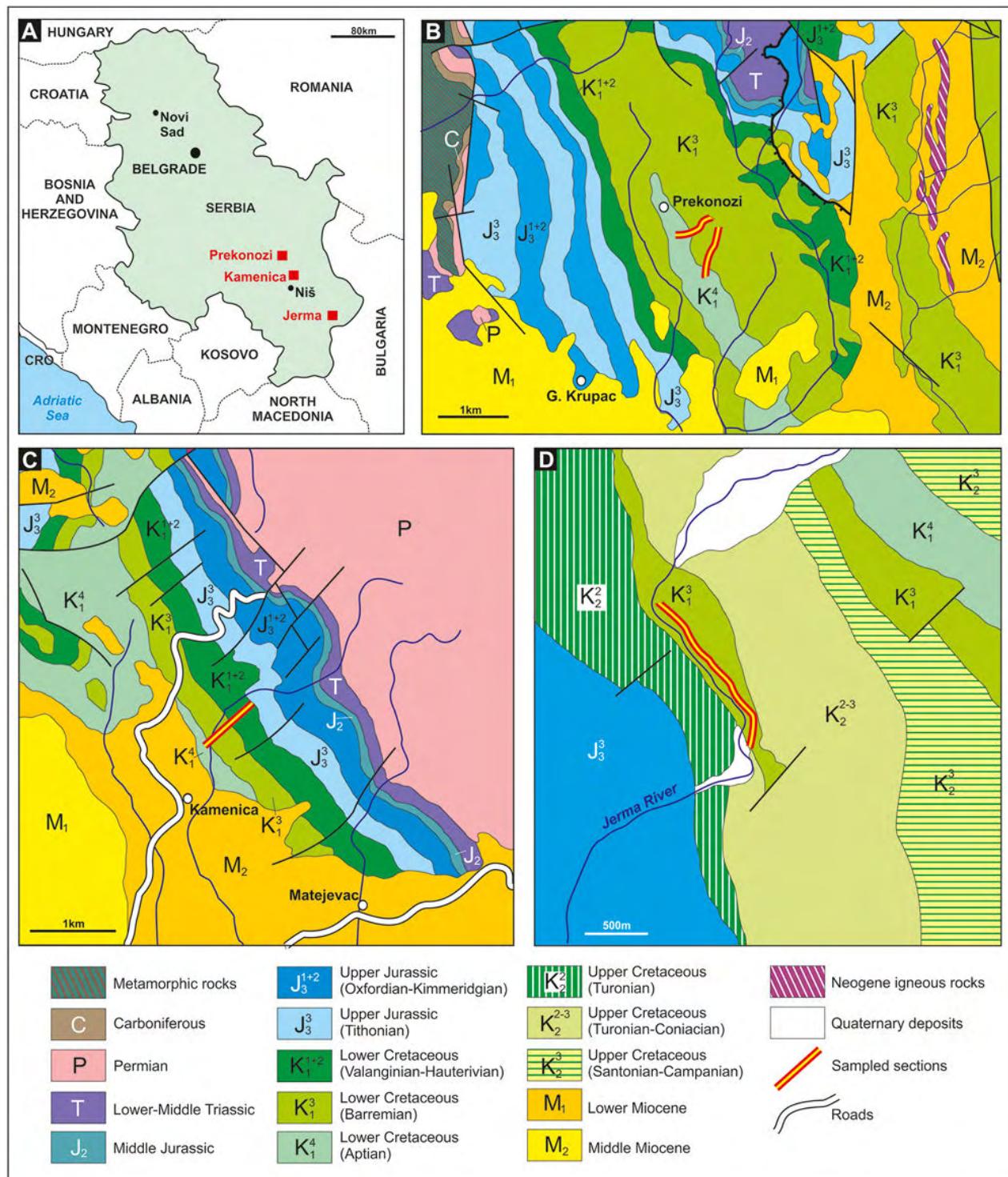


Figure 1: Location of the studied material (from BUCUR *et al.*, 2020, Fig. 1). A. General sketch map of Serbia with location of the three studied sections. B. Geological map of the Prekonozi area. Part of the Basic Geological Map of SFRY, 1:100,000, Sheet Aleksinac (K 34-20) (KRSTIĆ *et al.*, 1978), modified. C. Geological map of the Kamenica area. Part of the Basic Geological Map of SFRY, 1:100,000, Sheet Aleksinac (K 34-20) (KRSTIĆ *et al.*, 1978), modified. D. Geological map of the Jerna River Canyon area, redrawn and modified from BUCUR *et al.* (1995).

The Kurilovo folded structure (PETKOVIĆ, 1935), including the studied Kamenica section (Fig. 1.C) consists of an asymmetrical anticline associated with several minor folds (KRSTIĆ *et al.*, 1978, 1980). The core of this structure is made of Paleozoic deposits (Devonian, Carboniferous, and Permian) being flanked by Mesozoic (Triassic, Jurassic, and Lower Cretaceous) sequences. Ac-

cording to KRSTIĆ *et al.* (1980), the Lower Cretaceous deposits are represented by Valanginian-Aptian carbonates succeeded by a sequence of Aptian sandy limestones. Towards the NW, Lower Cretaceous deposits are outcropping near to Prekonozi (belonging to the Ozren folded structure) characterized by similar lithostratigraphic features as in Kurilovo (Fig. 1.B). The age of a part

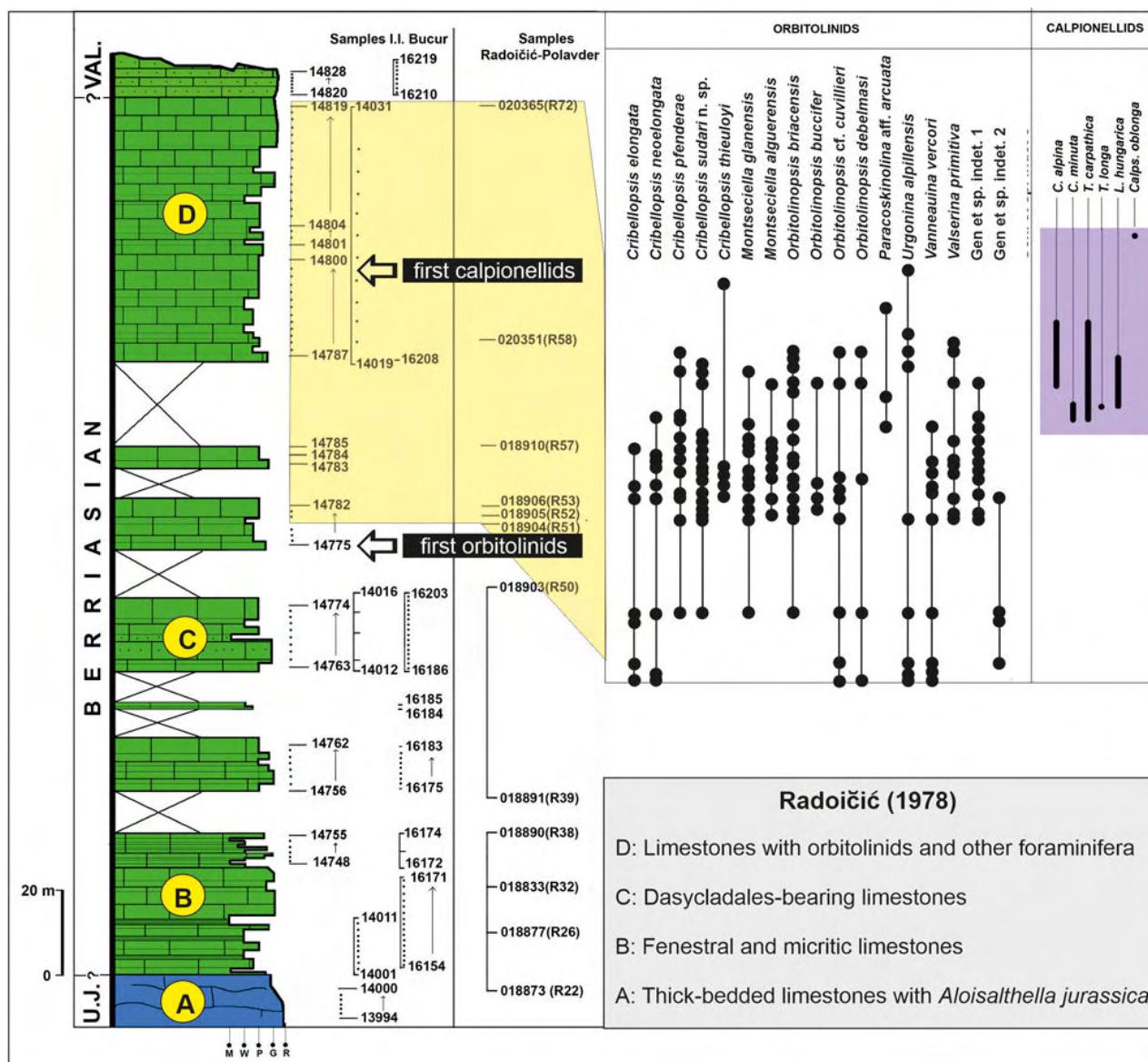


Figure 2: Kamenica section showing distribution of Orbitolinidae and Calpionellidae (modified from BUCUR *et al.*, 2020). Lithologic units (A to D) in accordance with RADOIĆIC (1978). Note: Gen. et sp. indet. 3 is absent in the Kamenica section.

of the limestones from both structures (considered as Barremian-Aptian on the 1:100,000 geological map-sheet Aleksinac, KRSTIĆ *et al.*, 1978, 1980) was reconsidered by POLAVDER & RADULOVIĆ (2005) and POLAVDER (2014) as Upper Hauterivian-lower Barremian based on orbitolinid assemblages. In SE, close to the Serbian-Bulgarian border, the Lower Cretaceous carbonates outcrop in the Jerma River Canyon. On the geological map of this area (sheet Breznik, ANDELKOVIĆ *et al.*, 1975, 1977), they have been attributed to the Barremian, forming a narrow strip, flanked by two faults between an Upper Cretaceous sedimentary sequence. Based on the dasycladales and benthic foraminifera, the age of the Jerma River Canyon limestones (Fig. 1.D) was revised by BUCUR *et al.* (1995) and assigned to the Berriasian-Valanginian. For the lithological evolution of the three sections, stratigraphic and micropalaeontological data reference is made to BUCUR *et al.* (2020). In all three sections, the orbitolinids

occur together with rare calpionellids in the upper part of the succession. Generally, the higher energy deposits (e.g., grain-supported fabrics) from the Prekonozi section reflect an outer platform setting compared to the inner platform facies (e.g., mud-supported fabrics) of the Kamenica section. This trend is also suggested by a less diverse assemblage of orbitolinids. Therefore, the main data included in the systematic part and the discussion on other aspects such as phylogeny refers essentially to the Kamenica section (Fig. 2).

3. Biostratigraphy

For the studied Lower Cretaceous orbitolinid-bearing sections of eastern Serbia, there is no calibration with ammonite zones, unlike southeastern France (e.g., CLAVEL *et al.*, 2014). There, the biostratigraphy of the occurring orbitolinids is well constrained based on ammonoids and calpionellids due to their occurrence in resediments within platform-to-basin depositional settings. In



the Serbian sections, numerous benthic foraminifera and Dasycladidae have been observed that are also occurring in the Lower Cretaceous of Switzerland and southeastern France (e.g., DARSAC, 1983; BLANC, 1996; GRANIER, 2019). The biostratigraphic setting of the studied sections has been discussed in detail by BUCUR *et al.* (2020). Therefore, only some remarks are provided herein.

Biostratigraphic important Dasycladidae are represented for example by *Salpingoporella steinhauseri* CONRAD *et al.* or *Falsolikanella campanensis* (AZÉMA & JAFFREZO). The latter species has recently been defined as an upper Berriasian marker taxon by GRANIER (2019). Although it has also been observed in the lower part of the Kamenica section that might be early Berriasian in age, *F. campanensis* has never been observed in Valanginian strata. Among the benthic foraminifera the occurrence of *Danubiella gracilima* NEAGU, *Pfenderina neocomiensis* (PFENDER) (Fig. 3.5-3.8), *Pseudotextulariella courtionensis* BRÖNNIMANN is worth mentioning because the FAD of *P. neocomiensis* consistently indicates the middle part of the upper Berriasian (base *alpiliensis* subzone) (DARSAC, 1983; BOISSEAU, 1987; VIRGONE, 1997; GRANIER, 2019). According to BLANC (1996, Fig. 58), the FAD's of *Pfenderina neocomiensis* (PFENDER) and the calpionellid *Lorenziella hungarica* KNAUER & NAGY (= *hungarica* Zone) are contemporaneously recorded from the base of the *alpiliensis* ammonoid zone referring to the middle part of the upper Berriasian. Both taxa are also recorded from upper Berriasian sections studied herein. In the Kamenica section, the first but undeterminable orbitolinids are recorded from sample 14776 (Fig. 2). Higher in the section, the Orbitolinidae appear contemporaneously with different taxa. *P. neocomiensis* appears about 20 m above the first orbitolinids and persists throughout the uppermost part of the section. Calpionellids (incl. *Lorenziella hungarica*) are recorded higher up in the section. The whole calpionellid assemblage (see BUCUR *et al.*, 2020) corresponds to the *Calpionellopsis* zone, and, most probably to the *oblonga* subzone that characterizes the upper Berriasian (REMANE *et al.*, 1986; POP, 1994; BLAU & GRÜN, 1997; REHÁKOVÁ & MICHALÍK, 1997; LAKOVA & PETROVA, 2013; BENZAGGAGH, 2020). The overall succession with fenestral limestones (intertidal) to subtidal foraminiferan-algal wackestones associated with rare calionellids in the upper part reflects a shift from internal to external platform settings. This might explain the time discrepancy between the offset occurrences of *P. neocomiensis* and *L. hungarica* in the Kamenica section (Fig. 2). The thickness of the orbitolinid-bearing strata in the Kamenica section is about 78 m, interrupted by two passages in the field without exposed rocks (Fig. 2). The first (not further determined) specimens occur in sample 14776 and slightly higher up, almost all the different taxa reported herein have been observed. There might be minor differences in the appearances of individual species in the studied

section, but these are difficult to verify. Taking into account sample biasing, incompleteness due to exposure gaps etc., all forms are treated as more or less contemporaneous herein, and assigned to the late Berriasian. In previous works, the upper orbitolinid-bearing part of the Kamenica section was attributed to the Late Hauterivian (POLAVDER, 2014; with kind assistance of B. CLAVER, see acknowledgements therein). This assignment was due to the occurrence of several Orbitolinidae that have their "first appearance datum" (FAD) in the Late Hauterivian times (e.g., CLAVER *et al.*, 2014). This assignment was state-of-the-art because these taxa have so far nowhere else been reported from older strata. The published data on the recovered orbitolinids from eastern Serbia, however, are in contradiction to our results, i.e., a late Berriasian age. Except those described as new or in open nomenclature herein, all other orbitolinid species from eastern Serbia are well known from the classical Urgonian of southeastern France (ARNAUD-VANNEAU, 1980; CLAVER *et al.*, 2009a, 2009b, 2010, 2014; GRANIER *et al.*, 2013a, 2013b, 2017). Based on numerous hemipelagic sections comprising ammonites and redeposited orbitolinids, a new detailed range chart ("nouvelle biostratigraphie des orbitolinidés") for 37 orbitolinid species [excluding the pfenderinid *Moulladella jourdanensis* (FOURY & MOULLADE); see BUCUR & SCHLAGINTWEIT, 2018; Fig. 3.1-3.4] has been provided by CLAVER *et al.* (2014) for this area. The first species are recorded from the lowermost Hauterivian (Sayni ammonite zone), and the latest from the lower Aptian (top Furcata zone). Among the numerous orbitolinids, just a few are considered as "marker species", such as *Valserina primitiva* for the Upper Hauterivian (CHAROLLAIS *et al.*, 2009, Fig. 2; CLAVER *et al.*, 2014, Fig. 5). Others like *Paracoskinolina arcuata* have a longer range, from the Late Hauterivian to the early Aptian (CLAVER *et al.*, 2014, Fig. 5). For the individual ranges of the orbitolinids (and other taxa), GRANIER *et al.* (2013a, p. 140; 2017, p. 118) highlighted the "calibration of the First Appearance Datum - FAD - (and eventually the Last Appearance Datum - LAD ...)". Both, the FAD and LAD define the total range (zone) of a given taxon (e.g., NICHOLS, 2009), that should ideally correspond to its origination and extinction (HOLLAND & PATZOWSKY, 2002, for details; GUEX *et al.*, 2016, p. 109: first phyletic appearance of a species). Lithostratigraphically, the first orbitolinids of southeastern France are recorded from the "Urgonien jaune" (e.g., CLAVER *et al.*, 2014, Fig. 39), nowadays replaced by the name Vallorbe Formation (STRASSER *et al.*, 2016). The Lower Hauterivian is represented by hemipelagic marls and other lithologies unsuitable for the proliferation of orbitolinids, in particular dictyocrinids (STRASSER *et al.*, 2016, e.g., Grand Essert Formation). In our opinion it concludes that the appearances of the orbitolinids in the Upper Hauterivian in southeastern France are facies-controlled, and cannot



be considered as FADs per definition as the first (oldest) appearances in the geological record. That in turn means that the "new biostratigraphy" from southeastern France (CLAVEL *et al.*, 2014) consists of regional and not supraregional individual ranges, and not taxon range zones. The transferation of these ranges from southeastern France to other areas (with differing lithostratigraphic evolution) led to the dating of the orbitolinid-bearing strata of the Kamenica section as Late Hauterivian (POLAVDER, 2014). This was based on the occurrence mainly of the "marker" species *Valserina primitiva*. Referring to the numerous publications of CLAVEL and co-workers, POLAVDER (2014, p. 12) stated that the "results are in agreement with recent integrated studies carried out in SE France and adjacent French-Suisse Jura". Following the general subdivision of the Lower Cretaceous strata by RADOIĆIĆ (1978), the Kamenica section comprises peritidal "fenestral and micritic limestones" (unit B), followed by "Dasycladale-bearing limestones" (unit C), and finally "limestones with orbitolinids and other foraminifera" (unit D). If unit B appears as not a very favourable environment for the orbitolinids, at least the subtidal inner platform facies of unit C can be considered as suitable facies realm. We therefore assume that the base of unit B is very close to the real FADs of the species described herein being aware that "the first occurrence of a species in any given local section is likely to postdate the time of origination of the species, and the last occurrence is likely to predate the extinction" (HOLLAND & PATZKOWSKY, 2002, p. 134). In any case, the stratigraphic ranges of several species have to be enlarged significantly. *V. primitiva* now spans about two stages (upper Berriasian to Upper Hauterivian), but still remains one of the stratigraphically more restricted species of the studied assemblage. For *V. primitiva*, the given interval most likely corresponds to the total taxon range. Others, like *Cribelopsis neelongata*, ranging over several stages, from the upper Berriasian to the lower Aptian. In this case, the correspondance of the youngest record to the LAD (see CLAVEL *et al.*, 2014, Fig. 5) is uncertain since the last orbitolinid occurrences in the late lower Aptian in southeastern France coincides with environmental changes, *i.e.*, to platform drowning and demise of shallow water carbonates. Summarizing, the detailed orbitolinid ranges in southeastern France (CLAVEL *et al.*, 2014) are in no case doubted. But the transferation of these data by subsequent workers to other regions should (i) keep in mind that these are local orbitolinid ranges and (ii) the usage of the terms FAD/LAD [First/Last Appearance Datum] or FO/LO [First/Last Occurrence] (*e.g.*, MASSE & FENERCI-MASSE, 2013) may be misleading. As GUEX *et al.* (2016, p. 109) summed up: "datum lost its original meaning" and is treated "synonymous with first local appearance and first local disappearance of a species" by many workers.

4. Material and methods

The present study is based on thin-sections coming from three localities or sections (Fig. 1): Kamenica and Prekonozzi (situated north of Niš city) and Jerma River Canyon (south of Pirot town, easternmost Serbia). More than 280 samples were collected (most of them, 198, from the Kamenica section) for thin-section preparation. In the framework of the present study, also 114 thin-sections collected from Kamenica section belonging to Rajka RADOIĆIĆ's collection were reanalysed. All of the used thin-sections are deposited in Rajka RADOIĆIĆ's private collection numbers RR 3412 to RR 4049 and in Ioan I. BUCUR collection (14001 to 14034; 14713 to 14739; 14748 to 14838; 16149 to 16227, and 16319 to 16370) from the Department of Geology (Babeş-Bolyai University in Cluj-Napoca).

The upper Berriasian orbitolinid fauna shows striking similarities to the one from the Urgonian type-area in southern Switzerland and southeastern France. Hence, the numerous works (including type descriptions) of (in alphabetical order) A. ARNAUD-VANNEAU (ARNAUD-VANNEAU, 1976, 1980; ARNAUD-VANNEAU & THIEULOT, 1972; ARNAUD-VANNEAU & SCHROEDER, 1976), B. CLAVEL (CHAROLLAIS *et al.*, 2009; CLAVEL in GRANIER *et al.*, 2013a, 2013b, 2017; CLAVEL *et al.*, 2014), G. FOURY (FOURY & MOULLADE, 1966; FOURY, 1968), M. MOULLADE (MOULLADE, 1960, 1966), and R. SCHROEDER (SCHROEDER & CHAROLLAIS, 1966; SCHROEDER *et al.*, 1969; CHERCHI & SCHROEDER, 1978, 1999) should be highlighted for determination purposes.

