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Lower Berriasian ammonites from Dedina (Golubac Mountains, eastern Serbia) and their biostratigraphic implication

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ABSTRACT

A rich ammonite fauna was collected from the Dedina section, which is part of the Getic nappe system of the Serbian Dacia Megaunit. More than three hundred ammonites were collected from the light grey to reddish bioclastic limestones of the lower part and light grey marlstones of the upper part. From this fauna, 10 genera with 17 species were described, and 4 aptychi species were recorded. The ammonites belong to the suborders Haploceratina, Perisphinctina, Olcostephanina, and Ancyloceratina. Perisphinctids belong to the genera *Pseudosubplanites*, *Hegaratella*, *Delphinella*, *Substeueroceras*, *Malbosiceras*, and *Strambergella*. Based on the occurrence of *Pseudosubplanites grandis*, the studied section can be considered to belong to the Grandis ammonite Subzone of the upper part of the lower Berriasian. The association described here appears to be close to the coeval ammonite association in Crimea.

1. Introduction

The worldwide definition of the base of the Berriasian is still not established and represents one of the most debatable points on the geological time scale, and it has been studied extensively over the last decades (e.g., Wimbledon, 2017; Arkadiev et al., 2018; Vaňková et al., 2019, and many others). The comprehensive biostratigraphic correlation of the Tithonian–Berriasian boundary sections between different regions provides important information for solving this problem.

The assumption that there are fossiliferous deposits in the area of the J/K boundary on the Serbian section at the Dedina locality initiated an integrated investigation of this site. Ammonites represent important international biostratigraphic markers that can contribute greatly to the definition of the base of the Berriasian stage. Despite the fact that the database on ammonite occurrences is very extensive (Wimbledon et al., 2011; Vašíček and Skupien, 2013; Arkadiev et al., 2018; among many others), examination of newly discovered sites bearing ammonite fauna could contribute to the definition of the base of the Berriasian stage.

Based on the recent investigations at the Dedina section near the Golubac town (eastern Serbia), it has been assumed the Tithonian–Berriasian boundary to be exposed in that location. During 2021 and 2022, several field trips visited the mentioned section as a result of joint research between experts from the Czech Republic (Geological Institute of the Academy of Science of the Czech Republic, VŠB–Technical University of Ostrava, Charles University in Prague and the Czech Geological Survey) and the Republic of Serbia (Geological Survey of Serbia, and Faculty of Mining and Geology, University of Belgrade). The research has been carried out within the international and Czech GACR project: "Leading edge instrumental methods in high resolution global Jurassic–Cretaceous border correlation". The study was accomplished by a multidisciplinary approach involving micropalaeontological, macropalaeontological, magnetostratigraphic and geochemical methods.

The Dedina section yields rich and diverse associations of macrofauna represented by cephalopods (ammonites, aptychi and belemnites), brachiopods, and bivalves. Among the most frequent and diverse are ammonites. The current study provides detailed description of many of those ammonites, as well as new results on

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the litho- and biostratigraphy of the studied section. Based on the ammonite species identified and described herein, the Dedina section is dated as early Berriasian in age (Jacobi? and Grandis ammonite Subzones), and the Jurassic–Cretaceous boundary cannot be constrained.

The aim of the current paper is to report the results of a detailed study of the representatives of the suborders Haploceratina, Perisphinctina, Olcostephanina, and three species of ribbed aptychi from the lower Berriasian of the Dedina section in eastern Serbia. In the described fauna, 10 genera with 17 species are described, and 4 aptychi species are recorded. The results published herein will be followed by an integrated study on belemnites, brachiopods, bivalves, microfossils, stable isotopes, and magnetostratigraphy.

2. Geological setting

The studied deposits of the Dedina area are within the Getic nappe system framework and have large extents and thicknesses. In that area, the Carpatho-Balkanides form a typical Alpine arcuate belt starting from southwestern Romania and then along eastern Serbia, crossing the Bulgarian territory from west to east. The Getic and Danubian are the most important nappe systems (Fig. 1A), along with several other small tectonic zones/terranes (Fig. 1B) (Anđelković and Nikolić, 1974, 1980; Karamata and Krstić, 1996). The first system is part of the Dacia Mega-unit, representing the Europe-derived units, and the last system is part of the Circum-Rhodope Unit, representing the Moesian-derived units (e.g., Schmid et al., 2020).

Within the sedimentary successions of the Getic Nappe, the Tithonian–Berriasian deposits represent pelagic depositional marine environments. The macroinvertebrate fauna is relatively rich, with ammonites being the most frequent fossils, followed by aptychi, brachiopods, belemnites, and bivalves. Calpionellids microfossils are abundant also. These layers in eastern Serbia are best exposed at the Dedina Stream, where the ammonites and aptychi studied herein were recently collected. This area has been geotectonically regarded as a part of the Kučaj–Svrljig tectono-sedimentary zone within the Karpatikum (Anđelković and Nikolić, 1974, 1980). It is also recorded in the Kučaj Terrane (Krstić et al., 1996).

The earliest data on the upper Tithonian macrofauna of the Golubac area were published by Uhlig (1884), who attributed one specimen to the genus *Simoceras* and listed *Perisphinctes dichotomus* Zittel and *Aptychus lammellosus* Voltz from the Tithonian light limestones. Toula (1891) mentions weathered marlstones with ammonoids in the vicinity of Golubac. Uhlig (1884) considered one specimen to be a new species of *Hoplites* that resembles some Berriasian forms. In the more compact layers of marlstones lying below, in addition to small aptychus, a belemnite was found, which Uhlig determined as *Belemnites ensifer* (Oppel).

On the eastern slope of Saš Hill, in the Dedina Stream, Žujović (1893) found *Perisphinctes dichotomus* Zittel and *Aptychus lamellosus* Voltz in the upper Tithonian bedded limestones. On the left side of the Dedina Stream, above the path, Petković (1935) recorded *Aptychus lammellosus* Voltz and specimens of *Perisphinctes* in the layered reddish limestones.

In the marly limestones and marlstones of the Dedina Stream, Sučić-Protić (1961) mentioned poorly preserved brachiopods, belemnites, ammonites and aptychi. They are listed as *Aulacosphintes eudichotomus* (Zittel) and *Lamelaptychus* cf. *beyrichi* (Oppel).

Rabrenović (1988) was the first to describe four ammonite species: *Pseudosubplanites* (*Hegaratella*) *lorioli* (Zittel), *Pseudosubplanites* (*H.*) *paramacilentus* (Mazenot), *Pseudosubplanites* (*H.*) *kaffae* (Rousseau in Retowski), and *Berriasella* (*B.*) *jacobi* (Mazenot) from the upper Tithonian–lower Berriasian limestones and marlstones, with calpionellid association at the locality; these fossils were located above the right side of the Dedina Stream and were not studied by earlier workers. Later, at the same locality, Carević and Jovanović (2007) and Carević (2009), based on the abundant occurrence of the calpionellid species *Calpionella alpina*, placed the boundary between the Tithonian and Berriasian. Recently, Carević et al. (2018) documented the late Tithonian in a succession of the Jelenska Stena Quarry, Danube River Gorge, approximately 5 km east of the Dedina locality, based on benthic foraminifers and calpionellid taxa.

The fossiliferous section of Dedina (Fig. 1A) is situated on the extreme northern slopes of the Golubac Mountains, near Golubac town, approximately 1.2 km southeast of the village of Dedina on the left side of the path that leads to Gurnja Hill (elevation 389 m). The studied sequence is 110 m thick, and 100 rock samples for microfossils were taken bed by bed along the outcrops (Figs. 2, 3) from the studied layers (GPS coordinates: start of profile: N 44°39′5.39″, E 21°39′44.27″; end of profile: N 44°39′ 7″, E 21°39′51.37″; 129 m above sea level).

In the Dedina Stream, the Palaeozoic schists are overlain by Middle Jurassic sandy limestones and Oxfordian—Kimmeridgian limestones with cherts. Above these limestones lie Tithonian–Berriasian limestones and marlstones, which attain a thickness of several hundred metres.