5. Systematics

The orbitolinid assemblage from the upper Berriasian of eastern Serbia comprises 17 taxa belonging to seven genera. Three taxa were described in open nomenclature. The majority of the observed genera belong to the subfamily Dictyocininae MOULLADE, and a single genus of the Dictyorbitolininae SCHROEDER: *Paracoskinolina* MOULLADE. No Orbitolininae (with complex embryo) were observed. According to present knowledge, they appear in the Late Hauterivian [SCHROEDER & CHERCHI, 2002; CLAVEL *et al.*, 2014: *Eopalorbitolina pertenuis* (FOURY)]. For each species, the occurrences in the studied three sections of eastern Serbia (Kamenica, Jerma, Prekonozzi) are indicated with semi-quantitative abundances (very rare, rare, common, abundant). These informal statements however must bear in mind that the data base (*e.g.*, number of thin-sections per studied section) is not balanced (see Material and Methods). For the already known species, reference is made to detailed descriptions available in the literature. Some additional remarks/observations from the Serbian material are provided along with informations on the biometric data (D = test diameter, H = test height).

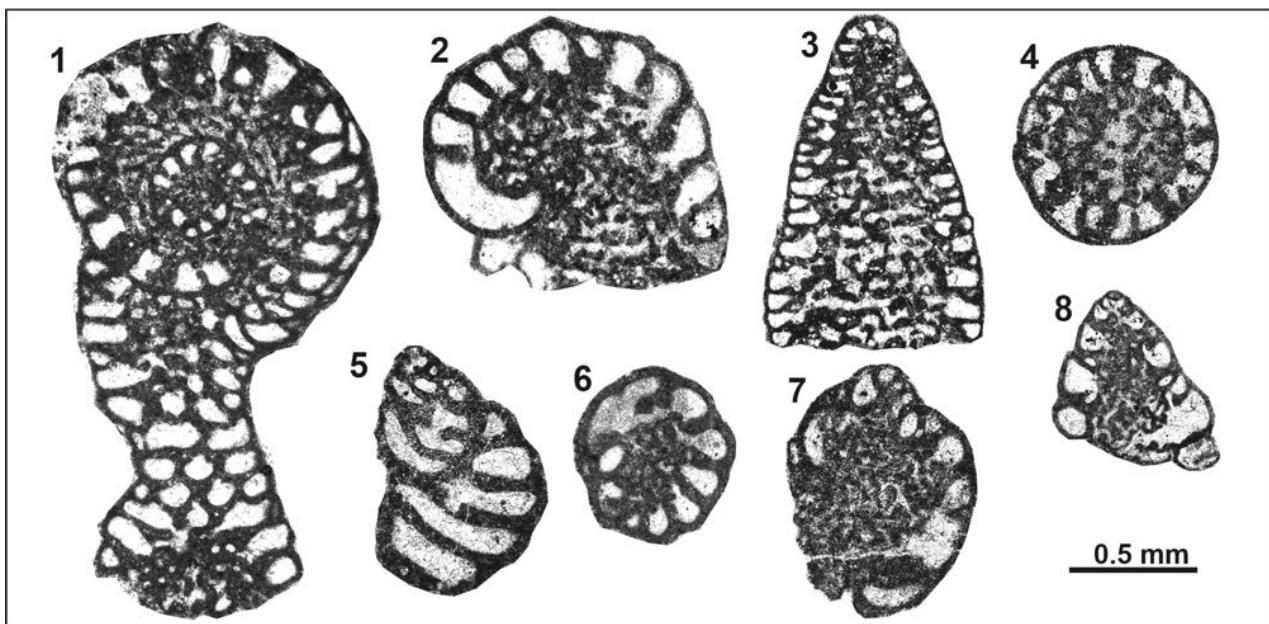


Figure 3: Pfenderinids *Moulladella jourdanensis* (FOURY & MOULLADE) (1-4) and *Pfenderina neocomiensis* (PFENDER) (5-8) from the upper Berriasian of the Kamenica section, Eastern Serbia. **1-2:** Subaxial sections of adult and juvenile microspheric specimens. Thin-section 14729, 14032. **3:** Axial section of a megalospheric specimen. Thin-section RR 4029. **4:** Transverse section. Thin-section 14808. **5:** Tangential section. Thin-section 14830. **6:** Transverse section. Thin-section 14803. **7:** Subaxial section. Thin-section 14805. **8:** Axial section. Thin-section 14792.

The high-rank classification follows PAWLowski et al. (2013). For the low-rank classification, see KAMINSKI (2014). For glossary, report to HOTTINGER (2006). Note: orientation of structures (e.g., pillars) with respect to chamber (floor versus ceiling or roof) in direction of growth (see HOTTINGER & DROBNE, 1980, p. 205). The common agglutinated conical species *Moulladella* (former *Paracoskinolina*) *jourdanensis* (FOURY & MOULLADE) is not treated herein due to its recent transfer to the Pfenderinidae (see BUCUR & SCHLAGINTWEIT, 2018) (Fig. 3.1-3.3).

Phylum Foraminifera ORBIGNY, 1826
Class Globothalamea PAWLowski et al., 2013
Order Loftusiida
KAMINSKI & MIKHALEVICH, 2004
Suborder Loftusiina
KAMINSKI & MIKHALEVICH, 2004
Superfamily Orbitolinoidae MARTIN, 1890
Family Orbitolinidae MARTIN, 1890
Subfamily Dictyoconinae SCHUBERT, 1912
Genus *Cribellopsis* ARNAUD-VANNEAU, 1980

Remarks: All species of *Cribellopsis* show more or less identical subdivision of the marginal zone: no horizontal partitions, and one to three intercalary beams between the main beams (ARNAUD-VANNEAU, 1980; CHIOCCHINI, 1989). The reticulate central zone may be well developed or reduced in different species. This means in turn that species are defined mainly by size and/or general morphology and in cases by indefinite features (more ..., less ...) (Fig. 4).

***Cribellopsis elongata* (DIENI et al., 1963)**
 (Pl. 1, figs. 1-9)

- 1963** *Orbitolinopsis elongatus* n. sp. - DIENI et al., p. 4; Pl. 1, figs. 1-2, 4
- 1980** *Cribellopsis elongata* (DIENI, MASSARI & MOULLADE) nov. comb. - ARNAUD-VANNEAU, p. 678; Pl. 96, figs. 3-8 (see comments of BECKER, 1999, below)
- 2009** *Cribellopsis elongata* - CHAROLLAIS et al.; Pl. 5, fig. 21
- 2010** *Cribellopsis elongata* - CLAVEL et al.; Pl. 1, specimen 6892-1b; Pl. 5, specimen GC13.4a; Pl. 7, specimen 161.29-1b, 471-16a, 387.4b1, 471-1b; Pl. 9, specimens 387.9-3b, 387.9-2b, 387.14-7a; Pl. 14, specimen 407.3c3; Pl. 20, specimens Ai31-11a, Ai19-12a, Ai19-1b; Pl. 27, 218.5-5b; Pl. 29, specimen 226.22-5e
- 2013a** *Cribellopsis elongata* - CLAVEL in GRANIER et al., p. 151; Pl. 5, figs. 1-5, 18, 20
- 2014** *Cribellopsis elongata* - CLAVEL et al.; Pl. 6, specimen MC233-6b; Pl. 8, specimen 511-12a; Pl. 10, specimen 400-7a; Pl. 12, specimen 470-5c; Pl. 14, specimen 464-6a; Pl. 16, specimen 493.3-24a; Pl. 21, specimen 6870-6a; Pl. 23, specimen 410-17a; Pl. 27, specimen LEST27-17a, Pl. 28 (topotypes!), specimens 7343-2a, 7343-1b, 7341-42a, 7341-12a; Pl. 29, specimens 7871-5b, 7871-8a; Pl. 31, specimens 6816-2a, 6816-1a, SANF1-1b, SANF1-1a, SANF10-1a
- 2015** *Cribellopsis elongata* - BONVALLET; Pl. 4.2, figs. 8-9
- 2017** *Cribellopsis elongata* - CLAVEL in GRANIER et al., p. 130; Pl. 5, figs. 1-5, 18, 20
- 2017** Dicycoconid foraminifera - UNGUREANU et al. 2017; Fig. 7.n
- non 2018** *Cribellopsis elongata* - GHAFOR & MOHALDEEN; Pl. 2, fig. c (= ?*Coscinoconus* sp., see GRANIER, 2020)

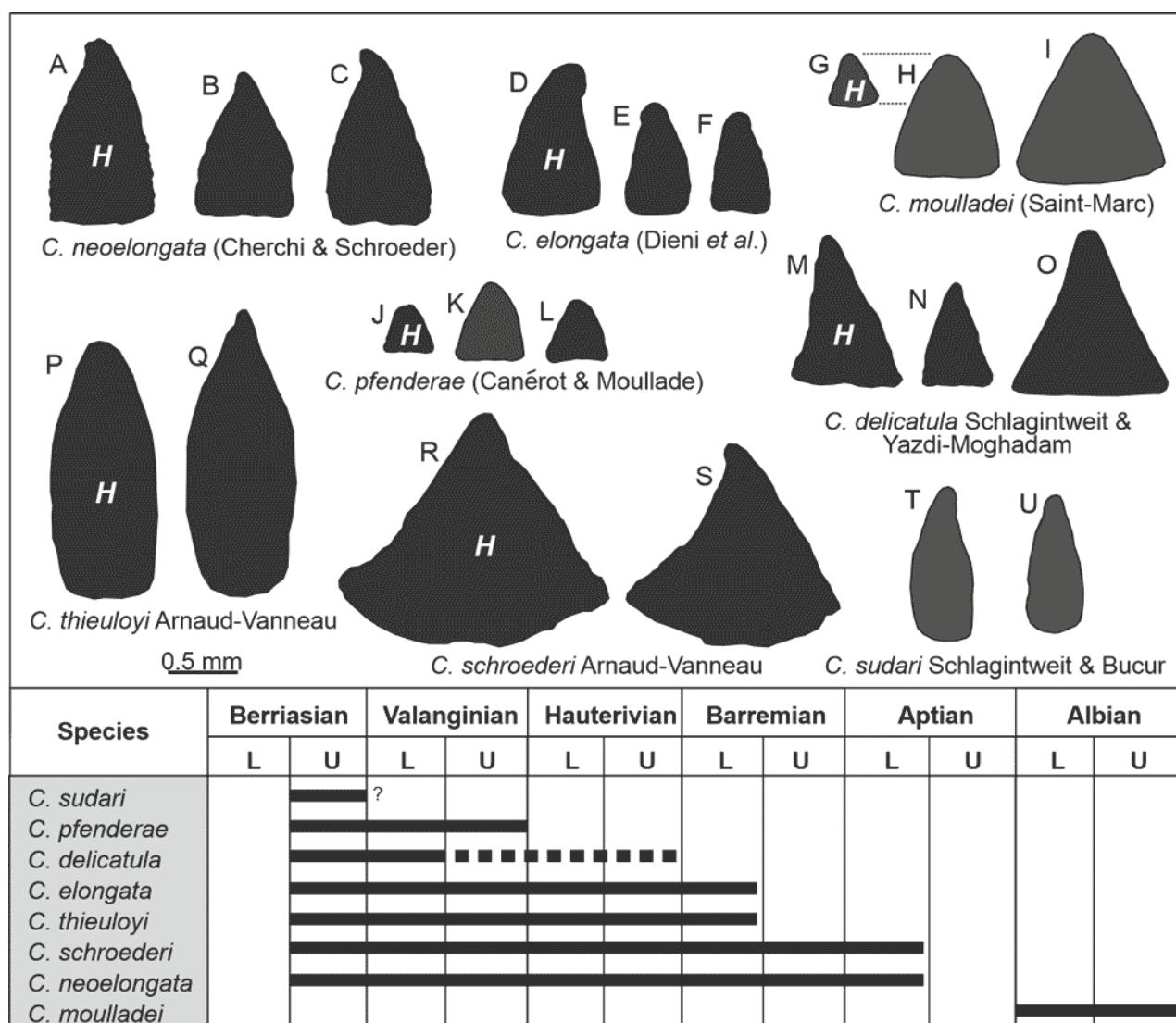


Figure 4: Morphological variety of different *Cribellopsid* species and known stratigraphic ranges.

Remarks: The species has witnessed differing views on its taxonomy and validity that is shortly summarized herein. DIENI *et al.* (1963) described two new species as *Orbitolinopsis elongatus* and *O. subkiliani* from the Barremian of the region of Orosei, Sardinia. All specimens illustrated are axial or subaxial sections; no transverse sections have been provided. From the four specimens of *O. elongatus*, only the holotype is from the type-locality, while the three paratypes are from southeastern France (Drôme and La Bédoule areas). It is worth mentioning here, that from the lower Barremian of Cassis-La Bédoule, CLAVEL *et al.* (2014, Fig. 28) illustrated four topotype specimens (Pl. 28, therein, see synonymy). From the Orosei area (incl. the type-locality of *O. subkiliani*), CHERCHI and SCHROEDER (1978) were studying the orbitolinid fauna, including the two forms described by DIENI *et al.* (1963). The authors state (p. 161) that *O. elongatus* and *O. subkiliani* should only differ from their dimensions (diameter, height, ratio d/h) and the number of chambers in the rectilinear stage. Summarizing, CHERCHI and SCHROEDER (1978) concluded that *O. elonga-*

tus represents a synonym of *O. subkiliani*. ARNAUD-VANNEAU (1980, p. 678) transferred *O. elongatus* to the genus *Cribellopsid* including the holotype, and two of the three paratypes of DIENI *et al.* (1963). ARNAUD-VANNEAU (1980) studying the type-material of DIENI *et al.* (1963) concluded that the internal structure of *O. elongatus* and *O. subkiliani* is "sensiblement différente" thereby rejecting the synonymization proposed by CHERCHI and SCHROEDER (1978). Whether *O. subkiliani* is a valid species has not been further considered by ARNAUD-VANNEAU. In any case it is lacking in the comparative table of *Orbitolinopsis* species occurring in the Vercors and Chartreuse areas of southeastern France (ARNAUD-VANNEAU, 1980, Fig. 226). BECKER (1999) followed the view of CHERCHI and SCHROEDER (1978) treating *O. elongatus* a synonym of *O. subkiliani*. She also noted that the specimens illustrated by ARNAUD-VANNEAU (1980) as *Cribellopsid elongatus* are not identical to the species described by DIENI *et al.* (1963) because of the presence of intercalary beams. The latter are not visible in the specimens from Sardinia (BECKER, 1999, p. 412), but this is, in our opinion,



just due to the axial/subaxial section planes. CLAVEL *et al.* (2010, p. 6) finally observed the structural identity ("structure absolument identique") of *O. subkiliani* and *O. kiliani*. Based on observations on a large number of specimens from southeastern France, CLAVEL *et al.* (2010) rejected the synonymization of *O. elongata* with *O. subkiliani*, as proposed by CHERCHI & SCHROEDER (1978) and BECKER (1999). Instead, these show generic differences (here: *Cribelopsis* vs. *Orbitolinopsis*, see ARNAUD-VANNEAU, 1980), a view that is followed here.

Dimensions: D = 0.35-0.55 mm; H = 0.5-0.85 mm; D/H 0.59-0.72

Occurrences: Rare in the Kamenica and Jarma sections.

Cribelopsis neelongata

(CHERCHI & SCHROEDER, 1978)

(Pl. 1, figs. 10-12; Pl. 2, figs. 1-12)

- 1966** *Orbitolinopsis* sp. (Gruppe1) - SCHROEDER & CHAROLLAIS, p. 103; Pl. 1, figs. 1-10
- 1978** *Orbitolinopsis* (?) *neelongata* n. sp. - CHERCHI & SCHROEDER, p. 162; Pl. 2, figs. 5-10
- 1980** *Cribelopsis neelongata* (CHERCHI & SCHROEDER) nov. comb. - ARNAUD-VANNEAU, p. 669; Pl. 59, figs. 4-7; Pl. 95, figs. 7-14, Fig. 228
- 2000** *Cribelopsis neelongata* (CHERCHI & SCHROEDER) - BERNAUS, p. 64; Pl. 5, figs. 15-18
- non 2000** *Cribelopsis neelongata* (CHERCHI & SCHROEDER) - HUGHES; Pl. 6, figs. 4 (= *Praechrysalidina infracretacea*) - 5 (= *Voloshinoides murgensis*)
- 2002** *Cribelopsis neelongata* (CHERCHI & SCHROEDER) - BERNAUS *et al.*; Fig. 5.G
- 2009a** *Cribelopsis neelongata* - CLAVEL *et al.*; Pl. 1, specimen DL101a; Pl. 2, specimens 6922-19a, 6922-22a, 6921-8a, 6923-23a, 6922, b14, 6923-1c
- 2010** *Cribelopsis neelongata* (CHERCHI & SCHROEDER) - CLAVEL *et al.*; Pl. 14, specimen 407.3-1c; Pl. 20, specimen Ai31-15b; Pl. 27, specimen 218.5-2a; Pl. 29, specimen 226.22-3b
- 2013a** *Cribelopsis neelongata* (CHERCHI & SCHROEDER) - CLAVEL in GRANIER *et al.*; p. 151, Pl. 5, figs. 9-14; Pl. 9, fig. 9; Pl. 10, fig. 10
- 2014** *Cribelopsis neelongata* (CHERCHI & SCHROEDER) - CLAVEL *et al.*; Pl. 9, specimen GF15-1c; Pl. 11, specimen 7833-9a; Pl. 13, specimen 470-8b; Pl. 14, specimen 464-44b; Pl. 17, specimen 575-1a; Pl. 22, specimen 407.3-1c; Pl. 23, specimen 409b43; Pl. 25, specimen 229.2-1b3; Pl. 26, specimen LEST54-31a; Pl. 28, specimen 7341-41a; Pl. 30, specimen 6943-10a; Pl. 31, specimen SANF50-1a2015
- 2014** *Cribelopsis neelongata* (CHERCHI & SCHROEDER) - POLAVER; Fig. 5a-l
- 2015** *Cribelopsis neelongata* - BONVALLET; Pl. 4.3, figs. 8-10
- 2017** *Cribelopsis neelongata* (CHERCHI & SCHROEDER) - CLAVEL in GRANIER *et al.*; p. 130, Pl. 5, figs. 9-14; Pl. 9, fig. 9; Pl. 10, fig. 10
- 2019** *Cribelopsis neelongata* (CHERCHI & SCHROEDER) - BONVALLET *et al.*; Figs. 10.27, 10.38-10.39

Remarks: A detailed description of the species has been provided by SCHROEDER in SCHROEDER & CHAROLLAIS (1966, p. 103-105) in open nomenclature as *Orbitolinopsis* sp. (Gruppe 1). Systematically, it has been described as *Orbitoli-*

nopsis (?) *neelongata* by CHERCHI & SCHROEDER (1978), later revised by ARNAUD-VANNEAU (1980). For instance, typical features are the often observed slight inclination of the rather acute apical part, a flat to slightly convex base, and the overall cylindro-conical morphology, resulting from the decreasing chamber diameter of the youngest chambers in adult specimens (CHERCHI & SCHROEDER, 1978, p. 162, "prima parte ... è conica, ... stadio tardoontogenetico è cilindrico"). Adult specimens consist of 20 to 30 uniserial chambers. *C. neelongata* is one of the most common taxa in the Kamenica section.

Dimensions: D = 0.70-0.95 mm; H = 0.80-1.35 mm; D/H 0.55-1.1

Occurrences: Common in the Kamenica and rare in the Jarma sections.

Cribelopsis pfenderae

(CANÉROT & MOULLADE, 1971) nov. comb.

(Pl. 3, figs. 1-11)

- 1971** *Paracoskinolina pfenderae* n. sp. - CANÉROT & MOULLADE, p. 216; Pl. 2, figs. 8-20
- 1976** *Paracoskinolina pfenderae* CANÉROT & MOULLADE - PEYBERNÈS; Pl. 14, figs. 17-20
- 1984** *Paracoskinolina pfenderae* CANÉROT & MOULLADE - CANÉROT; Pl. 1, figs. 14-16
- 1995** *Paracoskinolina pfenderae* CANÉROT & MOULLADE - BUCUR *et al.*; Pl. VII, figs. 10-11
- 2004** *Paracoskinolina pfenderae* CANÉROT & MOULLADE - IVANOVA & KOLEVA-REKALOVA; Pl. 4, figs. 8-12
- 2018** *Paracoskinolina?* *pfenderae* CANÉROT & MOULLADE - BUCUR & SCHLAGINTWEIT; Figs. 7e, h
- 2019** *Paracoskinolina pfenderae* CANÉROT & MOULLADE - GRANIER & CLAVEL; Figs. 5M-O

Remarks: The central zone of the small-sized "*Paracoskinolina*" *pfenderae* was originally described as possessing triangular pillars that are tapering towards the test base ("pointe en base"). The single slightly oblique transverse section does in our opinion not show pillars but radial main partitions reaching into the central part of the test where they anastomose (CANÉROT & MOULLADE, 1971: Pl. 2, fig. 12). They alternate between subsequent chambers (e.g., CANÉROT & MOULLADE, 1971: Pl. 2, figs. 10, 13, 19). The exoskeleton lacks horizontal partitions and exhibits one to three intercalary beams between two main partitions (Pl. 3, figs. 4, 7). Tests are medium-conical with up to 12 chambers in adult specimens. As revised by ARNAUD-VANNEAU (1980), the genus *Paracoskinolina* MOULLADE possesses pillars in the central zone that are aligned between subsequent chambers. Due to the inner test structure as defined above, the species is here transferred to the genus *Cribelopsis* ARNAUD-VANNEAU becoming its smallest representative (see Fig. 4). All reported occurrences are from the former Northern Neotethysian margin stretching from Spain to the west to Bulgaria-Serbia to the east (see synonymy).

Dimensions: D = 0.30-0.45 mm; H = 0.30-0.50 mm; D/H = 0.9-1.1

Occurrences: Common in the Kamenica and rare in the Jarma sections.

***Cribellopsis thieuloyi*****ARNAUD-VANNEAU, 1980**

(Pl. 3, figs. 12-17)

- 1980** *Cribellopsi thieuloyi* n. sp. - ARNAUD-VANNEAU, p. 675; Pl. 96, figs. 13-19
- 2010** *Cribellopsis thieuloyi* ARNAUD-VANNEAU - CLAVER et al.; Pl. 14, specimen DL105a; Pl. 20, specimen Ai31-8a; Pl. 24, specimen 6923-3a; Pl. 30, specimen 275.4-1a
- 2013a** *Cribellopsis thieuloyi* ARNAUD-VANNEAU - CLAVER in GRANIER et al., p. 151; Fig. 9A, Pl. 5, figs. 6-8, 17
- 2014** *Cribellopsis thieuloyi* ARNAUD-VANNEAU - CLAVER et al.; Pl. 8, specimen 7847-12a; Pl. 10, specimen 597-13a; Pl. 14, specimen 398-18b; Pl. 16, specimen 500.9d12; Pl. 19, specimen 263-28a; Pl. 21, specimen DL105a; Pl. 23, specimen 410-15b; Pl. 27, specimen LEST88.2-1b; Pl. 28, specimen 7341-19a, 7341-11a; Pl. 29, specimen 7339-15b
- 2017** *Cribellopsis thieuloyi* ARNAUD-VANNEAU - CLAVER in GRANIER et al., p. 131; Fig. 9A, Pl. 5, figs. 6-8, 17

Remarks: *C. thieuloyi* represents one of the largest species of the genus known so far only from southeastern France. It is of cylindro-conical morphology with acutely tapering apex; adult specimens consist of up 40 chambers. *C. thieuloyi* is comparably rare in the upper Berriasian orbitolinid assemblage of eastern Serbia.

Dimensions: D = 0.7-1.0 mm; H = 1.7-2.15 mm; D/H: 0.39-0.46; number of chambers last 0.5 mm: 5-8.

Occurrences: Common in the Kamenica and rare in the Jerma sections.

Cribellopsis sudari**SCHLAGINTWEIT & BUCUR n. sp.**

(Fig. 5, Pl. 4, figs. 1-13; Pl. 5, figs. 1-15)

Etymology: The species is dedicated to Milan SUDAR for his contribution to the study of Mesozoic deposits from Serbia.

Holotype: Specimen illustrated in Pl. 4, fig. 5, thin-section 16209-2.

Paratypes: Pl. 4, figs. 1 (14791-4) - 2 (14020), 10 (14796); Pl. 5, figs. 1 (14792-19) - 2 (14019).

Type horizon: Upper Berriasian carbonates, not yet assigned lithostratigraphically to any formation.

Type locality: Kamenica section located north of Kamenica (Fig. 1.A, .C). The locality can be found on the geological map of Yugoslavia 1:100.000 (sheet K34-20, Aleksinac) (KRISTIC et al., 1978). GPS coordinates: 43°13'48.2"N 21°33'38.5"E.

Description: High-conical to cylindroconical test displaying an acute tapering apex where the subspherical, simple embryo (diameter 0.06-0.13 mm) is positioned. It is followed by a high trochospirally coiled part of a few whorls, while the main part consists of up to 25 uniserial, slightly convex (in growth direction) chambers. The marginal zone is subdivided by beams and two to three intercalary beams; no rafters are present. The thickness of the intercalary beams equals the one of the marginal chamber wall. The beams are widening inwards where they form a coarse reticulate network. This central part (or zone) amounts roughly one third of the total diameter. In shallow tangential sections, a rectangular pattern, higher than wide, is present. Inwards, the partitions are widening at the base and top producing a rounded-triangular to trapezoidal pattern with foramina arranged cross-wise obliquely in diagonal lines. The wall is finely agglutinated. Test dimorphism has not been observed.

Dimensions: D = 0.39-0.51; H = 0.99-1.25 mm; D/H = 0.39-0.44; numbers of chambers last 0.5 mm: 8-12.

Comparisons: Shallow tangential sections (from apex towards base) showing the rectangular pattern of compartments (Pl. 4, fig. 10) can be confused with *Paracoskinolina maynci* (CHEVALIER). In the latter species the vertical elements (beams, pillars) are arranged in continuity; in *C. sudari* they are alternating (Pl. 4, fig. 10, middle part), and only in some chambers (e.g., lower and upper part of the same specimen) they appear as being aligned. The alternating arrangement becomes evident when the section plane passes from the random to the central parts in these specimens (Pl. 4, fig. 1). The general test morphology compares to some extent with *C. neelongata*, often showing a bell-shaped morphology. *C. sudari* has a more slender cylindroconical test expressed by a lower D/H ratio and a high trochospirally coiled initial part. The upper test of *C. sudari* rarely and only slightly bends. *C. thieuloyi* with its bullet-like test morphology is distinctly larger (D, H), also having chambers of greater height.

Occurrences: Rare in the Jerma and Preko-nozi sections.

Genus *Montseciella*
CHERCHI & SCHROEDER, 1999

Remarks: In contrast to the classification of KAMINSKI (2014), the genus *Montseciella* CHERCHI & SCHROEDER with its simple embryo is removed from the Orbitolininae and considered a representative of the Dictyoconinae here.

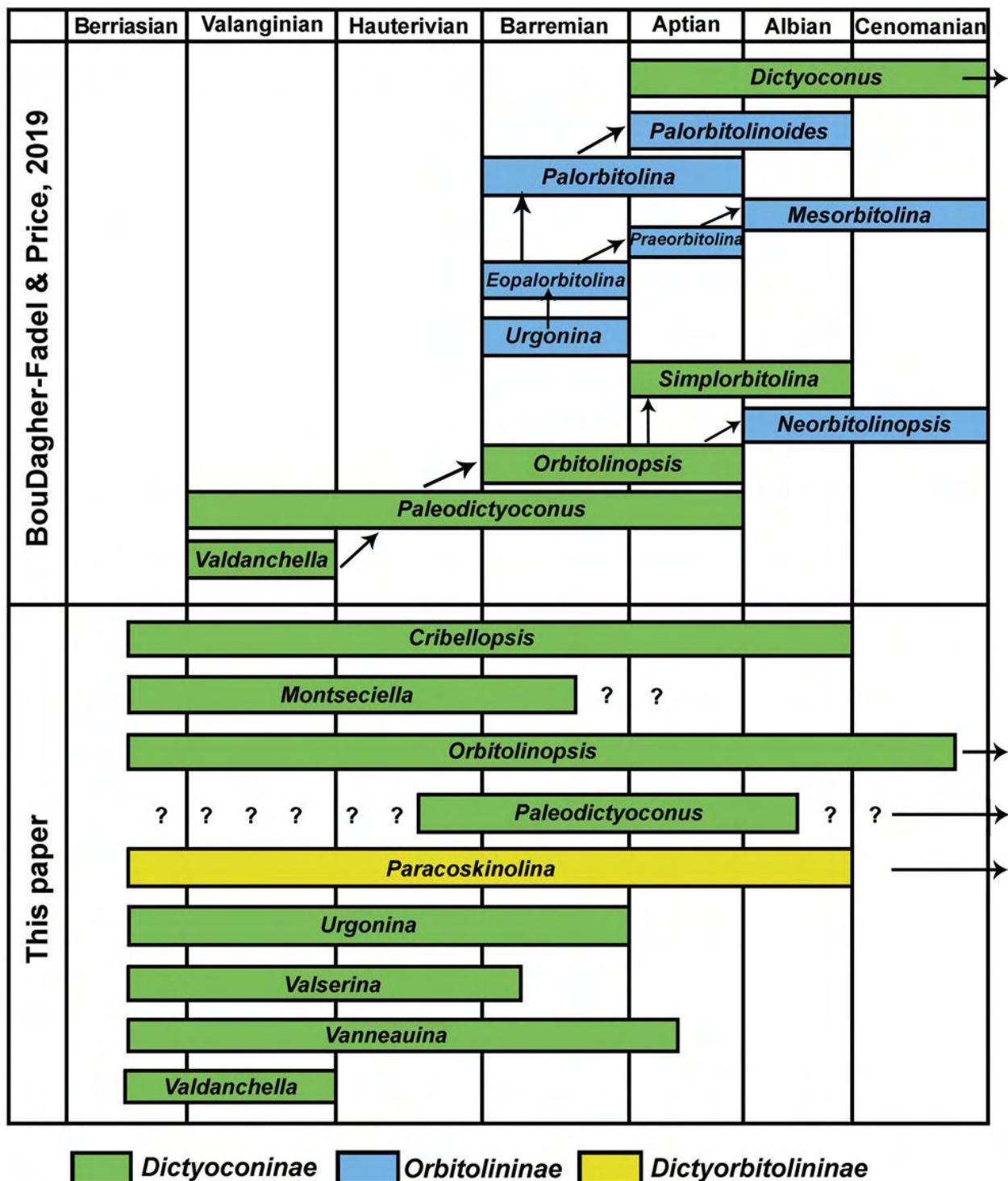


Figure 5: Evolution of Cretaceous Orbitolinidae, with special reference to the Dictyoconinae. **Above:** Concept of "gradual morphological changes" (redrawn after BOUDAGHER-FADEL & PRICE, 2019, Fig. 4). Note: Urgonina is not a member of the Orbitolininae but the Dictyoconinae (e.g., LOEBLICH & TAPPAN, 1987). **Below (this work):** Sudden burst evolution due to adaptive radiation in the upper Berriasian. Note that Valdanchella has been recorded from the upper Berriasian of southern Spain (BÁDENAS *et al.*, 2004, Fig. 2) and southwestern Switzerland (GRANIER *et al.*, 2014, Fig. 2).

- Montseciella glanensis (FOURY, 1968)**
(Pl. 6)
- 1968** *Paleodictyoconus glanensis* n. sp. - FOURY, p. 146; Pl. 18, figs. 1-12; Pl. 2, fig. 19 (fide SCHROEDER & CHERCHI, 1982)

- 1969** *Urgonina cf. alpiliensis* (FOURY) - SCHROEDER *et al.*, p. 93; Pl. 2, figs. 1-6; Pl. 3, fig. 6
- 1982** "*Paleodictyoconus*" *glanensis* FOURY - SCHROEDER *et al.*; Pl. 4, figs. 1, 4, 6
- 1999** *Montseciella glanensis* (FOURY) n. gen., n. comb. - CHERCHI & SCHROEDER, p. 9; Pl. 1, figs. 1-6; Pl. 2, figs. 1-7



- 2010** *Montseciella glanensis* (FOURY) - CHAROLLAIS et al.; Pl. 4, figs. 1-7; Pl. 2, figs. 1-5, 22; Pl. 6, figs. 1-4
- 2010** *Montseciella glanensis* (FOURY) - CLAVERE et al.; Pl. 5, specimens PA16.17-2a and CA1-6a; Pl. 8, specimens 471-2a, 387.12-2b, 471-13a, 387.12-1a, 387.12-2a, 161.29-1e, 387.11-6a and 387.11-8a; Pl. 13, specimen PL19.0-4d; Pl. 15, specimens DL80a, DL78a, DL88a, DL84b and DL88a; Pl. 19, specimen Ai19-8b; Pl. 21, specimens Ai31-16a and Ai31-3b; Pl. 25, specimens 6922-13a, 6923-4a and 6923-13a; Pl. 27, specimen 218.5-4a; Pl. 29, specimen 226.22-4a and 226.22-11a; Pl. 30, specimen 275.4-5a, 275.3-7a, 275.3-6b and 275.5-2b
- 2013a** *Montseciella glanensis* (FOURY) - CLAVERE in GRANIER et al., p. 152; Pl. 6, figs. 13, 16-17, 19-21; Pl. 8, fig. 13; Pl. 9, fig. 5
- 2014** *Montseciella glanensis* (FOURY) - CLAVERE et al., 2014; Pl. 4, specimen 8504-9b; Pl. 7, specimens RH 352-51 and MC233-5b; Pl. 8, specimen GF15-3a; Pl. 12, specimen 471-2a; Pl. 15, specimen 7864-9a; Pl. 16, specimen 500.2-2b; Pl. 19, specimen 7402-1a; Pl. 21, specimen DL60a; Pl. 23, specimen 375-4a; Pl. 27, specimen LEST84.5-4b; Pl. 28, specimen 7341-44b and 7341-c6; Pl. 29, specimen 6933-a2; Pl. 31, specimen 6812-4c, 6816a5 and SANF10-2b
- 2014** *Montseciella glanensis* (FOURY) - POLAVDER; Fig. 9.A
- 2017** *Montseciella glanensis* (FOURY) - CLAVERE in GRANIER et al., p. 132; Pl. 6, figs. 13, 16-17, 19-21; Pl. 8, fig. 13; Pl. 9, fig. 5

Remarks: It was initially described as *Paleodictyoconus glanensis* by FOURY (1968) from the Barremian of southeastern France noting structural differences to *P. cuvillieri* that "might finally justify the creation of a generic or subgeneric taxonomic unit" (FOURY, 1968, p. 148, translated). This taxon represents the type-species of the genus *Montseciella* CHERCHI & SCHROEDER, 1999. CRUZ-ABAD (2018) noted structural differences of the specimens from Sardinia that were included in the description and diagnosis of *Montseciella* by CHERCHI and SCHROEDER (1999). In fact, we note that none of the specimens of *Paleodictyoconus glanensis* as described by FOURY (1968) shows a very prominent initial coil that is defined as one typical feature of the genus *Montseciella* CHERCHI & SCHROEDER. "*Paleodictyoconus*" *glanensis* should possess a slightly eccentric embryo followed by only a small spire, accepted by CRUZ-ABAD (2018, p. 86). CHERCHI and SCHROEDER (1999, p. 10) on the other hand interpreted that this embryo "laterally of the apical region" with a "thick semicircular sparitic wall" absolutely unusual for Orbitolinidae..." does not belong to the figured specimen"... and "could be a transversal section of an encrusting organism, perhaps an annelid tube". This view is accepted herein. Any further taxonomic discussion based solely on our material from eastern Serbia however is beyond the scope of the present paper. Contrasting *M. alguerensis*, *M. glanensis* only occasionally has "a vertical plate" (= intercalary beam) in the marginal zone (CHERCHI & SCHROEDER, 1999). CHERCHI and SCHROEDER (1999, p. 10) noted that "horizontal plates are lacking in our specimens", but there

seems to be rare individual rafters in adult chambers in the type-material (FOURY, 1968, Pl. 18, fig. 9, penultimate chamber, left side; re-illustrated herein in Pl. 6, fig. 2, arrow). In the upper Berriasian material, *M. glanensis* has preferentially been observed in grainstones.

Dimensions: D up to 1.2 mm, H up to 1.1 mm; due to the majority of incomplete and/or oblique sections, dimensional data are not provided.

Occurrences: Common in the Kamenica and Prekonozi sections.

Montseciella alguerensis
CHERCHI & SCHROEDER, 1999
(Pl. 7)

- 1999** *Montseciella alguerensis* n. sp. - CHERCHI & SCHROEDER, p. 10; Pl. 3, figs. 1-3; Pl. 4, figs. 1-5
- 1999** *Paleodictyoconus?* *leridanus* n. sp. - BECKER, p. 409; Pl. 14, figs. 1-6; Pl. 15, figs. 1-2, 4
- 2014** *Montseciella alguerensis* CHERCHI & SCHROEDER - CLAVERE et al.; Pl. 8, specimen OV288a; Pl. 10, specimen 524-4a; Pl. 15, specimen 7864-4b; Pl. 16, specimen 500.9m85; Pl. 19, specimen 275.5-2b; Pl. 21, DL67b

Remarks: The species was described separately as *Paleodictyoconus?* *leridanus* and *Montseciella alguerensis* in the same year (BECKER, 1999; CHERCHI & SCHROEDER, 1999). In this case, the ICZN (1999, article 24.2.2) regulates that the "first reviewer" stating the synonymy may fix the name in a published work (see CHERCHI & SCHROEDER in SCHROEDER et al., 2000, p. 22). According to CHERCHI & SCHROEDER (1999, p. 11), it is "a species of *Montseciella* characterized by the regular occurrence of horizontal plates within the marginal zone". Medium, rarely high-conical tests with up to 25 chambers in adult specimens (Pl. 7, fig. 1). There is one short rafter, and one to three intercalary beams in the marginal zone. The central zone consists of vermicular partitions that form a labyrinthic structure (Pl. 7, figs. 6, 8). The structure of the central zone ("structural elements ... forming an imperfect network", BECKER, 1999, p. 409 ... unvollkommenes Geflecht; FOURY, 1968: "pseudoréticulaire") was the reason for BECKER (1999) to assign the specimens only with reservation to *Paleodictyoconus* MOULLADE. The pores in the central area show a predominantly vertical arrangement. A chronological order (1, *M. glanensis*; 2, *M. alguerensis*) at the beginning of the "*Montseciella* - *Rectodictyoconus* lineage" (CHERCHI & SCHROEDER, 1999; SCHROEDER et al., 2002) cannot be verified in the upper Berriasian of eastern Serbia. Also the belonging of *Dictyoco-nus?* *arabicus* HENSON, 1948, to the genus *Montseciella* is highly debatable; again this topic is beyond the scope of the present paper.

Dimensions: D = up to 1.3 mm, H = up to 1.5 mm. Like with *Orbitolinopsis buccifer*, *Vaneauina vercori*, *Montseciella glanensis*, and other taxa reported herein also the dimensions of the upper Berriasian specimens are reduced in comparisons to the respective younger type-material.



Occurrences: Rare to common in the Kamenica section.

Genus *Orbitolinopsis* HENSON, 1948
Orbitolinopsis cf. briacensis
ARNAUD-VANNEAU, 1980
(Pl. 8, figs. 1-9)

1978 *Orbitolinopsis gr. flandrini* DIENI, MASSARI & MOULLADE - GARCÍA-HERNÁNDEZ; Pl. 25, figs. 13-14

1980 *Orbitolinopsis briacensis* n. sp. - ARNAUD-VANNEAU, p. 644; Pl. 10, figs. 8-10; Pl. 94, figs. 1-8, Fig. 225

2013a *Orbitolinopsis briacensis* ARNAUD-VANNEAU - CLAVEL in GRANIER et al., p. 152; Pl. 2, figs. 17, 20; Pl. 9, fig. 4 (cf.); Pl. 10, figs. 1-3

2014 *Orbitolinopsis briacensis* ARNAUD-VANNEAU - CLAVEL et al.; Pl. 13, specimen 470-3a; Pl. 14, specimen 464-14a; Pl. 15, specimen 7864-19a; Pl. 18, specimens 500.9-19a and 500.9-44b; Pl. 20, specimen 336-2c; Pl. 24, specimen 410-14a; Pl. 26, specimen LEST84.5-a19; Pl. 30, specimens 7339-1a and 6937-2b; Pl. 32, specimens SANF48-1b and SANF46-1a

2015 *Orbitolinopsis briacensis* ARNAUD-VANNEAU - BONVALLET; Pl. 4.6, figs. 5, 6?, 8

2017 *Orbitolinopsis briacensis* ARNAUD-VANNEAU - CLAVEL in GRANIER et al., p. 132; Pl. 2, figs. 17, 20; Pl. 9, fig. 4 (cf.); Pl. 10, figs. 1-3

2019 *Orbitolinopsis briacensis* ARNAUD-VANNEAU - BONVALLET et al.; Fig. 10/57, 10/60?, 10/61

non 2018 *Orbitolinopsis briacensis* - GHAFOR & MOHIALDEEN; Pl. 1a, any litho- or bioclast?

Remarks: Medium-sized species of *Orbitolinopsis*, superficially similar to *O. kiliani* with intercalary beams in the marginal zone (ARNAUD-VANNEAU, 1980, Fig. 226; CLAVEL in GRANIER et al., 2013a, 2017). The test structure and many parameters of the Serbian specimens agree with the type-material of southeastern France except that the chamber height is distinctly reduced and the maximum value of the test diameter (see below); there are 14-15 chambers in the last 0.5 mm of the test in the former compared to 8-9 (ARNAUD-VANNEAU, 1980). A separation of a new species only based on this feature would not make sense in our opinion. It might be just a phylogenetic increase in the chamber height from the late Berriasian to the Late Hauterivian-Barremian.

Dimensions: D = 0.45-0.62 mm (ARNAUD-VANNEAU, 1980: up to 1.0 mm); H = 0.5-0.95 mm (ARNAUD-VANNEAU, 1980: up to 1.0 mm); D/H: 0.65-0.9; number of chambers last 0.5 mm: 14-15.

Occurrences: Common to frequent in the Kamenica section, common in the Prekonozi section, rare in the Jerma section.