Within the deposits studied, two distinct lithofacies occur in the investigated outcrop (Fig. 3). The lower lithofacies consists of light grey to reddish, thinly bedded bioclastic limestones (wackstones/packstones) and contains abundant ammonites. The uppermost part comprises light grey marly limestones with intercalations of marlstones that contain rare brachiopods but are rich in ammonites. These layers are also very rich in calpionellids.

3. Material and methods

The first ammonite material in this study was collected in 2007 by D. Rabrenović. Further material was collected in September 2021 and May 2022 by the authors of this contribution and colleagues from Charles University in Prague, the Czech Academy of Sciences and the Geologic Survey in Brno.

The studied collection (359 pieces) consists only of crushed, sometimes also laterally deformed, predominantly fragmentary ammonites, as well as external moulds and impressions. Only less than one-third of the specimens could be used for determination and a detailed taxonomic elaboration. As far as size parameters are concerned, specimens with shell diameters in the range of 20—30 mm and a smaller number that within 30—60 mm completely predominate. The remaining ten consist of even smaller, juvenile specimens; only five specimens belong to fragments of whorls of larger shells. Ribbed specimens represent the bulk of the collection. Smooth shells represent only approximately 10% of the collection. The aforementioned circumstances make it possible to measure the dimensional parameters of the shells on one dimension only and, on the ribbed shells, to count the number of ribs lying at the umbilicus and outside of the half-whorl. The specimens, with a few exceptions, do not have the ventral side exposed. Because of this latter condition, the widths or cross-sections of the whorls are not observable.

The poorly preserved specimens of the stratigraphically insignificant ammonites were usually determined on a generic level without a description. Some of them are shown in Figs 4—6. The present aptychi are determined at the species level. They are shown in Fig. 6.

Identification of the studied material is usually difficult by the juvenile size of the specimens, the accompanied planar deformation or lateral deformation, the unknown shape of the ventral side,

and the frequent lack of preservation of the inner whorls or the body chamber. Due to the nature of the preservation, no suture lines are observable. When specimens were identified, preference was given to specimens in which the entire whorl or at least half of it was preserved. For the measurements of such specimens, the diameter of the shell, D, for which the measurement was made to one-tenth of a mm (or Dmax, indicating the maximum preserved shell size), as well as the height of the whorl (H), width of the umbilicus (U), and the ratios of H/D and U/D are given in parentheses. The width of the whorl (B), although exceptionally measurable, would not usually be worth measuring due to the deformation of the shells. Where possible, the number of ribs at the umbilicus and by the ventral side was counted on half of the whorl.

The studied and illustrated material is housed in the Geological Museum, Department of Geological Engineering, VSB – Technical University of Ostrava, Czech Republic.

4. Taxonomy of ammonites

As already mentioned, the bulk of the ammonite collection consists of ribbed shells, especially of the so-called perisphinctoid type. Historical monographs starting from the second half of the previous century, and several subsequent publications (as is evident from the synonymies of the species described) are significant too.

Based on the current concept of the taxonomy of ammonites, the presented work mainly considers studies from the last 30 years. Among them, it is necessary to mention at least Besnosov and Mikhailova (1991), Wright et al. (1996), Kvantaliani et al. (1999), Klein (2005), Arkadiev and Bogdanova (2004, 2005), Bogdanova and Arkadiev (2005), Arkadiev and Bogdanova (2012), Arkadiev (2014), Bulot et al. (2014), Frau et al. (2016a,b), Hoedemaeker et al. (2016), and Szives and Főzy (2022). With minor exceptions (suborders Haploceratina and Olcostephanina), the most basic classical taxonomy of ammonites used by Hoedemaeker in Hoedemaeker et al. (2016) is adopted in the presented work.

Published synonymies of species tend to be very extensive, complex, and inconsistent. In the species descriptions here, the synonymies begin with the work in which the species was first described. Next, works showing the subsequent development of the taxonomy of the species or its geographical occurrence or citations adding further relevant data or removing typists' errors in synonymies by earlier authors are cited. Many imperfectly preserved specimens could only be determined in open nomenclature. However, we consider useful to provide synonymies also for the cf. species. They indicate their geographic distribution and the age of the deposits.