***Orbitolinopsis cf. cuvillieri* MOULLADE, 1960**
(Pl. 8, figs. 10-17)

1960 *Orbitolinopsis cuvillieri* n. sp. - MOULLADE, p. 190; Pl. 2, figs. 1-7

1980 *Orbitolinopsis cuvillieri* MOULLADE - ARNAUD-VANNEAU, p. 634; Pl. 60, figs. 1-3; Pl. 93, figs. 1-13, fig. 223

2010 *Orbitolinopsis cuvillieri* MOULLADE - CLAVEL et al.; Pl. 15, specimens DL 81a and DL86a; Pl. 25, specimen 6922-25a; Pl. 29, specimen 226.22-9a

2013a *Orbitolinopsis cuvillieri* MOULLADE - CLAVEL in GRANIER et al., p. 152; Pl. 2, figs. 1-5, 8-10, 12,

16, 21; Pl. 9, figs. 16-19

2014 *Orbitolinopsis cuvillieri* MOULLADE - CLAVEL et al.; Pl. 9, specimen MM319az; Pl. 11, specimen 400-10c; Pl. 13, specimen 470-2a; Pl. 14, specimen 398-8a; Pl. 15, specimen 462-8a; Pl. 18, specimens 500.9-13a and 500.9-22c; Pl. 20, specimens 348-2b? And 348-1a; Pl. 22, specimens DL86a and 407.2-19b; Pl. 24, specimens 409-2a, 375-36a and 410-19b; Pl. 25, specimen 229.1-2a Pl. 26, specimen LEST27-2a and LEST26.6-7a; Pl. 30, specimens 6935-12ab, 7339-4a and 7339a3; Pl. 32, specimens SANF4-1a (cf.), SANF46-1b and SANF48-1c

2017 *Orbitolinopsis cuvillieri* MOULLADE - CLAVEL in GRANIER et al., p. 132; Pl. 2, figs. 1-5, 8-10, 12, 16, 21; Pl. 9, figs. 16-19

Remarks: There are two very close forms: the type-species *Orbitolinopsis kiliani* SILVESTRI, 1932, and *O. cuvillieri* MOULLADE, 1960. In the literature there are differing views on the validity of both. SCHROEDER et al. (1969, p. 97) considered *O. cuvillieri* as a junior synonym of *O. kiliani* since "structural differences between both species are not recognizable". And even MOULLADE (1966), who was describing the former species, reported other specimens later as *Orbitolinopsis gr. kiliani-cuvillieri*. ARNAUD-VANNEAU (1980, p. 636) remarked that both are "quite close" but treated them as separate species. According to ARNAUD-VANNEAU (1980), *O. cuvillieri* is smaller, possesses a reduced central part, and the cupules, being more spaced-away, have a more regular shape. ARNAUD-VANNEAU (1980) assumed that *O. kiliani* was deriving from *O. cuvillieri*. According to the studies of CLAVEL et al. (2014, Fig. 5), both have their first local appearances in southeastern France at the base of the Barremian. The upper Berriasian specimens from Serbia are directly comparable to those from the Barremian of France, namely the two (subaxial) sections of *O. cuvillieri* by MOULLADE (1960, Pl. 2, figs. 2-3). Unlike *O. briacensis*, *O. cuvillieri* exhibits a less complex marginal zone lacking intercalary beams (Pl. 8, figs. 13-15).

Dimensions: D = 0.6-0.8 mm, H = 0.48-0.9 mm, D/H = 0.9-1.3

Occurrences: Common in the Kamenica, and rare in the Prekonozi sections.

Orbitolinopsis buccifer
ARNAUD-VANNEAU & THIEULOY, 1971
(Pl. 9)

1970 *Orbitolinopsis* n. sp. - FOURCADE; Pl. 34, figs. 3-4

1972 *Orbitolinopsis buccifer* n. sp. - ARNAUD-VANNEAU & THIEULOY; Pl. 1, figs. 1-9; Pl. 2, figs. 1-11

1974 *Orbitolinopsis buccifer* ARNAUD-VANNEAU & THIEULOY - CANÉROT; Pl. 16, Figs. 1-2

1978 *Orbitolinopsis buccifer* ARNAUD-VANNEAU & THIEULOY - GARCÍA-HERNÁNDEZ; Pl. 25, figs. 15-16

1979 *Orbitolinopsis buccifer* ARNAUD-VANNEAU & THIEULOY - AZÉMA et al.; Pl. 4, fig. 7

1980 *Orbitolinopsis buccifer* ARNAUD-VANNEAU & THIEULOY - ARNAUD-VANNEAU, p. 636; Pl. 60, fig. 6; Pl. 92, figs. 9-12

1984 *Paleodictyoconus?* n. sp. - CANÉROT; Pl. 1, fig. 20

1988 *Orbitolinopsis buccifer* - BUCUR & COCIUBA; Pl. 2, figs. 12-13



- 2001** *Orbitolinopsis buccifer* - CASTRO *et al.*; Fig. 5.G
2008 *Orbitolinopsis buccifer* ARNAUD-VANNEAU & THIEULOUY - SUDAR *et al.*; Fig. 9.9-9.11
2012 *Orbitolinopsis buccifer* ARNAUD-VANNEAU & THIEULOUY - LÉONIDE *et al.*; Fig. 7.C
2013a *Orbitolinopsis buccifer* - CLAVER in GRANIER *et al.*, p. 152; Pl. 2, figs. 11, 13-14, 18-19; Pl. 9, figs. 11-15; Pl. 11, fig. 7
2014 *Orbitolinopsis buccifer* - CLAVER *et al.*; Pl. 9, specimen OV177b; Pl. 11, specimen 7862-1a; Pl. 13, specimen 470-9a; Pl. 14, specimen 464-31a; Pl. 18, specimen 500.9-18b; Pl. 22, specimens DL77a, 257.4-37a; Pl. 24, specimens 6874-2a, 410a18; Pl. 25, specimen 229.2-3b; Pl. 26, specimen LEST54-2a; Pl. 30, specimen 7338-d2; Pl. 32, specimens 6816-2c, SANF46-1a, SANF43-1b
2015 *Orbitolinopsis buccifer* - BONVALLET; Pl. 4.6, figs. 7, 11
2017 *Orbitolinopsis buccifer* - CLAVER in GRANIER *et al.*, p. 132; Pl. 2, figs. 11, 13-14, 18-19; Pl. 9, figs. 11-15; Pl. 11, fig. 7
non 2018 *Orbitolinopsis buccifera* - GHAFOR & MOHIAL-DEEN; Pl. 1, fig. B (= any calcitic bioclast?); Pl. 2, fig. E (= superficial ferruginous ooid, see GRANIER, 2020)
2019 *Orbitolinopsis buccifer* ARNAUD-VANNEAU & THIEULOUY - BONVALLET *et al.*, Figs. 10.55-56

Remarks: Among the different *Orbitolinopsis* species, *O. buccifer* is outstanding due to its morphology and size. The test is generally rather broad, low- to medium-conical. The adult chambers may be sigmoidal to annular with margins bending upwards (= reflexed convexo-concave type of HENSON, 1948: Fig. 12u-v). Like with *Orbitolinopsis briacensis*, the upper Berriasian specimens of *O. buccifer* do not attain the large sizes as the younger type-material (Upper Hauterivian-lower Aptian) from southeastern France, especially the microspheric generation.

Dimensions: D = up to 2.1 mm; H = up to 1.3 mm.

Occurrences: Rare in the Kamenica and Prekonozi sections.

Orbitolinopsis debelmasi MOULLADE & THIEULOUY, 1965 (Pl. 10)

- 1960** *Orbitolinopsis kiliani* - MOULLADE, p. 190; Pl. 3, Figs. 6-12
1965 *Orbitolinopsis debelmasi* n. sp. - MOULLADE & THIEULOUY, p. 4178
1974 *Orbitolinopsis debelmasi* MOULLADE & THIEULOUY - CANÉROT; Pl. 16, fig. 3
1980 *Orbitolinopsis debelmasi* MOULLADE & THIEULOUY - ARNAUD-VANNEAU, p. 642; Pl. 60, fig. 7; Pl. 94, figs. 9-16, Fig. 225
2006 *Orbitolinopsis kiliani?* - ALBRICH *et al.*; Pl. 6, fig. 14
2010 *Orbitolinopsis debelmasi* MOULLADE & THIEULOUY - CLAVER *et al.*; Pl. 15, specimen DL139a; Pl. 24, specimen 6923-9a; Pl. 27, specimen 218.5-5b
2013a *Orbitolinopsis debelmasi* MOULLADE & THIEULOUY - CLAVER in GRANIER *et al.*; p. 152 Pl. 7, figs. 1-5
2014 *Orbitolinopsis debelmasi* MOULLADE & THIEULOUY - CLAVER *et al.*; Pl. 4, specimen 8509-1b; Pl. 6, specimen EB H22.4; Pl. 8, specimen OV275; Pl. 10, specimen 524-5a; Pl. 13, specimen 458-7a; Pl. 16, specimen 500.6-1b; Pl. 19, specimen

7401-5a; Pl. 21, specimen 258.15-1a; Pl. 23, specimen 409-4a; Pl. 27, specimen LEST54-23a; Pl. 28, specimens 7341c5, 7341-48a and 7341-52a; Pl. 29, specimens 7339-18a, 7338-13a and 7338-10b; Pl. 31, specimens 6812-4a and SAN21-1a

- 2014** *Orbitolinopsis debelmasi* MOULLADE & THIEULOUY - POLAVDER; Fig. 7A-C
2015 *Orbitolinopsis debelmasi* - BONVALLET; Pl. 4.2, figure 10
2019 *Orbitolinopsis debelmasi* - BONVALLET *et al.*; Fig. 10.25

Remarks: Initially, the type-specimens were illustrated as *Orbitolinopsis kiliani* PREVER by MOULLADE (1960, Pl. 3, figs. 6-12), later described as a new species, *Orbitolinopsis debelmasi* by MOULLADE & THIEULOUY (1965). At the type-locality, it occurs in high-energetic deposits (grainstones; "Faciès microconglomératique", MOULLADE, 1960, p. 188). In the studied sections of eastern Serbia, *O. debelmasi* has been observed in comparable facies, grainstones with ooids, e.g., in the upper parts of the Prekonozi and Jerma sections. *O. debelmasi* is characterized by its large-sized test of high-conical (apical angles 40 to 70 degrees) morphology (often with an ultimate cylindrical part, Pl. 10, figs. 8-9), a wide central zone with a pattern of regularly alternating cupules, and vertical plates (intercalary beams) in the marginal zone. The pattern of the foramina cross-wise obliquely arranged in diagonal lines is well discernible (Pl. 10, figs. 4, 6, 12). Adult specimens consist of up to 35 uniserial chambers.

Dimensions: D = 0.7-0.95 mm, H = 1.0-1.5 mm, D/H = 0.5-0.75; number of chambers last 0.5 mm = 9-11.

Occurrences: Rare in the Kamenica section, common in the Prekonozi and Jerma sections.

Genus *Urgonina* FOURY & MOULLADE, 1966

Remarks: Correctly, the genus *Urgonina* is classified as belonging to the Dictyoconinae (LOEBLICH & TAPPAN, 1987; KAMINSKI, 2014), and not to the Orbitolininae (BOUDAGHER-FADEL & PRICE, 2019, p. 6, Fig. 4).

Urgonina alpiliensis (FOURY, 1963) (Pl. 11, figs. 1-9)

- 1963** *Coskinolina alpiliensis* n. sp. - FOURY; Pl. 1, fig. 7, non 8; Pl. 3, figs. 1-9
1966 *Urgonina protuberans* n. sp. - FOURY & MOULLADE, p. 252; Pl. 1, figs. 7-19; Pl. 2, figs. 1-11
1969 *Urgonina cf. alpiliensis* (FOURY) - SCHROEDER *et al.*, p. 93-96; non Pl. 2, figs. 1-6 [= *Montseciella glanensis* (FOURY) *fide* CHERCHI & SCHROEDER, 1999]; Pl. 3, fig. 6
1980 *Urgonina alpiliensis* (FOURY) - ARNAUD-VANNEAU, p. 617; Pl. 91, figs. 1-9
2007 *Urgonina alpiliensis* (FOURY) - BUCUR *et al.*; Fig. 4/2
2006 *Orbitolinopsis?* sp. - ALBRICH *et al.*; Pl. 5, fig. 4
2009a *Urgonina alpiliensis* - CLAVER *et al.*; Pl. 2, specimen 6922-22a
2010 *Urgonina alpiliensis* - CLAVER *et al.*; Pl. 12, specimens PL18.3-2c, PL19.1-5a; Pl. 14, specimen 407.1-2b; Pl. 19, specimens Ai19-1a, Ai19-6d, Ai19-17d; Pl. 24, specimen 6923-1b



2013a *Urgonina alpiliensis* (FOURY) - CLAVEL in GRANIER et al., p. 153; Pl. 6, figs. 1-3; Pl. 9, fig. 6

2014 *Urgonina alpiliensis* (FOURY) - CLAVEL et al.; Pl. 6, specimen 372-43a; Pl. 8, specimen 7847-24a; Pl. 10, specimen 527-14a; Pl. 12, specimens 387.4-3a and 470-9b; Pl. 15, specimen 7865-11b; Pl. 16, specimen 493.3-3b; Pl. 19, specimen 263a1; Pl. 23, specimen 375-35b; Pl. 27, specimen LEST54-25c; Pl. 28, specimens 7341a17, 7341-14b, 7341-33c, 7341-38a; Pl. 29, specimens 6935-21a and 7338c 2; Pl. 31, specimens 6812-2b, SAN16-1c, SAN21-1c and SANF1-1c

Remarks: The synonymy between *Coskinolina alpiliensis* FOURY and *Urgonina protuberans* FOURY & MOULLADE was discussed by SCHROEDER et al. (1969) leading to the new combination *Urgonina alpiliensis* (FOURY) (see also CLAVEL in GRANIER et al., 2013a, 2017) and the monotypy of the genus. It is worth mentioning that ARNAUD-VANNEAU (1980) raises the question of two sub-species, *alpiliensis protuberans* and *alpiliensis alpiliensis* with different stratigraphic abundances in the Vercors area, SE France. *U. alpiliensis* is characterized by a well-developed initial spire (Pl. 11, fig. 1), massive test elements (septa, marginal chamber wall, pillar-like vertical elements) and vertical pores. Shallow tangential sections show an undivided marginal zone (for test reconstruction see ARNAUD-VANNEAU, 1980, Fig. 219). The upper Berriasian specimens from eastern Serbia are smaller in dimensions than the Barremian type-material (e.g., H = 1.0 to 1.875 mm according to FOURY & MOULLADE, 1966). We consider this variation as a simple intraspecific evolution (without any structural differences) or example of COPE's rule (e.g., GUEX, 2020).

Dimensions: D = 0.6-0.9 mm, H = 0.85-1.0 mm, D/H = 0.9 (1 value)

Occurrences: Common in the Kamenica section, rare in the Jarma section (in grainstones).

Genus *Valserina*

SCHROEDER & CONRAD in SCHROEDER et al., 1967

Remarks: Although described more than half a century ago, the suprageneric status of *Valserina* is still pending in our opinion. In LOEBLICH & TAPPAN (1987) it is included in the subfamily Orbitolininae ("complex embryonal apparatus", p. 163 therein), whereas in the genus diagnosis (p. 168, therein), an "embryonic apparatus of simple protoconch and deutoeroconch" is mentioned, that would consequently lead to its attribution to the Dictyoconinae SCHUBERT. The current classification of KAMINSKI (2014) also lists *Valserina* among the Orbitolininae (see also CLAVEL in GRANIER et al., 2013a, 2017). This is obviously due to the fact that the type-species *V. broennimanni* has a simple embryo (without partitions) while *Valserina turbinata* (FOURY, 1968) an embryo with partitions. Trivially, a genus cannot have species that belong to different subfamilies. It is noteworthy that *Eyalierina turbinata* FOURY is treated as belonging to *Palorbitolina* in SCHROEDER [1993: *Palorbitolina turbinata* (FOURY)] followed by

BECKER (1999). In the same work, *Eopalorbitolina charollaisi* SCHROEDER in SCHROEDER & CONRAD, 1968, is newly combined as *Valserina charollaisi* (SCHROEDER) and *Eopalorbitolina* regarded as a junior synonym of *Valserina*. Later, *Eopalorbitolina* is again regarded as an individual genus different from *Valserina* and *Eopalorbitolina charollaisi* reinstated (SCHROEDER et al., 2010). A further increased taxonomic complexity arises from the reinstatement of *Eyalierina turbinata* FOURY in SCHROEDER et al. (2002) and the giving up of its former transfer to *Valserina*. Last but not least, the validity of the three genera *Valserina* SCHROEDER & CONRAD, *Alpillina* FOURY, 1968, and *Eyalierina* FOURY, 1968, has also been discussed by ARNAUD-VANNEAU (1980, p. 680) concluding that *Eyalierina* represents a junior synonym of *Alpillina*. Excluding the species *turbinata* (with complex embryo) from *Valserina* would speak for the inclusion of the latter into the Dictyoconinae that is provisionally accepted herein.

Valserina primitiva SCHROEDER et al., 1969

(Fig. 6, Pl. 11, figs. 10-18)

1969 *Valserina brönnimanni primitiva* n. ssp. - SCHROEDER et al., 99; Pl. 3, figs. 1-5

1999 *Valserina primitiva* SCHROEDER, CHAROLLAIS & CONRAD - BECKER, p. 393; Pl. 5, figs. 1-4

1999 *Valserina primitiva* SCHROEDER, CHAROLLAIS & CONRAD - SCHROEDER et al.; Fig. 2

2002 *Valserina primitiva* SCHROEDER, CHAROLLAIS & CONRAD - SCHROEDER et al.; Pl. 2, fig. 9

2009a *Valserina primitiva* SCHROEDER, CHAROLLAIS & CONRAD - CLAVEL et al.; Pl. 1, specimen PL19.2-2a

2009 *Valserina primitiva* SCHROEDER, CHAROLLAIS & CONRAD - CHAROLLAIS et al.; Pl. 4, figs. 12-16; Pl. 5, figs. 6-7; Pl. 6, figs. 8-10, 14-15

2010 *Valserina primitiva* SCHROEDER, CHAROLLAIS & CONRAD - CLAVEL et al.; Pl. 2, specimen 6894-3a; Pl. 4, specimens BC8Ga, BA19a.02-1a; Pl. 5, specimens BC23.05b, PA16.15a; Pl. 7, specimens 161.29-1b, 471-16a, 387.4b1; Pl. 12, specimen PL18.3-1c

2014 *Valserina primitiva* SCHROEDER, CHAROLLAIS & CONRAD - CLAVEL et al.; Pl. 6, specimen 7878-31a; Pl. 8, specimen GF9-2a; Pl. 10, specimen 447-21a; Pl. 12, specimen 161.29-1b; Pl. 21, specimen PL18.3-1c

2014 *Valserina primitiva* SCHROEDER, CHAROLLAIS & CONRAD - POLAVDER; Fig. 3.a-i

Remarks: The radial zone of *Valserina* (incl. the type-species *V. broennimanni* and *V. primitiva*) is well developed with meandering septules that are thickening inwards and foramina arranged in linear rows (Fig. 6.2, Pl. 11, figs. 12-13, 15-17). The reticular zone shows meshes with polygonal to elongated-branchy outlines. In the reticular (or central) zone, the chambers are connected by cross-wise oblique pores arranged in diagonal line, as in the genus *Orbitolinopsis*. The subaxial section illustrated in Figure 6 shows a specimen of a Chinese hat morphology ("chapeau chinois", ARNAUD-VANNEAU, 1980, legend Fig. 206), that due to its low apical angle and size is interpreted as a microspheric specimen. The same morphotype of a microspheric form has

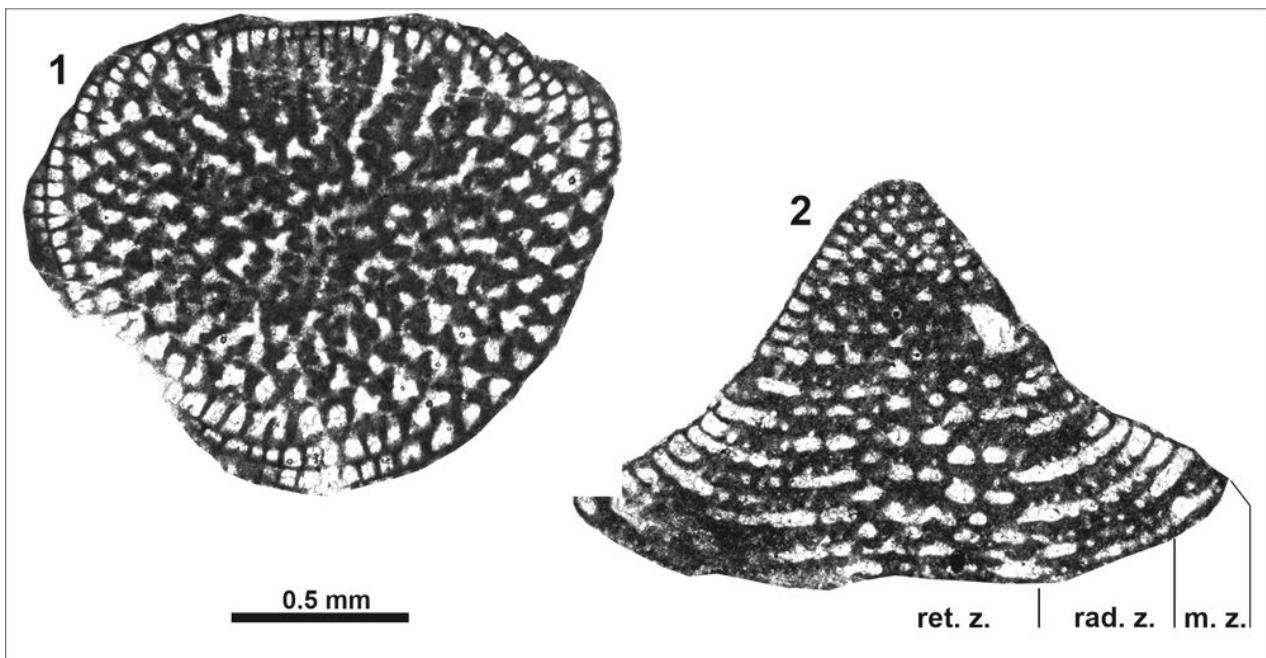


Figure 6: *Valserina primitiva* SCHROEDER & CHAROLLAIS from the upper Berriasian of the Kamenica section, eastern Serbia. **1.** Tangential section of a low conical specimen, presumably microspheric; thin-section 16208, Kamenica section. **2.** Subaxial section, specimen of Chinese hat morphology ("chapeau chinois", ARNAUD-VANNEAU, 1980, legend fig. 206), thin-section 14790. Abbreviations: m. z. = marginal zone, rad. z. = radial zone, ret. z. = reticular zone.

also been observed from the type-species *Valserina broennimanni* has been reported by SCHROEDER in SCHROEDER *et al.* (1968, Fig. 4). The upper Berriasian specimen consists of 25 chambers; it has a test diameter of ~1.85 mm and a height (almost complete) of ~1.2 mm. There are 22 chambers for the last mm axial test length.

Dimensions: D = 0.8-1.0 mm, H = 0.95-1.6 mm (megalospheric specimens)

Occurrences: Rare to common in the Kamenica section.

Genus *Vanneauina* SCHLAGINTWEIT, 2020
***Vanneauina vercorii* (ARNAUD-VANNEAU, 1980)**
 (Pl. 12)

1980 *Dictyoconus?* *vercorii* n. sp. - ARNAUD-VANNEAU, p. 653; Pl. 61, figs. 1-8; Pl. 97, figs. 1-10, Fig. 227

2011 *Dictyoconus* (collection DELOFFRE, origine inconnue) - MATHIEU *et al.*; Photos 8-9

2013a *Dictyoconus?* *vercorii* ARNAUD-VANNEAU - CLAVEL in GRANIER *et al.*, p. 151; Pl. 8, figs. 10-12; Pl. 9, fig. 7; Pl. 10, fig. 4

2014 *Dictyoconus?* *vercorii* ARNAUD-VANNEAU - CLAVEL *et al.*; Pl. 8, specimen 7847-11a; Pl. 10, specimen 7833-1c; Pl. 12, specimen 6898-2a; Pl. 17, specimen 575-1b; Pl. 22, specimen 407.2-16b. Pl. 25, specimen 229.1-1a1; Pl. 26, specimen LEST54-36a; Pl. 29, specimen 6935-4b; Pl. 32, specimen SANF10-2c

2020 *Vanneauina vercorii* (ARNAUD-VANNEAU) n. gen., n. comb. - SCHLAGINTWEIT, p. 2; Fig. 2A-G

Remarks: This taxon is characterized by its cylindroconical test with a small initial spire, solid coalescing pillars (often largely filling the central chamber lumen and appearing as micritic masses or patches), and the lack of rafters (ARNAUD-VAN-

NEAU, 1980, p. 650). Incompatible with *Dictyoconus* BLANCKENHORN, it has been described as the new genus *Vanneauina* by SCHLAGINTWEIT (2020). The dimensions of the upper Berriasian specimens are reduced compared to the Lower Cretaceous type-material of southeastern France (ARNAUD-VANNEAU, 1980). Specimens with comparable dimensions however have been illustrated by CLAVEL in GRANIER *et al.* (2013a, Pl. 8, figs. 10-12; 2017, Pl. 8, figs. 10-12) or CLAVEL *et al.* (2014, e.g., Pl. 8, specimen 7847-11a) from the Barremian-lower Aptian of the same area (see synonymy).

Dimensions: D = 0.65-1.0 mm, H = 0.9-1.2 mm, D/H 0.55-0.75

Occurrences: Common in the Kamenica section, rare in the Prekonozi section.

Gen. et sp. indet 1 (no rafters)
 (Pl. 13, figs. 1-6)

Remarks: This common taxon is characterized by medium- to high-conical tests, with adult chambers often reduced in width, and an almost plane base (e.g., Pl. 13, fig. 1). There are no rafters in the marginal zone, and the vertical main partitions are alternating between subsequent chambers; in axial sections the chambers are subdivided by numerous vertical pillar-like elements, their arrangement in the central zone remains unclear due to the lack of adequate transverse sections (Pl. 13, figs. 3, 5). Similar specimens have been illustrated by POLAVDER (2014) from the Kamenica section as belonging to *Paleodictyoconus beckerae* CLAVEL *et al.*, 2009b. This species has, like any other species of



the genus, a prominent early coil in the megalospheric form; the initial part of our specimens is unknown so that a preference is made herein for an open nomenclature.

Dimensions: D up to 0.85 mm, H up to 1.1 mm.

Occurrences: rare to common in the Kamenica section.

Gen. et sp. indet 2 (no rafters)
(Pl. 13, figs. 7, 9-10)

Remarks: This rare taxon is characterized by a coarse test structure, comparably high chambers and pillar-like elements in the central zone often triangular in shape (= the acute end pointing towards the apex = "pointe en haut"). In oblique sections, these elements do not regularly reach the septum of the chamber (= hemi-pillars; e.g., CLAVEL in GRANIER et al., 2013a, p. 153; 2017, p. 133) thus leaving a free space at its base. The poor material does not allow for a better characterization. The test habitus shows affinities to *Paracoskinolina hispanica* PEYBERNÈS, 1976, a species that has been described from the Barremian of the Spanish Pyreneans, later recorded from the Upper Hauterivian - lower Barremian of various localities in southeastern France (CLAVEL et al., 2010, 2014; CLAVEL in GRANIER et al., 2013a, 2017). For comparison purpose one oblique section of *Paracoskinolina? hispanica* from southeastern France is re-illustrated herein (CLAVEL et al., 2014, Pl. 6, specimen EB H 27.4). In any case, the revision of this taxon is still pending; it cannot belong to the genus *Paracoskinolina* as the vertical main partitions are alternating between subsequent chambers (e.g., PEYBERNÈS, 1976, Pl. 1, figs. 2 and 8, each in the upper test part).

Dimensions: D up to 0.85 mm, H up to 1.1 mm; noting a poor database.

Occurrences: Rare in the Kamenica section.

Gen. et sp. indet 3 (with rafters)
(Pl. 14, figs. 6-11)

Remarks: This rare and rather large-sized taxon is characterized by high-conical tests with up to 35 uniserial chambers; the initial part is unknown. The marginal zone is subdivided by one rafter per chamber; the number of intercalary beams (at least one up to ?) is unknown. The main partitions and vertical elements (pillars?) of the central zone are alternating between subsequent chambers. These structural features exclude the assignment to *Cribellopsis* on the one hand and *Paracoskinolina* on the other hand. More sections including the initial part and transverse sections showing the structure of the central zone and the vertical subdivision of the marginal zone are needed.

Dimensions: H up to 1.8 mm, D up to 0.75 mm, D/H = 0.5, number of chambers per last mm = 12-15

Occurrences: Lacking in the Kamenica section, gen. et sp. indet 3 has been observed only in the upper part of the Jerma section within high-energy deposits such as grainstones with ooids.

Subfamily DICTYORBITOLININAE
SCHROEDER in SCHROEDER et al., 1990

Remarks: The three genera *Paracoskinolina* MOULLADE, *Praedictyorbitolina* SCHROEDER, and *Dictyorbitolina* CHERCHI & SCHROEDER are attributed to the subfamily Dictyorbitolininae in the Lower Cretaceous. According to SCHROEDER in SCHROEDER et al. (1990, p. 196, translated), it is defined as follows: "The genera assigned to this subfamily are characterized by the presence of marginal foramina, situated at the periphery of the central zone forming a circular row. These apertures are arranged along vertical lines from the apex to the base. The primary septules show the same arrangement as the apertures". In the central zone, pillars may alternate (*Dictyorbitolina*, *Praedictyorbitolina*), or are aligned (*Paracoskinolina*).

**Genus *Paracoskinolina* MOULLADE, 1965,
emend. ARNAUD-VANNEAU, 1980**

Remarks: The genus *Paracoskinolina* was originally established as a subgenus of *Meyendorffina* of the subfamily Dictyoconinae defined by a distinct initial trochospire, pillars in the central zone and the lack of horizontal partitions (MOULLADE, 1965, p. 4033). *Paracoskinolina* was emended by ARNAUD-VANNEAU (1980, p. 602) defined by the alignment of both the main partitions of the marginal zone and the pillars of the central zone (from apex to base). It is generally accepted that horizontal partitions are present in some species of the genus, e.g., *P. arcuata* (ARNAUD-VANNEAU) or *P. reicheli* (GUILLAUME). In the 70s and 80s *Paracoskinolina* became a wastebasket for orbitolinids with differing internal structures, and in any case incompatible with the emended diagnosis: *P. fleuryi* DECROUEZ & MOULLADE, 1974, *P. pfenderae* CANÉROT & MOULLADE, 1971 (see this work), *P. prestati* PEYBERNÈS & DELMAS, 1981, *P. querolensis* CANÉROT & PEYBERNÈS, 1981, and *P. hispanica* PEYBERNÈS, 1976.

***Paracoskinolina* aff. *arcuata*
(ARNAUD-VANNEAU, 1976)**
(Pl. 14, figs. 1-4, 5?)

1976 *Dictyoconus maynci arcuatus* n. ssp. - ARNAUD-VANNEAU, p. 9; Pl. 1, figs. 4-8; Pl. 2, figs. 6-9.

1980 *Paracoskinolina arcuata* (ARNAUD-VANNEAU) - ARNAUD-VANNEAU, p. 609; Pl. 61, fig. 12; Pl. 99, figs. 11-13

2010 *Paracoskinolina arcuata* (ARNAUD-VANNEAU) - CLAVEL et al.; Pl. 1, specimen 136.2-4c; Pl. 14, specimen 407.2-1a; Pl. 24, specimen 6922a1

2014 *Paracoskinolina arcuata* (ARNAUD-VANNEAU) - CLAVEL et al.; Pl. 9, specimen MM373a; Pl. 13, specimen 6901-1a; Pl. 17, specimen 500.5-1a; Pl. 21, specimen 407.2-1a,

2019 *Paracoskinolina arcuata* (ARNAUD-VANNEAU) - BONVALLET et al.; Figs. 10/42, 10/51, 10/53, 10/59.



Remarks: The present rare oblique sections belong to medium- to high-conical tests displaying one rafter per chamber and aligned skeletal elements (Pl. 14, fig. 2). The latter feature is not always well constrained due to the obliqueness of the section plane. The specimens might belong to the high-conical to cylindro-conical *P. arcuata*. The presence of several orders of intercalary beams in the oblique transverse section (Pl. 14, fig. 5) however points to *Paracoskinolina reicheli* GUILLAUME, 1956, at least for this specimen rather than *P. arcuata* that has just one intercalary beam (ARNAUD-VANNEAU, 1976).

Dimensions: no data are provided to the rare oblique sections.

Occurrences: Rare in the upper parts of the Kamenica and Jerma sections.

6. Discussion

The earliest Orbitolinidae

The range of the family Orbitolinidae is indicated as Middle Jurassic to Oligocene in the fundamental work of LOEBLICH and TAPPAN (1987). The Middle Jurassic "record" of these taxa refers to *Gutnicella* (former *Lucasella*) (GUTNIG & MOULLADE, 1981; MOULLADE et al., 1981) including also "*Dictyoconus*" *cayeuxi* (LUCAS, 1938), and *Meyendorffina* AUROZE & BIZON (see MOULLADE, 1965; LOEBLICH & TAPPAN, 1987, p. 159-160). *Gutnicella*, the oldest "foraminifère orbitolinomorphe" (SEPTFONTAINE et al., 1991, p. 263), has been assigned to the Hauraniidae as well as *Meyendorffina* (SEPTFONTAINE, 1988, fig. 3; KAMINSKI, 2014). *Ataxella* PEYBERNÈS, 1988 (type-species *Paracoskinolina occitanica* PEYBERNÈS, 1974), from the Middle Jurassic of France, previously assigned to the Dictyoconinae has not been included in the classification of KAMINSKI (2014). It was assigned to the genus *Gutnicella* by BOUDAGHER-FADEL (2008), later retained in the genus *Ataxella* PEYBERNÈS, 1988 (not BASSOULET & LORENZ, 1988, as indicated in BOUDAGHER-FADEL, 2018), and assigned to the Hauraniidae. Due to the rather homogeneous and massive columella, *Ataxella* is in our opinion better placed within the Pfenderinidae. The Upper Jurassic "record" refers to the taxa *Kilianina* PFENDER, 1933, respectively the type-species *K. blancheti* PFENDER, 1933, and *K. rahonensis* FOURY & VINCENT, 1967 (= *Neokilianina* acc. to SEPTFONTAINE, 1988), and *Parurgonina* CUVILLIER et al., 1968. According to the classification of KAMINSKI (2014), *Kilianina* belongs to the Paravalvulinidae BANNER et al. whereas *Parurgonina* belongs to the Parurgoninidae SEPTFONTAINE. Summarizing, all Middle and Upper Jurassic species previously assigned to the Orbitolinidae have meanwhile been included in other families. The first records of the Orbitolinidae date back to the upper Berriasian (DARSAC, 1983; GRANIER, 2019; BUCUR, et al., 2020; SCHLAGINTWEIT & YAZDI-MOGHAMAD, 2020: *Cribellopsis delicatula*). Another form, *Valdanchella miliani* (SCHROEDER), considered by many workers as a Valanginian marker taxon (AZÉMA et

al., 1977; MARTÍN-CLOSAS & SALAS, 1998; CHERCHI & SCHROEDER in SCHROEDER et al., 2000) has also been reported from upper Berriasian strata (BÁDENAS et al., 2004; GRANIER et al., 2014, Fig. 2). The reported assemblage herein from eastern Serbia further manifests the late Berriasian age of the first representatives of the family. The outstanding species enrichment from the upper Berriasian of eastern Serbia with 18 taxa is highlighted by the contrast to just three different taxa recognized by DARSAC (1983) from the upper Berriasian of the French Jura Mountains.

Phylogenetic aspects

The discussion of phylogenetic relationships and models for any fossil group requires detailed knowledge on the stratigraphic ranges of the taxa involved. This prerequisite is even more important for a group such as the Orbitolinidae that lack any modern representatives, and thus exclude the application of molecular data analyses (e.g., PAWLOWSKI et al., 2013). Otherwise, the assumption of different stratigraphic ranges must necessarily result in contradictory views on the phylogeny of the group. In the literature there are different views on the phylogeny of the Orbitolinidae (or the genus *Orbitolina*) of which the most important ones have been summarized by HENSON (1948, p. 73). HENSON already recognized the most important "variation(s) from older to younger communities", namely increase of (i) test size, (ii) complexity of the marginal zone ("sub-epidermal layer"), (iii) the size and complexity of the megalospheric embryo along with its (iv) shift from a spiral-eccentric towards a central (apical) position. Note that the increasing complexity in the marginal zone is a prominent criterion for the subfamily Dictyoconinae, while in the Orbitolininae it is the increasing complexity of the embryo. It is worth mentioning that the principles of HENSON are still the base for the widely accepted temporary concept of different lineages within the three subfamilies Dictyoconinae, Orbitolininae, and Dictyorbitolininae (e.g., SCHROEDER, 1975; SCHROEDER et al., 2002, 2010). In his review, HENSON (1948, p. 75), distinguished the four structurally different groups of *Dictyoconus*, *Dictyoconella*, *Orbitolinopsis*, and *Orbitolina*. Direct relationships (e.g., ancestor-descendant) between different genera were not refined certainly also due to the lack of knowledge on the accuracy of stratigraphic ranges. Numerous genera that might have functioned as missing links, have also been described later. A phylogeny, that took "into account not only the morphologic stage of development but also the stratigraphic occurrence" was proposed almost 20 years later by DOUGLASS (1960, p. 249). DOUGLASS regarded *Coskinolinoites texanus* KEIJZER, a "primitive" form without horizontal partitions (= rafters) as the ancestor from which other genera evolved in "several directions", namely *Orbitolina* (= *Mesorbitolina*) *texana*, *Simplorbitolina manasi* CIRY & RAT, *Iraqia simplex* HENSON, and two branches with the Eocene *Dictyoconus* (= *Coskinon*) *floridanus* (COLE)



and the Albian *Dictyoconus walnutensis* (CARSEY), and another one with the Eocene *D. indicus* DAVIES (DOUGLASS, 1960, Fig. 3). This scheme is not commented in detail. We only want to stress that the stratigraphic distribution of these genera does not fit such a reconstruction: the Albian *C. texanus* cannot be the ancestor of the older forms *S. manasi* or *I. simplex*.

Several (if not all) authors however agree that the Orbitolinidae represent a morphologically rather heterogeneous group composed of convergent evolutionary lines (e.g., POKORNÝ, 1963). The most recent contribution to this topic was provided by BOUDAGHER-FADEL & PRICE (2019, Fig. 4) with a phylogenetic evolution scheme where "gradual morphological changes" occurred through time. Among several points that would be worth mentioning, we just name two. First, the stratigraphic ranges indicated for the genera following each other (ancestor-descendant) are, independently from the new data from Serbia (BUCUR *et al.*, 2020), not accurate. The range of *Orbitolinopsis* for example is indicated as Aptian-Albian to stress its descendence from *Paleodictyoconus* with an inferred range of late Valanginian to Aptian. It is already widely known that the oldest record of both *Orbitolinopsis* and *Paleodictyoconus*, previously known, dates back to the Late Hauterivian (CHAROLLAIS *et al.*, 2010; CLAVER *et al.*, 2010, 2014; GRANIER *et al.*, 2013a, 2017). In addition, the assumed evolution from forms with hemi-pillars (*Paleodictyoconus*; e.g., SCHROEDER in SCHROEDER & CHAROLLAIS, 1966, p. 109-110) to forms with cupules in the central zone (*Orbitolinopsis*; e.g., ARNAUD-VANNEAU, 1980) appears quite arbitrarily and has not been further discussed. Last but not least, the presentation may create the appearance of facts rather than of one hypothesis. Anyway, the new data give evidence that numerous genera display a near-simultaneous appearance (or FAD) in a parallel manner, not one after the other. Independently from the evolutionary first appearance, the lower part of the Kamenica section appears unsuitable from a facies point of view (e.g., fenestral limestones) for the proliferation of the group (see Fig. 2). Higher up in the stratigraphic section the establishment of inner platform conditions allowed the occupation and colonization of available or new ecospaces, e.g., muddy lagoonal facies (wackestones) and external shoal facies (grainstones). In the latter, the preference of some taxa is evident (*Orbitolinopsis debelmasi*, *Urgonina alpicensis*, *Paracoskinolina* aff. *arcuata*, gen. et sp. indet 3). Thus, the early history of the Orbitolinidae can be interpreted as an example of adaptive radiation where a clade displays a rapid diversification (18 taxa recorded herein!) and ecological exploitation (SIMPSON, 1944). This kind of evolution is also often referred to as "early bursts" (e.g., PUTTICK, 2018). The major part of the genera that later lead to the "Urgonian" diversification (e.g., ARNAUD-VANNEAU, 1980; CLAVER *et al.*, 2014) were already present at the very be-

ginning of the group. Therefore, the new data provide a solid data base for future further refinements of phylogenetic traits within the Orbitolinidae. The explosive radiation of the Orbitolinidae in the late Berriasian is accompanied by the FAD of several other large benthic foraminifera including mostly agglutinating (e.g., *Ammocycloloculina* MAYNC, *Choffatella* SCHLUMBERGER, *Drevennia* ARNAUD-VANNEAU, *Eclusia* SEPTFONTAINE, *Moulladella* BUCUR & SCHLAGINTWEIT, *Pfenderina* HENSON, *Pseudotextulariella* BARNARD) but also complex porcellaneous taxa (*Pavlovcevina* LOEBLICH & TAPPAN) (e.g., GRANIER, 2019; BUCUR *et al.*, 2020) providing evidence for a thus far unknown bioevent in this time period that exceeds the number of taxa originating in the previous (Tithonian) and the following stage (Valanginian) (e.g., KAMINSKI *et al.*, 2008, Fig. 1). Last but not least, the Berriasian also witnessed the appearance of new genera of the aragonitic Robertinida described only recently by RIGAUD *et al.* (2021).

Palaeobiogeographic aspects

A "remarkable stratigraphic identity" between the Urgonian of southeastern France and the southern Pyreneans (France-Spain) has been stated by BECKER (1999) and SCHROEDER *et al.* (2000, p. 34). This cross reference is provided here, due to species common to both this area and eastern Serbia. The orbitolinid microfauna of southeastern France also shows many species in common with Sardinia, Italy (e.g., DIENI *et al.*, 1963; CHERCHI & SCHROEDER, 1978, 1999). This accordance is not really astonishing bearing in mind that during the Lower Cretaceous the Corsica-Sardinia microplate was in a position proximal to the European continent (here: Provence area of southeastern France) (e.g., GATTACCECA *et al.*, 2007). The diversity of Lower Cretaceous Orbitolinidae from these northern Tethysian occurrences is distinctly greater than the one recorded from its southern margin, e.g., northern Africa (e.g., PEYBERNÈS, 1982). There, the records are also younger lacking any late Berriasian taxa. It is worth mentioning that later, for example during the Cenomanian, the diversity of the southern Tethysian margin (with special reference to the Arabian Plate) exceeds the one observed from the northern Neotethysian margin (SCHROEDER & NEUMANN, 1985; YAZDI-MOGHADAM & SCHLAGINTWEIT, 2021).

7. Conclusions

The upper Berriasian orbitolinid microfauna of eastern Serbia is characterized by very high diversity including at least 18 taxa belonging to at least seven genera. One species is described as the new species *Cribellopsis sudari*. Morphologically, high-conical forms with predominantly simple exoskeleton (= lack of rafters) are dominating. The observed taxa belong to the Dictyorbitolininae (genus *Paracoskinolina*) and Dictyoconinae (all other genera observed); Orbitolininae are absent.



With presumably inconvenient environmental conditions in the lower Berriasian (e.g., fenestral limestones), the appearing of inner platform facies favoured the rapid (explosive) adaptive radiation of the group. The sudden and more or less time-equivalent appearance of all these genera, contrasts evolutionary concepts with "gradual morphological changes" and ancestor-descendant relationships. This observation does not question lineages among the Dictyoconinae (e.g., with increasing complexity of the marginal zone) and the Orbitolininae (e.g., increasing complexity and size of the embryo).