The stratigraphic position of the ammonites is based on data from other localities. Older literature data are usually questionable based on earlier different conceptions and zonation of the Tithonian, Berriasian, and lower Valanginian. The most recent data on the stratigraphic range of ammonite species come primarily from sites with multidisciplinary studies as part of the international J/K boundary project. However, even at these sites, data on their exact range are not yet clear.

Order Ammonitida Haeckel, 1866
Suborder Haploceratina Beznosov and Mikhailova, 1983

Because we consider the ontogeny of the septal suture lines as the standard for the taxonomy of ammonites, earlier obsolete classifications, e.g., Hyatt (1889, 1900) and Callomon (1981), are omitted here. According to the form of the suture line in agreement with Beznosov and Mikhailova (1983) and Besnosov and Mikhailova (1991), we place the haploceratids in the suborder Haploceratina, in contrast to older concepts.

Superfamily Haploceratoidea Zittel, 1884
Family Haploceratidae Zittel, 1884

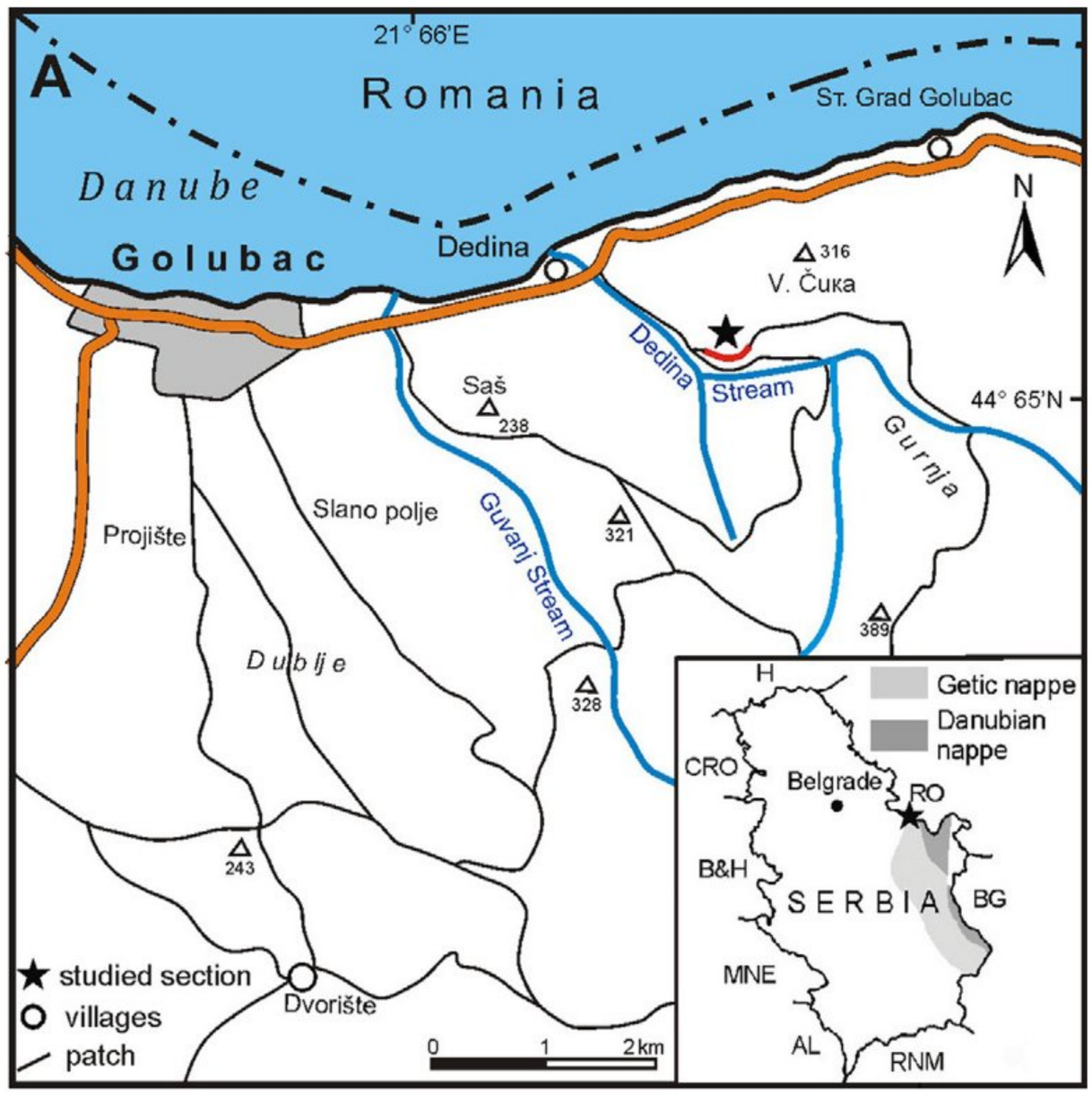
Genus *Hypolissoceras* Breistroffer, 1947
Type species. *Ammonites carachtheis* Zejszner, 1846