Almost all taxa observed herein are known from the Lower Cretaceous (Upper Hauterivian-lower Aptian) of southeastern France. With the distinct extension of the stratigraphic ranges, the biostratigraphic value of several species is distinctly lowered.

The rich assemblages of the Orbitolinidae of eastern Serbia (upper Berriasian) and south-eastern France (Upper Hauterivian-lower Aptian) belong to the former northern Neotethysian margin contrasting an impoverished assemblage from the southern Neotethysian margin, where upper Berriasian taxa have so far not been recorded.

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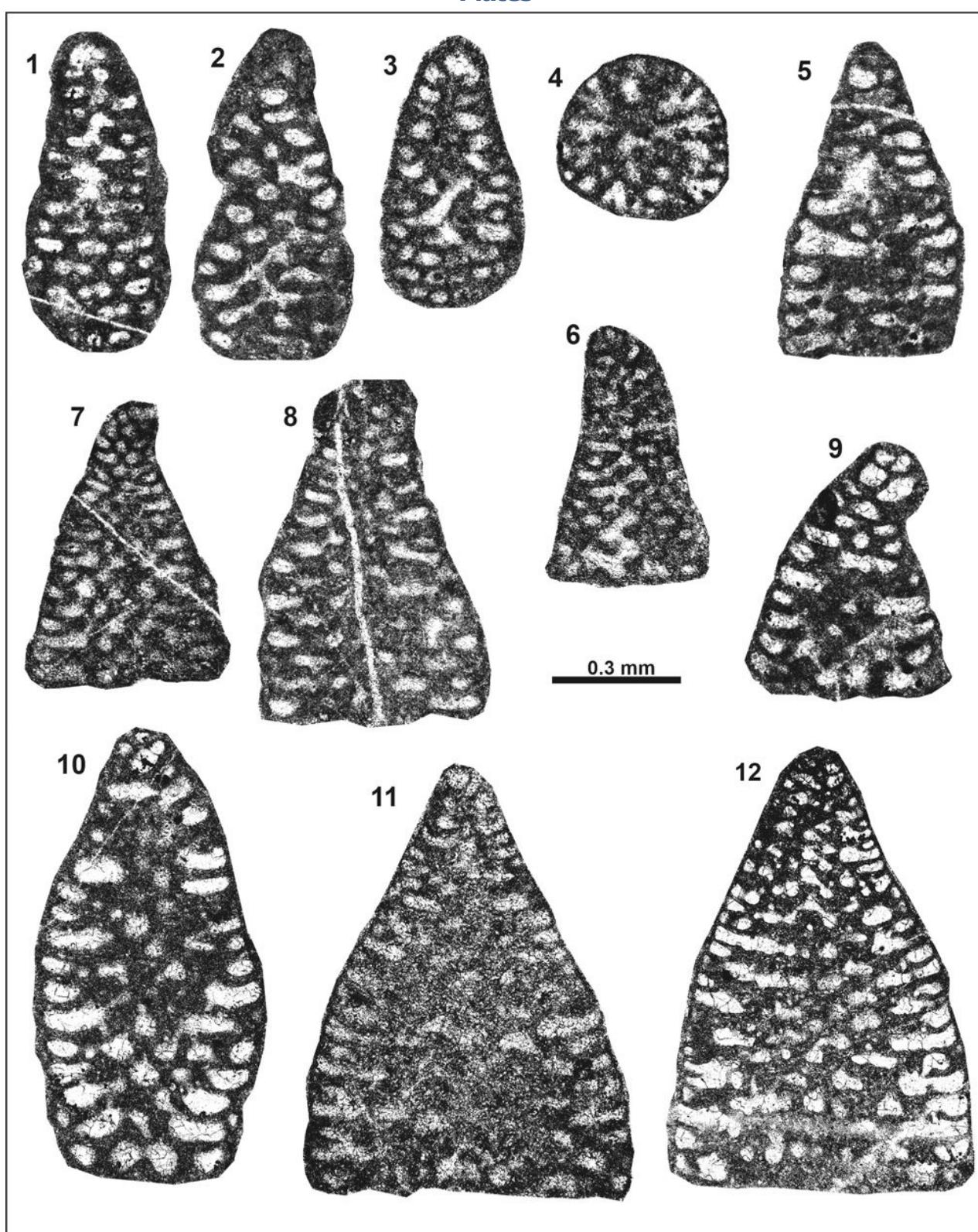


State of the art and description of *Ebrahimiella* *dercourti* (DECROUEZ and MOULLADE, 1974) gen. et comb. nov. (family Coskinolinidae) from the

Sarvak Formation (SW Iran, Zagros Zone).-
Cretaceous Research, vol. 126, article 104885,
12 p.



Plates

**Plate 1:**

Upper Berriasian Orbitolinidae from the Kamenica (1-8, 10-12), Jerma (4), and Prekonozi (9) sections, eastern Serbia. *Cribelopsis elongata* (DIENI et al.) (1-9), and *Cribelopsis neoelongata* (CHERCHI & SCHROEDER) (10-12).

Figs. 1-3, 5-6: (Sub)Axial sections. Thin-sections 14778, 14782, RR4025, 14783, 14791-3.

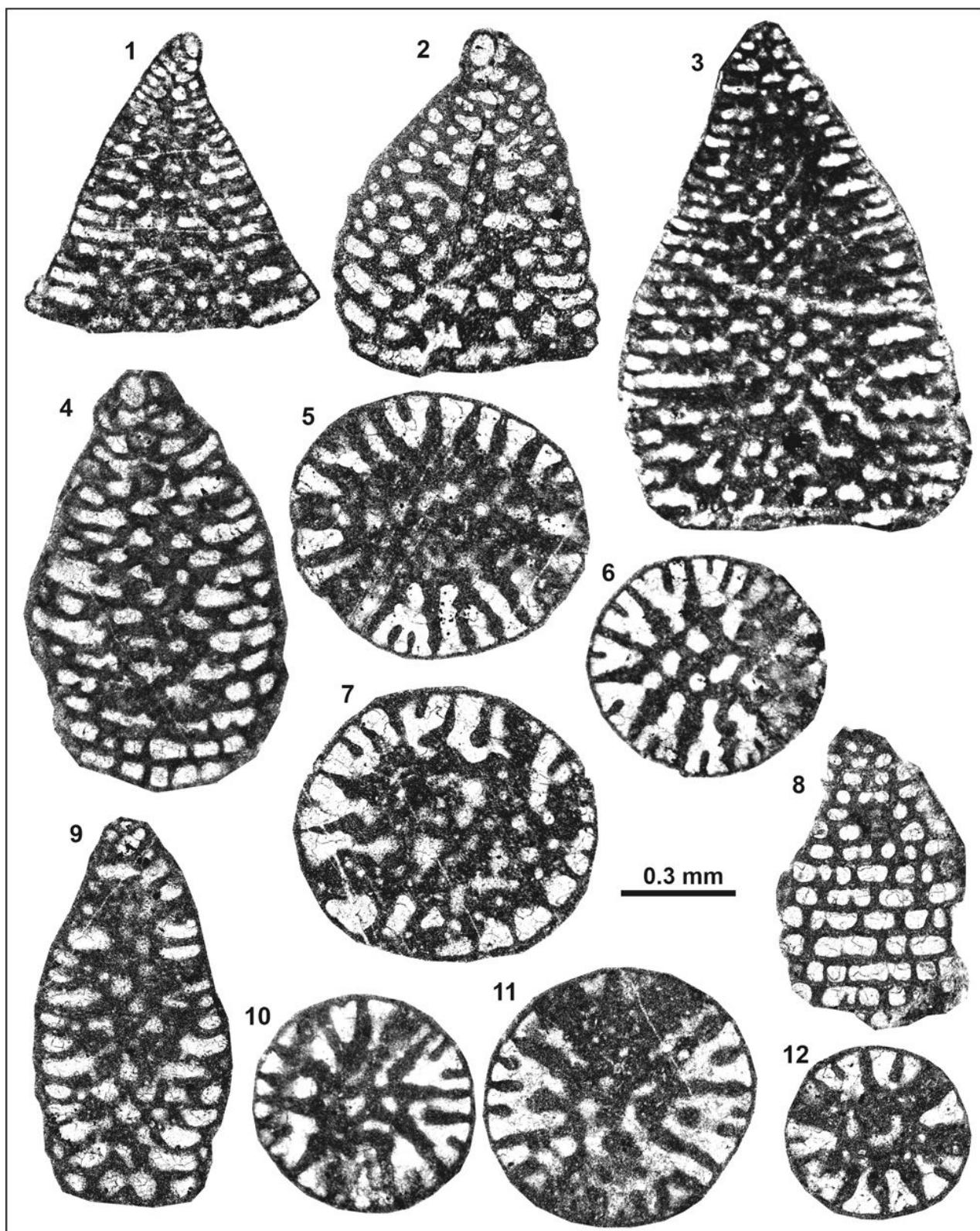
Fig. 4: Slightly oblique transverse section. Thin-section 14739.

Figs. 7-9: Axial sections. Thin-sections 14796, 14783, 16352.

Fig. 10: Oblique section. Thin-section RR3988.

Fig. 11: Axial section. Thin-section 14024-2.

Fig. 12: Subaxial section. Thin-section RR4015.

**Plate 2:**

Upper Berriasian Orbitolinidae from the Kamenica section, eastern Serbia. *Cribellopsis neelongata* (CHERCHI & SCHROEDER)

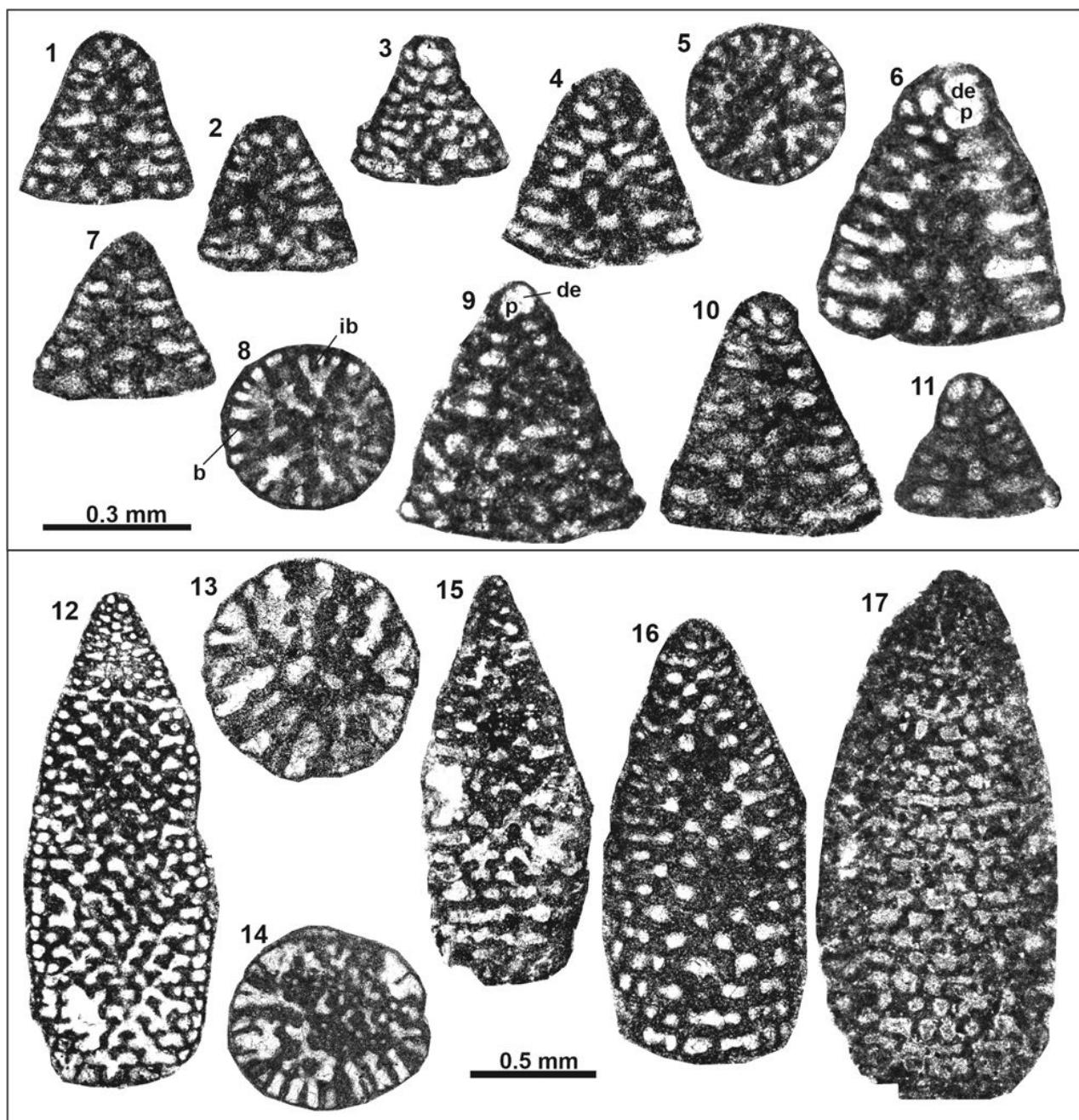
Fig. 1: Axial section. Thin-section 14800.

Figs. 2, 4, 9: Oblique axial sections. Thin-section RR3982, 14784, RR3988.

Fig. 3: Subaxial section. Thin-section 14793.

Figs. 5-7, 10-12: Transverse sections, partly slightly oblique. Thin-sections RR3990, RR3993, RR3988, RR3993, RR3992, RR3990.

Fig. 8: Tangential-oblique section. Thin-section RR3982.

**Plate 3:**

Upper Berriasian Orbitolinidae from the Kamenica section, eastern Serbia. *Cribellopsis pfenderae* (CANÉROT & MOULADE) nov. comb. (1-11), and *Cribellopsis thieuloyi* ARNAUD-VANNEAU (12-17).

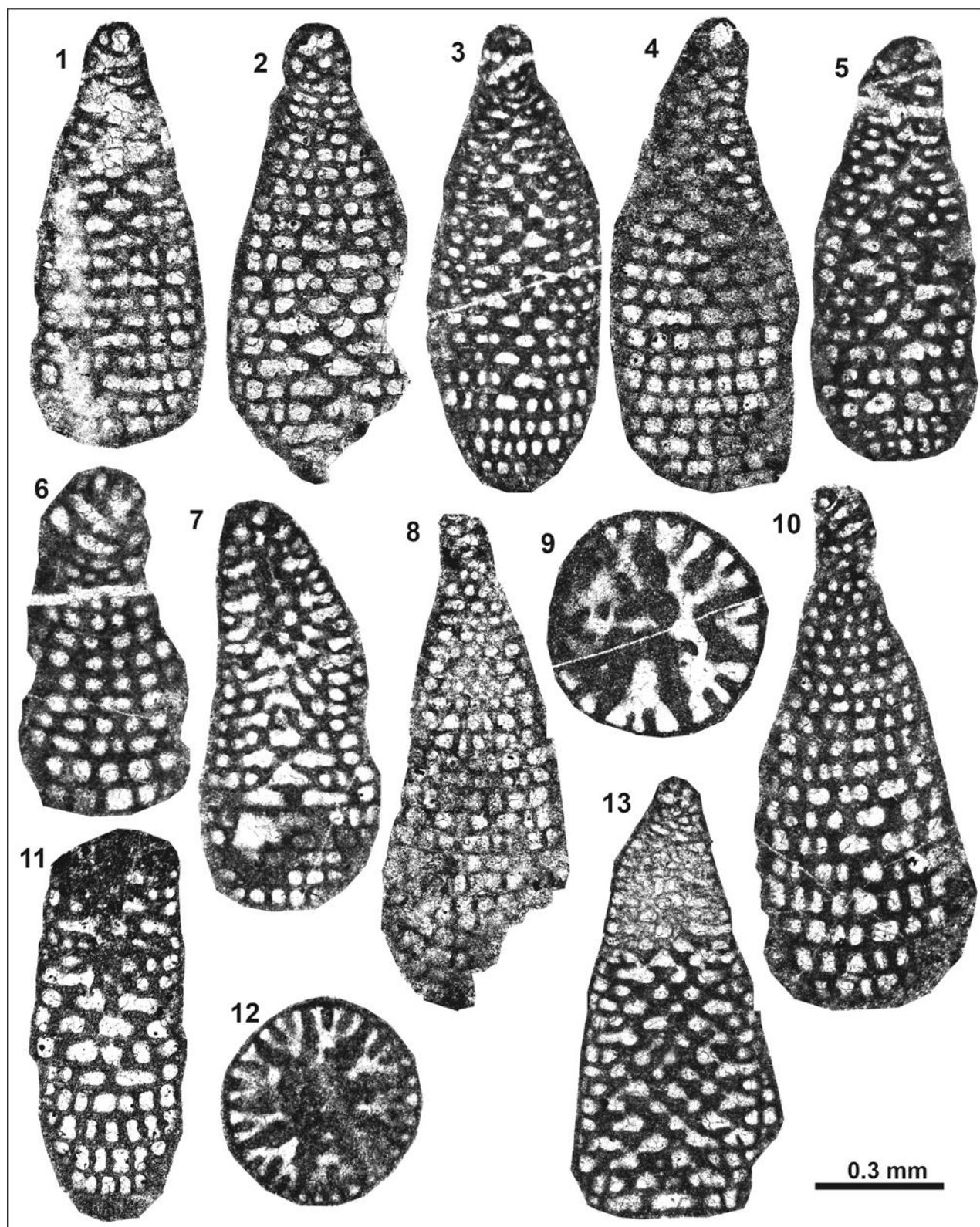
Figs. 1-2, 4, 7: Subaxial sections. Thin-sections 14793-2, 14788-3, RR4017, 14022.

Figs. 3, 6, 9-11: Axial sections; note embryo in 3, 6, and 9. Thin-sections 14792-2, 14796-2, 14800, 14790-4, 14019.

Figs. 5, 8: Transverse sections. Thin-sections 14799, 14796-2.

Figs. 12, 15-17: (Sub) axial sections. Thin-sections 14791-3, RR4040, 14791-3, 14816.

Figs. 13-14: Slightly oblique transverse sections. Thin-sections RR3992, RR3986.

**Plate 4:**

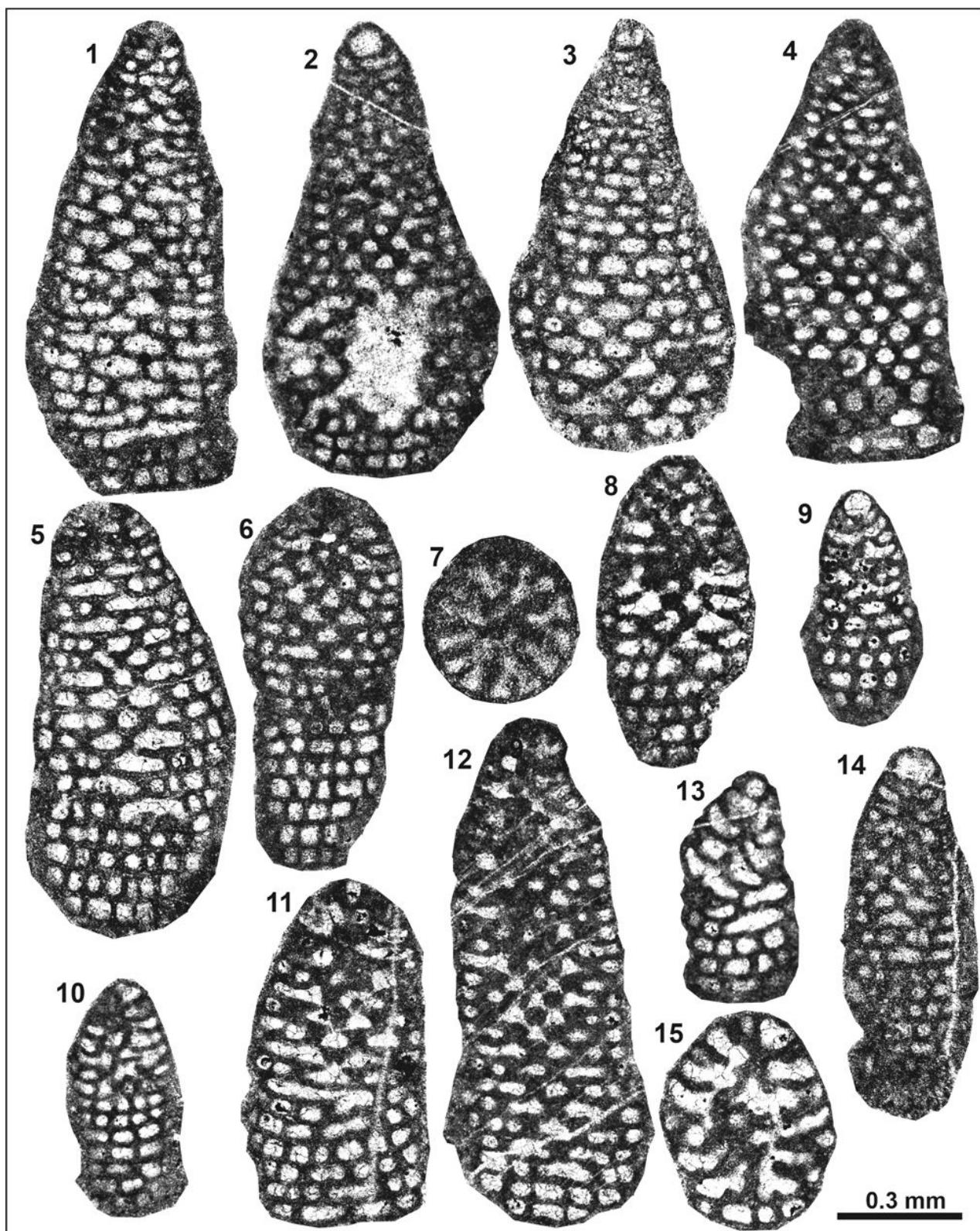
Upper Berriasian Orbitolinidae from the Kamenica section, eastern Serbia. *Cribellopsis sudari* n. sp.

Figs. 1-5, 7, 13: (Sub) axial, p.p. tangential sections. Thin-sections 14791-4, 14020, 14796-3, 14794, 16209-2, 14796-2, 14792-5.

Fig. 6: Tangential section passing through the initial spire. Thin-section 14806.

Figs. 8, 10-11: Tangential sections. Thin-sections 14795-2, 14796, RR3979-1.

Figs. 9, 12: Transverse sections. Thin-sections 14778-3, 14796.

**Plate 5:**

Upper Berriasian Orbitolinidae from the Kamenica (1-6, 8, 10-15) and Jerma (7) sections, eastern Serbia. *Cribellopsis sudari* n. sp.

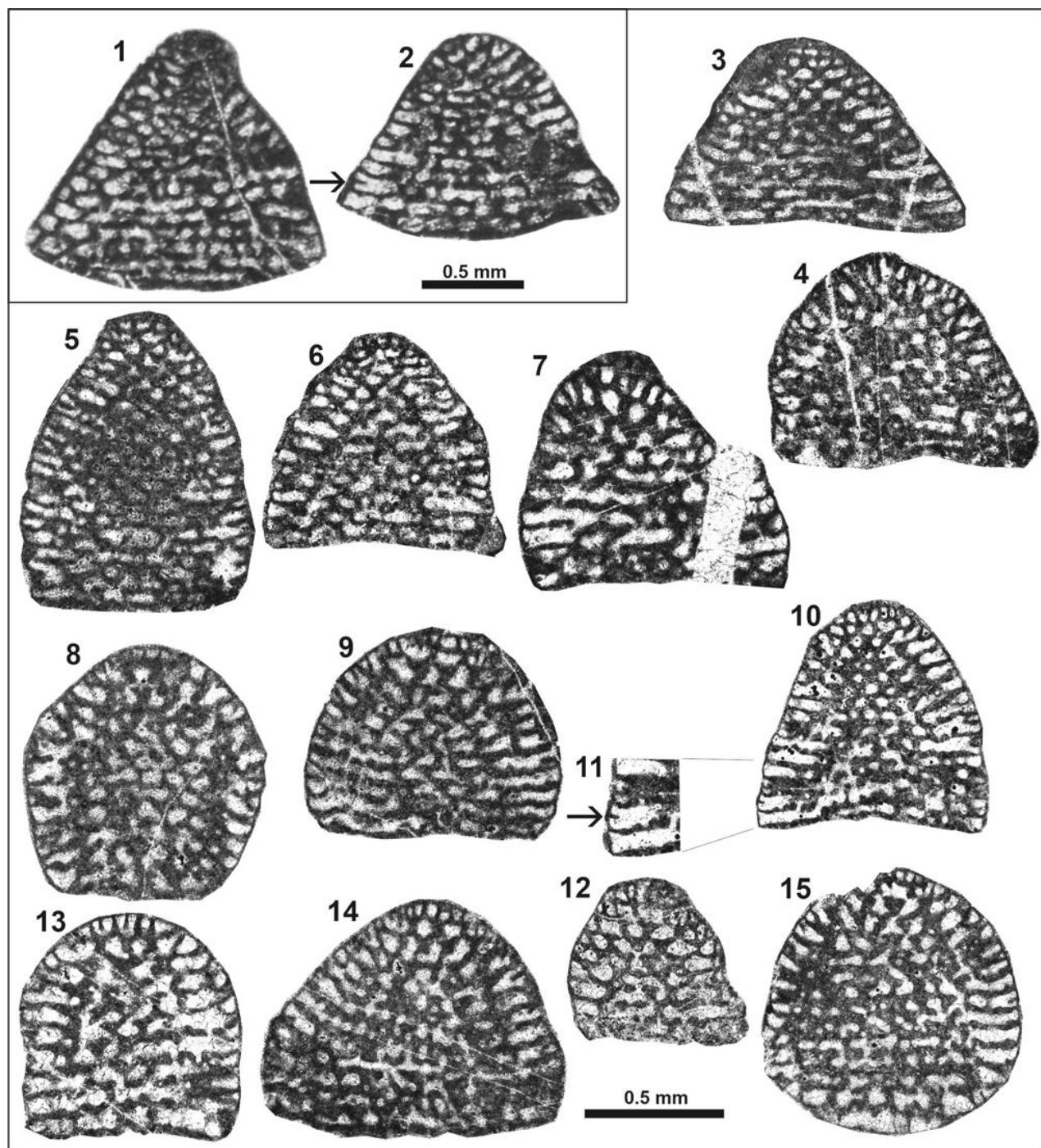
Figs. 1-4, 9, 12, 14: (Sub) axial, p.p. tangential sections. Note embryo in 2-3, 9, and 14.
Thin-sections 14792-1, 14019, 14797, 14784-6, 14797, 14802, 14793.

Figs. 5-6, 8, 10-11: Tangential-oblique sections. Thin-sections 14797, 14793, 14787-2, 14792-7, 14798.

Fig. 7: Transverse section of juvenile test part. Thin-section 14720.

Fig. 13: Oblique section through the trochospirally coiled initial part. Thin-section 14784-6.

Fig. 15: Oblique transverse section of adult test part. Thin-section 14792-7.

**Plate 6:**

Lower Cretaceous Orbitolinidae of southeastern France (1-2), and the upper Berriasian of the Kamenica section, eastern Serbia (3-15). *Montseciella glanensis* (FOURY)

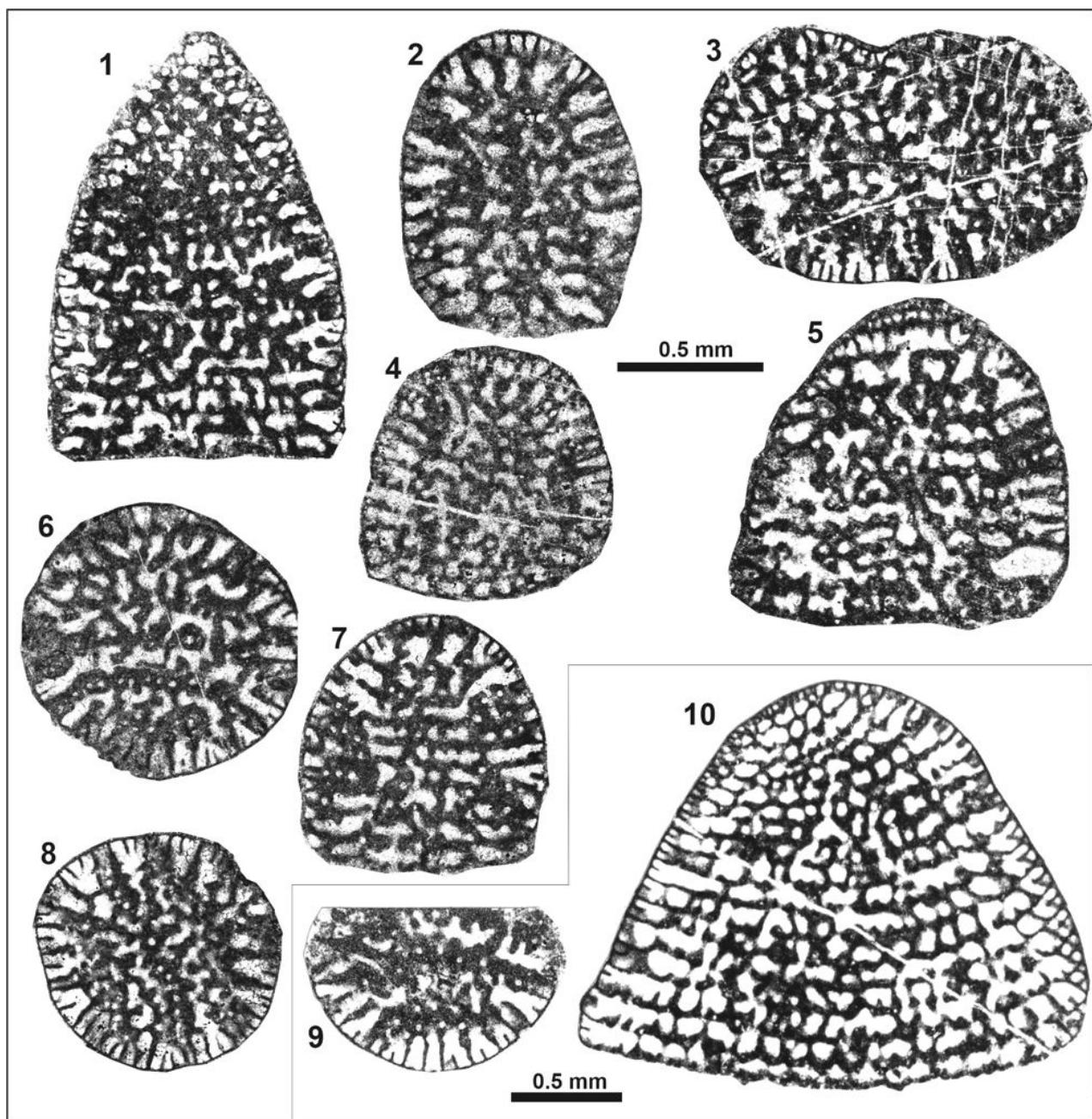
Fig. 1-2: Subaxial sections (from FOURY, 1968, Pl. 18, figs. 7, 9).

Figs. 3, 5-6, 9-11: Subaxial sections, partly oblique. Thin-sections 14025, 14021, 14797, 14019, 14792-1. Note the occurrence of a single, rather short horizontal partition in the penultimate chamber (left side, detail in 11).

Figs. 4, 7, 13-14, 15: Oblique sections. Thin-sections 14810, 16209-2, 14787, 14797.

Fig. 8: Oblique transverse section. Thin-section 14792-1.

Fig. 12: Tangential section. Thin-section 14788-3.

**Plate 7:**

Lower Cretaceous Orbitolinidae of Sardinia, Italy (9-10, from CHERCHI & SCHROEDER, 1999, Pl. 3, fig. 1; Pl. 4, fig. 1), and the upper Berriasian of the Kamenica section, eastern Serbia (1-8). *Montseciella algerensis* CHERCHI & SCHROEDER.

Figs. 1, 10: Subaxial sections. Thin-section 14796-2 (1), (10) from CHERCHI & SCHROEDER (1999).

Figs. 2-5, 7: Oblique sections. Thin-sections 14795, 14796, 14798, 14794-2, 14795-2.

Figs. 6, 8-9: Transverse sections, partly oblique. Thin-sections 14022, 14792-7, and from CHERCHI & SCHROEDER (1999).

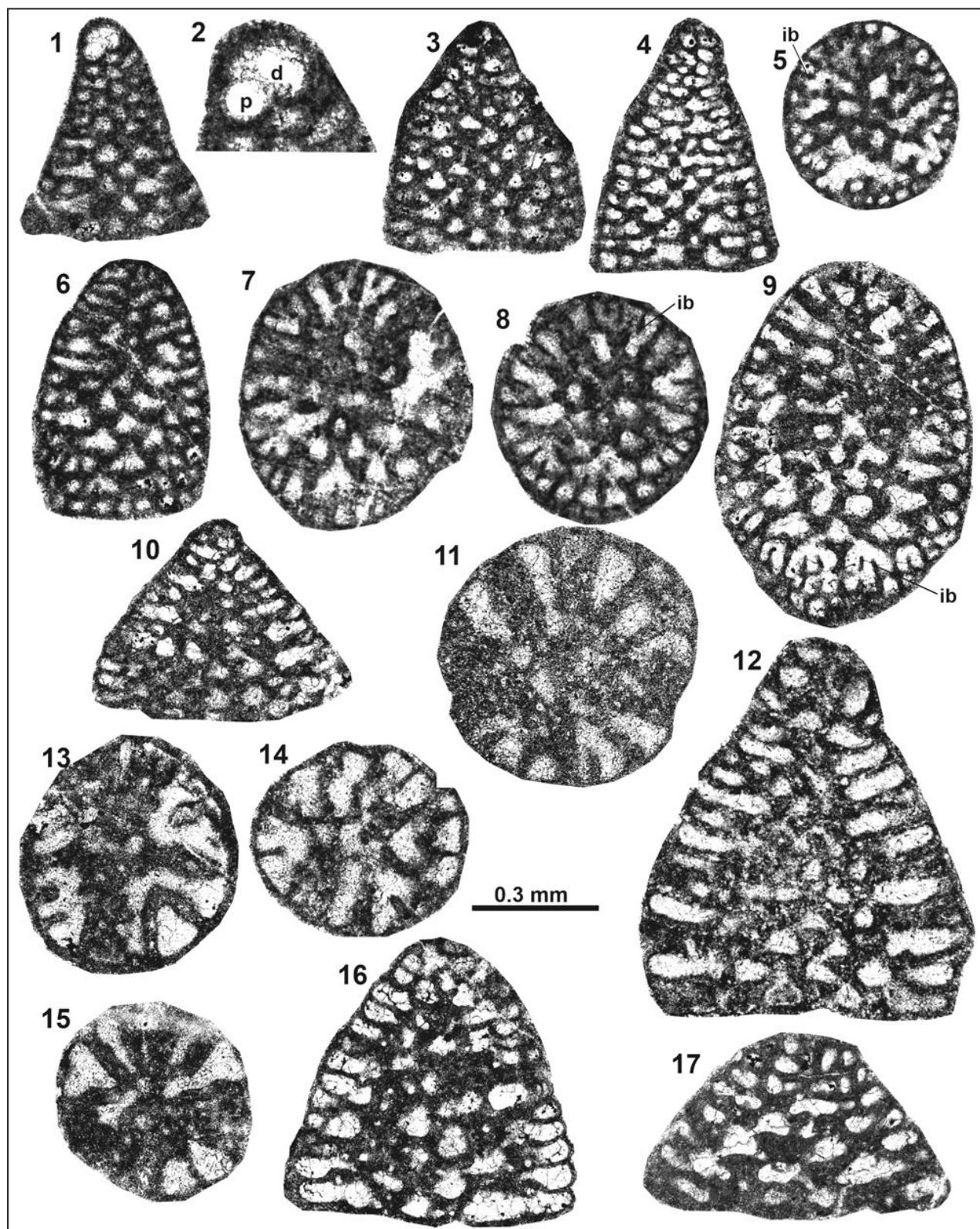


Plate 8: Upper Berriasian Orbitolinidae from the Kamenica (1-11, 13), and Prekonozi (12, 14) sections, eastern Serbia. *Orbitolinopsis briacensis* ARNAUD-VANNEAU (1-10), and *Orbitolinopsis cuvillieri* MOULLADE (11-17). Abbreviation: ib = intercalary beam.

Figs. 1-2: Axial section of megalospheric specimen showing slightly eccentric bilocular embryo (proloculus, deuteroconch; see detail in 2). Thin-section 14019.

Figs. 3-4: Subaxial sections Thin-sections 14019, 14794-2.

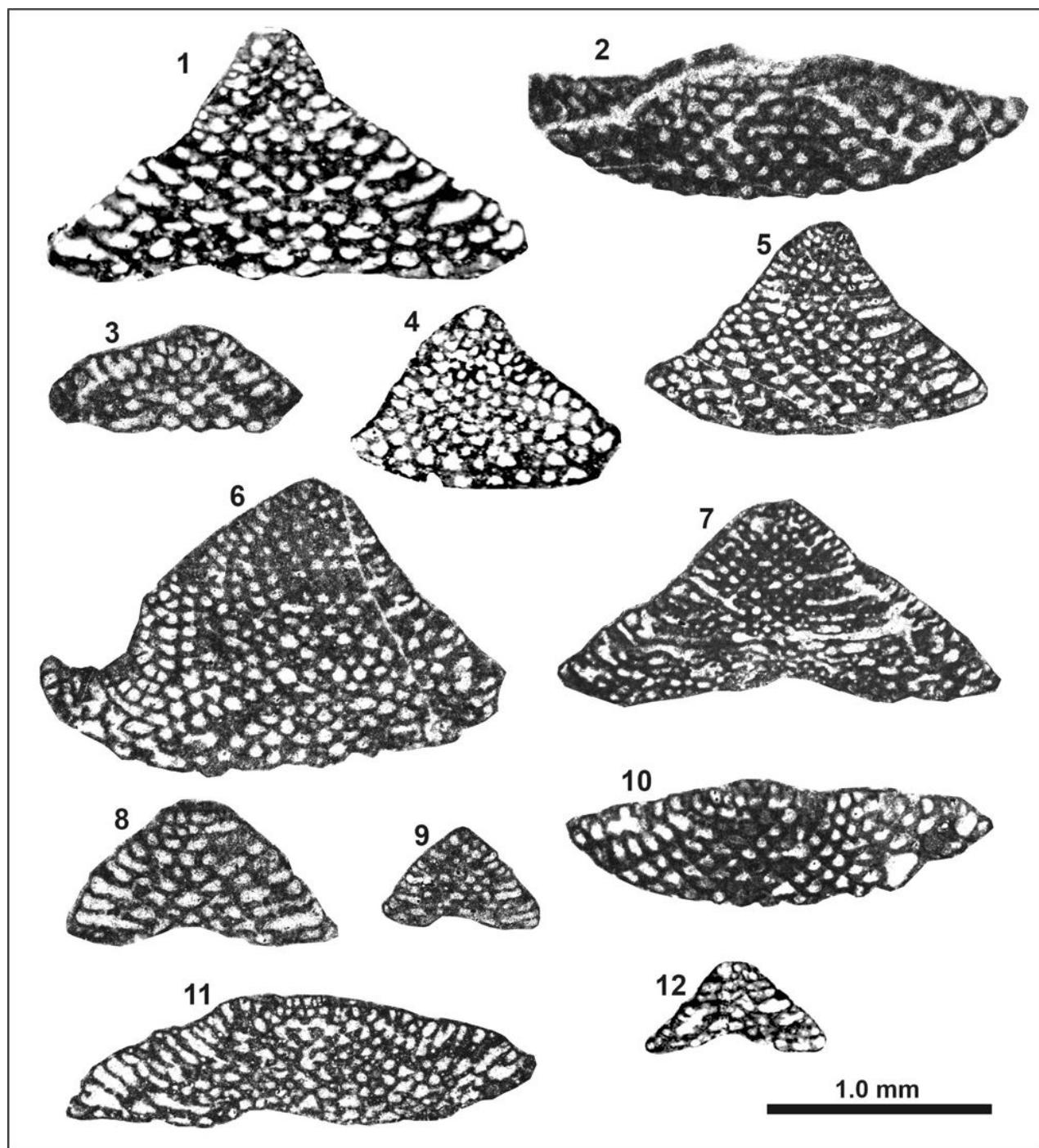
Figs. 5, 8, 14: Oblique transverse sections. Thin-sections 14787-3, 14027, 16331.

Figs. 6-7, 9-10: Oblique sections. Thin-sections 14019, 14025, 14792-1, RR4024.

Figs. 11, 13, 15-16: (Sub)axial sections, thin-sections RR4982, 14786, 14784, 14792-1.

Fig. 12: Axial section. Thin-section 16331.

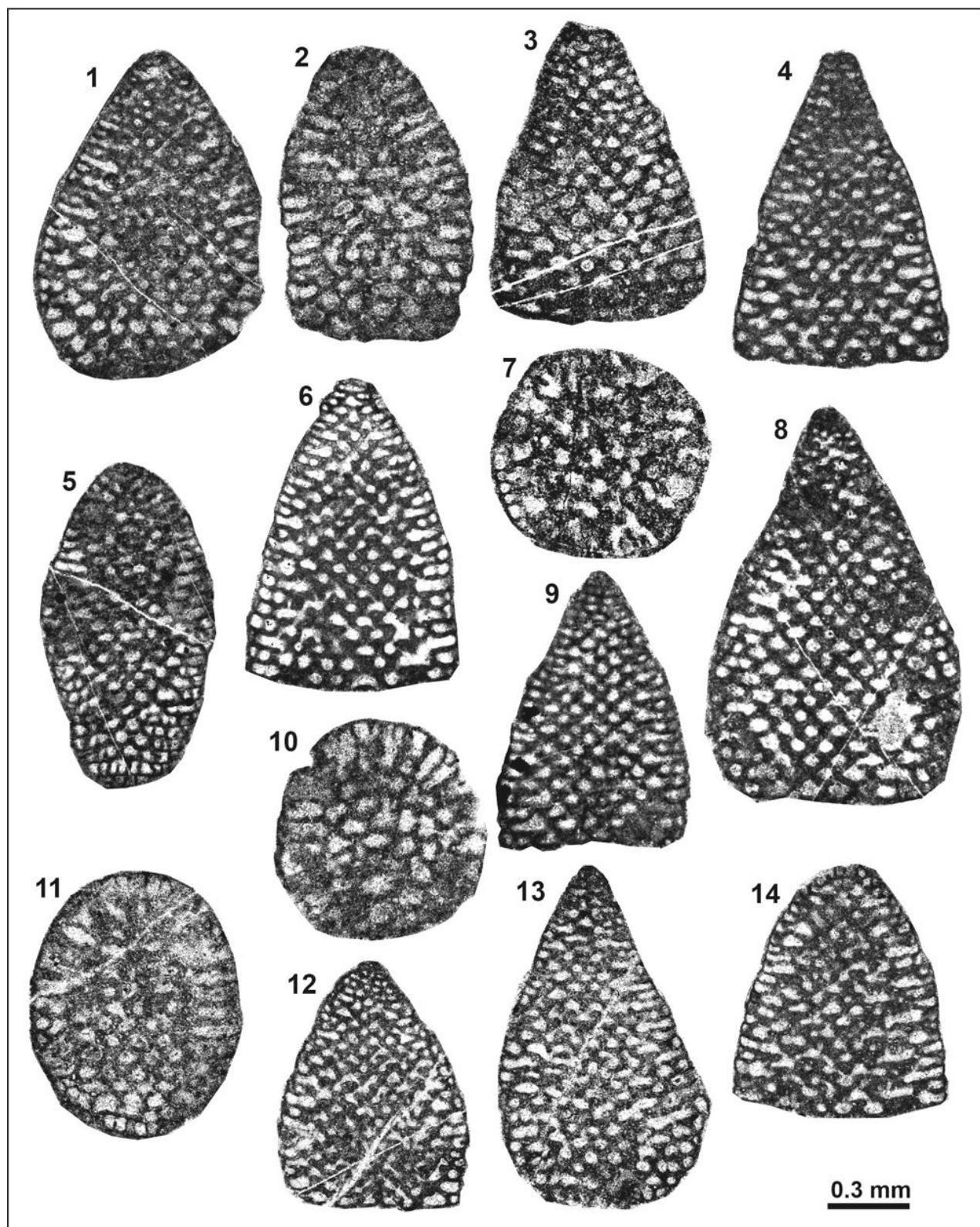
Fig. 17: Tangential section. Thin-section 14784-6.

**Plate 9:**

Upper Berriasian Orbitolinidae from the Kamenica (3, 5-11), Jerma (2) section, eastern Serbia, and Lower Cretaceous of southeastern France (1, 4, 12) *Orbitolinopsis buccifer* ARNAUD-VANNEAU & THIEULOUY

Figs. 1, 6, 9-12: (Sub)axial sections. Juvenile specimens in 9 and 12. Specimen OV 177b, thin-section 16209, 14733, RR4024, specimen 7803-9a.

Figs. 2-4, 5, 7-8: Tangential sections. Thin-sections 14436, 14804, specimen 7039-10a, thin-section 14803, 14790, 14804.

**Plate 10:**

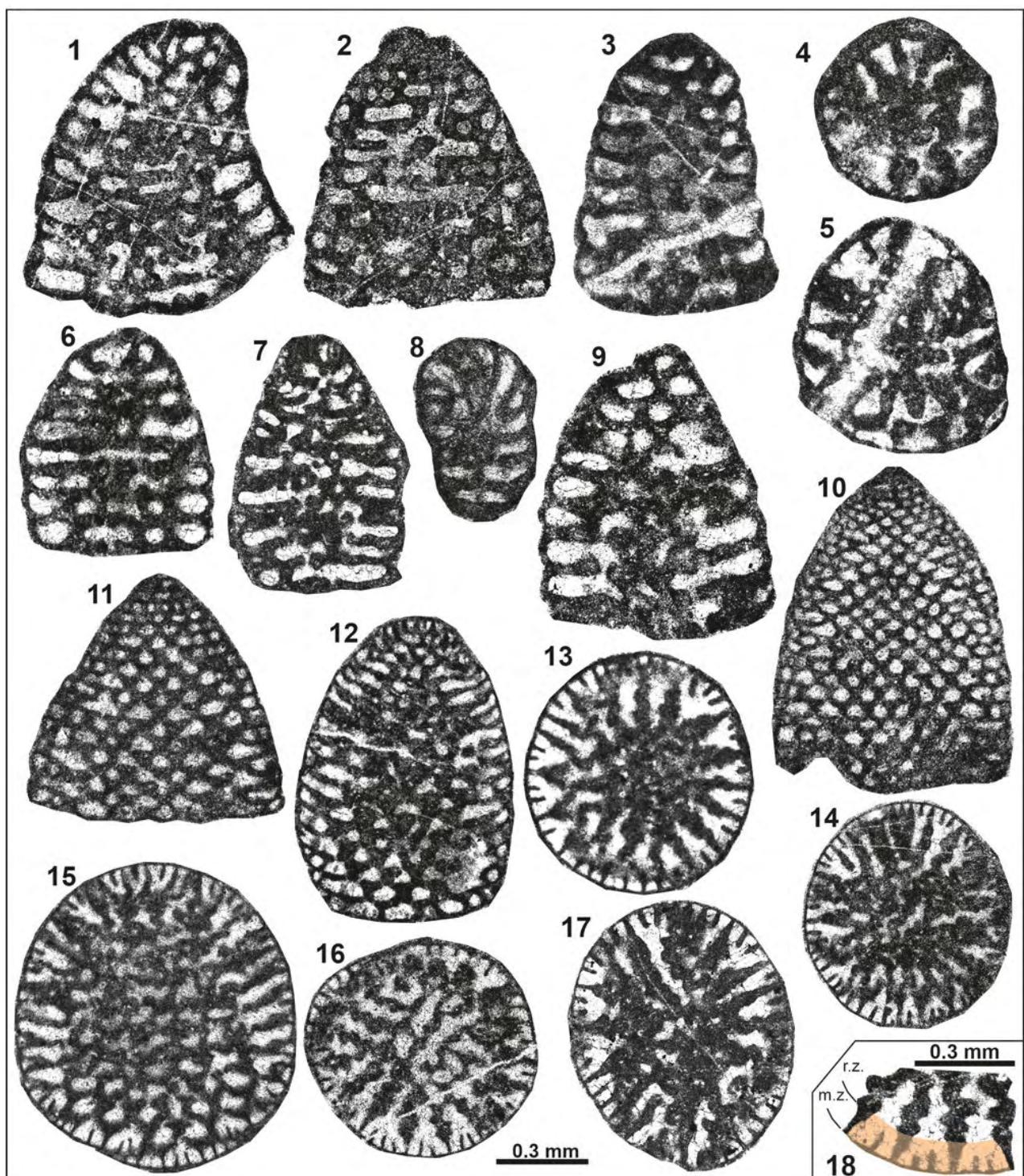
Upper Berriasian Orbitolinidae from the Kamenica (3-6, 8-10, 12, 14) section, Prekonozi section (1-2), and Jerma section (7, 11, 13), eastern Serbia. *Orbitolinopsis debelmasi* MOULLADE & THIEULOY

Figs. 1, 3-4, 6, 8-9, 12-14: (Sub)Axial sections. Thin-sections 16362, 14787-2, 14019, 14788-2, 14800, 14022, 14787, 14715-2, 14020.

Figs. 2, 11: Oblique sections. Thin-sections 16361B, 14715.

Fig. 5: Tangential-oblique section. Thin-section 14022.

Figs. 7, 10: Transverse sections. Thin-sections 14034, 14804.

**Plate 11:**

Upper Berriasian Orbitolinidae from the Kamenica section (1-7, 9-18) and Jerma section (8), eastern Serbia. *Urgonina alpiliensis* (FOURY) (1-9), and *Valserina primitiva* SCHROEDER & CHAROLLAIS (10-18)

Fig. 1: Axial section. Thin-section 14810.

Figs. 2-3, 6-7, 9: Subaxial sections. Thin-sections 14818, 14786, 14028, 14778, 14806.

Fig. 4: Transverse section. Thin-sections 14778-2.

Fig. 5: Oblique section. Thin-section 14779-2.

Fig. 8: Oblique section passing through the initial coil. Thin-section 14721.

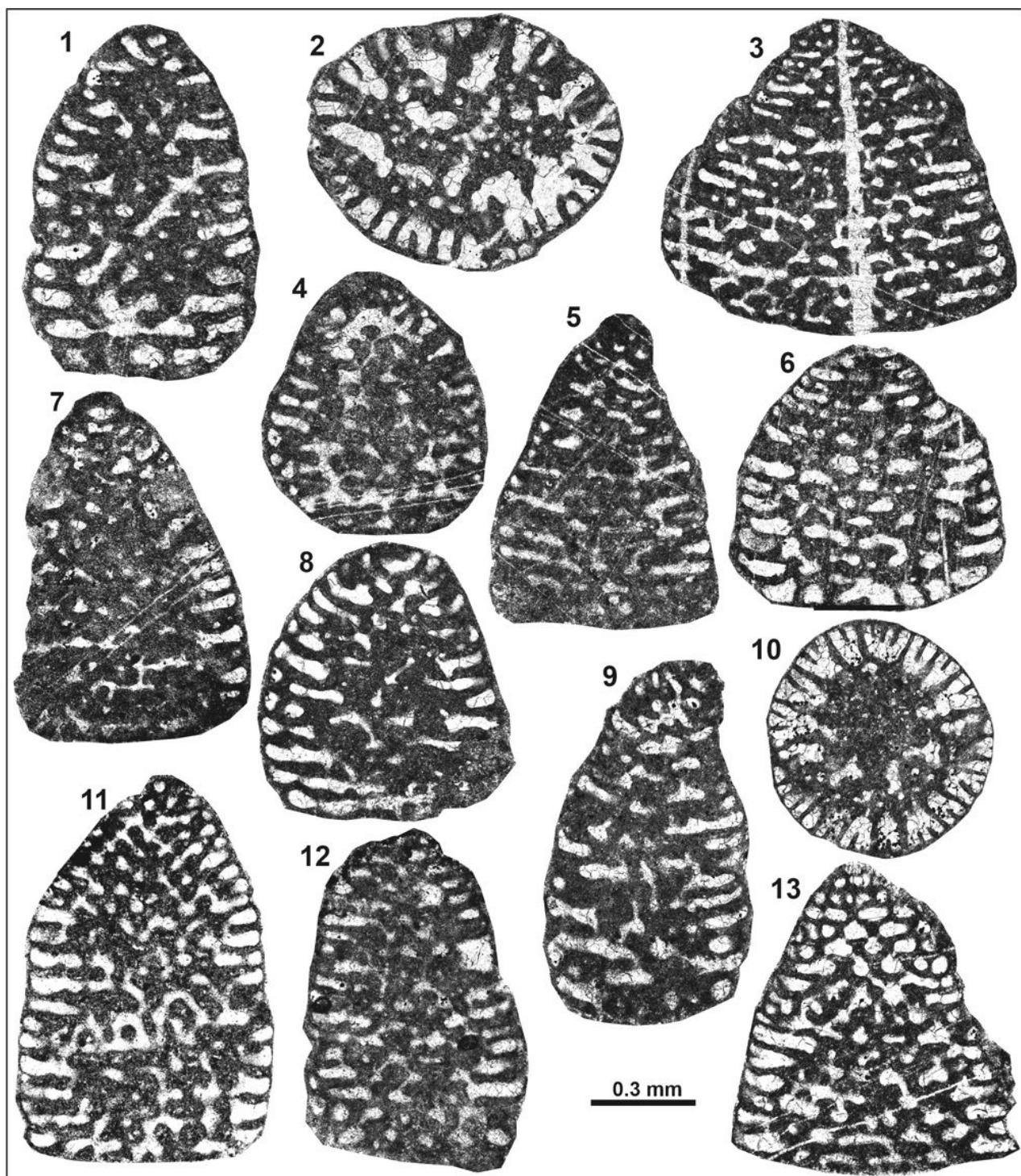
Fig. 10: Tangential section. Thin-section 14804.

Fig. 11: Subaxial sections. Thin-sections 14020.

Figs. 12, 15: Oblique section. Thin-sections 14208, 14804.

Figs. 13-14, 16-17: Transverse sections, partly slightly oblique. Thin-sections: 14787-2, 14022, 14794, 14793.

Fig. 18: Detail of the marginal (m.z., in orange) with one to two vertical partitions between two meandering septulae of the radial zone (r.z.).

**Plate 12:**

Upper Berriasian Orbitolinidae from the Kamenica (1-11, 13) and Prekonozi (12) sections, eastern Serbia. *Vanneauvercorii* (ARNAUD-VANNEAU)

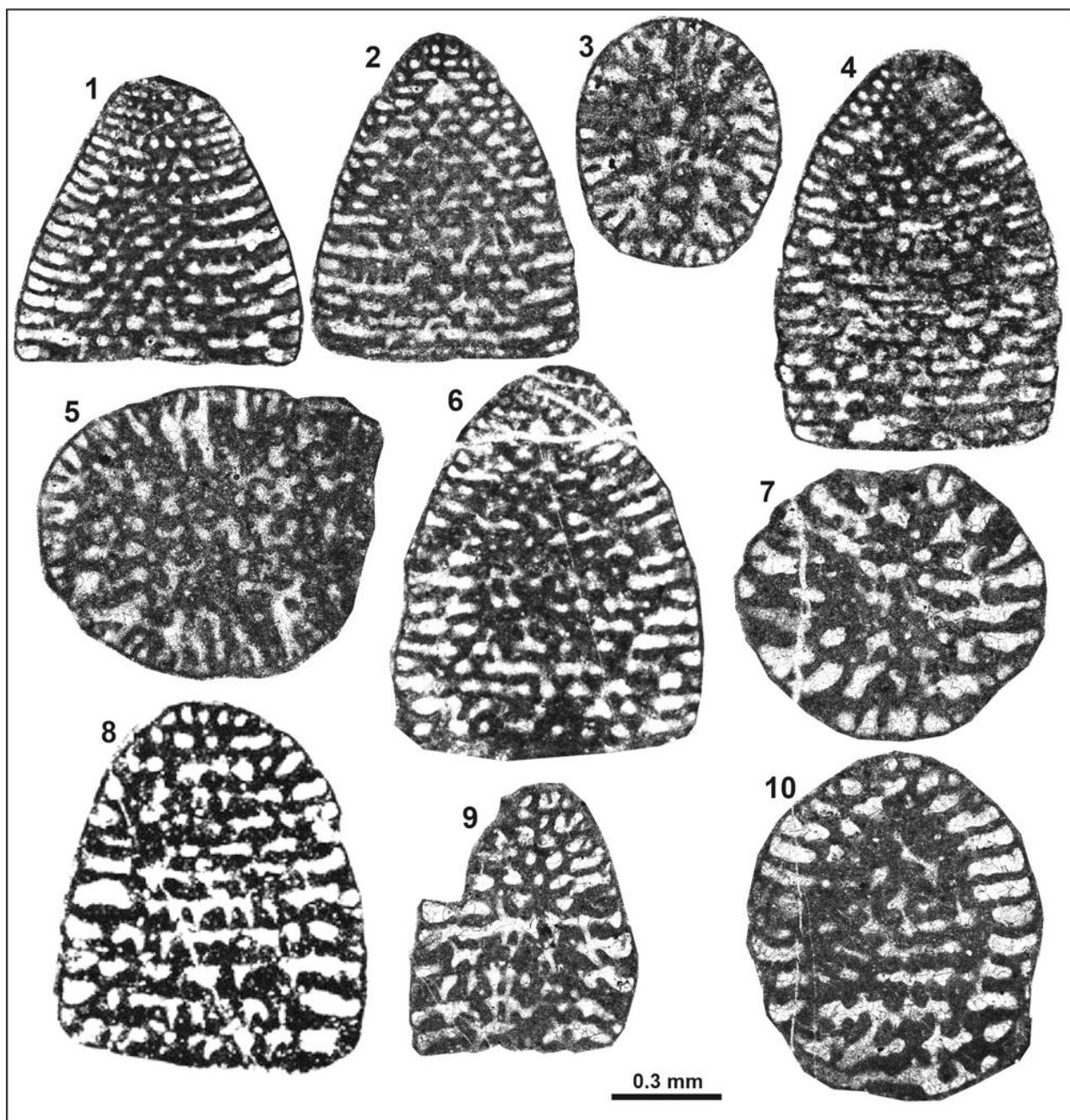
Figs. 1, 7, 11-12: Subaxial sections. Thin-sections 14778, 14779, RR3990, 16352A.

Figs. 2, 10: Partly oblique, transverse sections. Thin-sections: RR3982, 14799.

Fig. 3: Subaxial section of a presumably microspheric specimen. Thin-section 14778.

Figs. 4, 6, 8, 13: Oblique sections. Thin-sections 14779, 14784, 14778-2, 14787-2.

Figs. 5, 9: Axial sections: Thin-sections 14778, 14794.

**Plate 13:**

Upper Berriasian Orbitolinidae from the Kamenica section, eastern Serbia (1-7, 9-10) and the Lower Cretaceous of southeastern France (8). Gen. et sp. indet 1 (1-6), Gen. et sp. indet 2 (7-10), *Paracoskinolina?* *hispanica* PEYBERNÈS (from CLAVEL et al., 2014, Pl. 6, specimen EB H27.4 (8)). Abbreviations: h.p. = hemi-pillars, pi? = possible pillars.

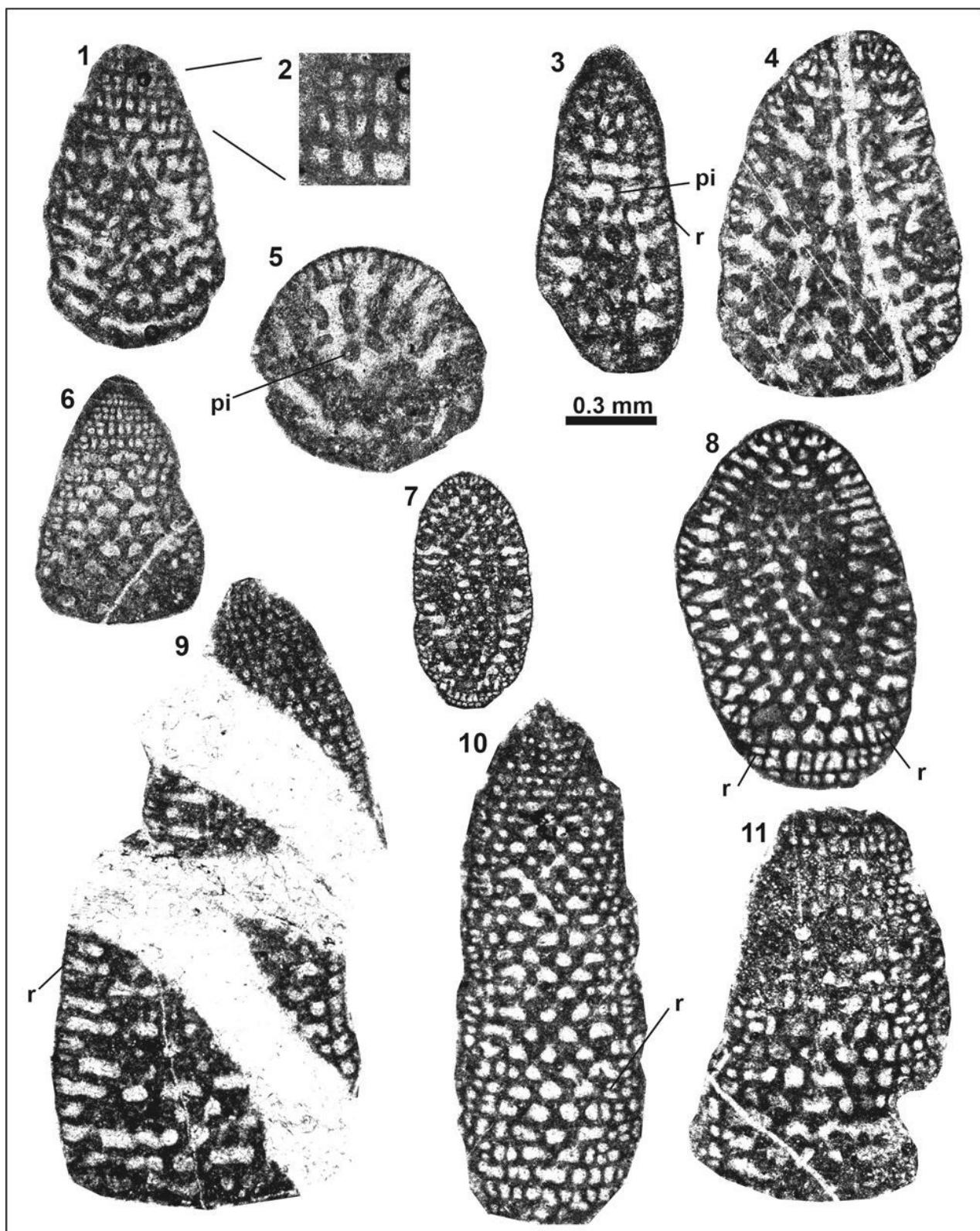
Figs. 1-2, 4, 6: Subaxial sections. Thin-sections 114792-7, 14791, 14797, 14800.

Figs. 3, 5: Oblique transverse sections. Thin-sections: 14797, 14793.

Figs. 7, 9: Oblique sections. Thin-sections RR3391, RR3988, 14783.

Fig. 8: Subaxial section showing hemipillars of zagged appearance towards the apex (from CLAVEL et al., 2014).

Fig. 10: Almost axial section. Thin-section 14784.

**Plate 14:**

Upper Berriasian Orbitolinidae from the Kamenica section (1, 4, 8) and Jerma section (3, 5-7, 9-11), eastern Serbia. *Paracoskinolina* aff. *arcuata* (ARNAUD-VANNEAU) (1-4, ?5) and gen. et sp. indet 3 (6-11). Abbreviations: r = rafter, pi = pillar.

Figs. 1-4: Oblique sections. Detail in 2 shows the aligned arrangement of the main vertical partitions. Thin-sections 14023, 14719, 14030.

Fig. 5: Oblique transverse section. Thin-section 14720-2.

Fig. 6: Oblique section showing the presence of rafters and main partitions alternating between subsequent chambers. Thin-section 14720.

Figs. 7-8: Oblique sections. Thin-section 14715-2, 14787-3.

Fig. 9: Subaxial section. Thin-section 14714.

Figs. 10-11: Tangential sections. Thin-section 14727, 14732.



Nomenclatural note:

Life Sciences Identifier (LSID)

<http://zoobank.org/References/E00D3DCB-77DD-4FF9-9692-826E174333D0>

- *Cribelopsis sudari* SCHLAGINTWEIT & BUCUR, 2021

<http://zoobank.org/NomenclaturalActs/40A5B99E-4DBC-4F4E-9328-AF3CE767CA85>