In the 19th century, the Tithonian and basal Cretaceous haploceratids of the genus *Haploceras* were first studied by Zittel (partly together with Oppel in Zittel, 1868) and Zittel (1870). Much later, Breistroffer (1947) separated and defined the genus *Hypolissoceras* from the genus *Haploceras*. Based on the facts observed in our recent study of haploceratids from the Štramberk Limestone, in the presented contribution, we tend towards the older version of Breistroffer (1947), as opposed to the newer concept of Hoedemaeker (in Hoedemaeker et al., 2016) or Sarti (2020). The genus *Haploceras* lacks crenulate ribbing on the ventral side compared to the genus *Hypolissoceras*. We consider this ribbing to be the basic distinguishing characteristic of the last genus.

Hypolissoceras leiosoma (Oppel, 1865)
Fig. 4A, B

1865 *Ammonites leiosomus* Opp.; Oppel, p. 550.
1868 *Ammonites leiosoma* Opp.; Zittel, p. 86, pl. 14, figs. 5a, b (lectotype), 6a, b.
2013 *Haploceras carachtheis* (Zeuschner); Főzy and Scherzinger, p. 215, pl., fig. 3a, b, *non* pl. 4, fig. 4a, b; *non* pl. 5, figs. 1a, b, 2, 10 (= *H. carachtheis* /Zejszner/).
?2020 *Haploceras carachtheis leiosoma* (Zittel); Sarti, p. 91, pl. 4, fig. 6a, b.

Material. Small, partially deformed, and corroded outer mould (specimen S36.3/1).
Description. Involute specimen with a high whorl and narrow umbilicus. The flanks of the whorl are slightly arched, with a low umbilical wall passing to the line of coiling. The ventral side is narrow and arched. The flanks of the whorl are smooth. Faint, numerous, short and dense ribs are visible on the incomplete terminal half of the whorl only in the siphonal region.
Measurements. At Dmax = 24.5 mm, H = 11.3 (0.46) and U = 5.0 (0.20).
Remarks and relations. The circumstance that fine crenulate ribbing is developed on the venter is evidence of belonging to the genus *Hypolissoceras*. The dense, thin, and short ventral ribs distinguish this specimen from the type species of the genus *Hypolissoceras* (*H. carachtheis*), which attains a larger size. The intensity and character of crenulation on the specimen figured in Sarti (2020) corresponds more to *Hypolissoceras carachtheis*. The species *H. leiosoma* is a relatively little-known species established in ancient history. The specimens illustrated by Zittel are characterised by flat flanks of the whorls, which are not evident in the Serbian specimen. A related species, also in terms of size, is *Hypolissoceras subtilior* (Zittel, 1870). It differs in dimensional parameters, especially in the greater width of the umbilicus.
Distribution. This species is probably known only from the Štramberk Limestone from Štramberk, Koňákov, and recently, also from Hungary. The exact stratigraphic position is unknown. Tithonian or lower Berriasian age are possible.
Occurrence. Marlstones at layer 36 (10 cm from the base).


A
21° 66'E
Romania
Danube
Golubac
Dedina
St. Grad Golubac
N
316
V. Čuka
Dedina Stream
Saš
238
44° 65'N
Gurnja
Slano polje
Guvanj Stream
321
Projište
Dublje
328
389
243
Dvorište
studied section
villages
patch
0 1 2km
H
Getic nappe
Danubian nappe
CRO
Belgrade
RO
B&H
SERBIA
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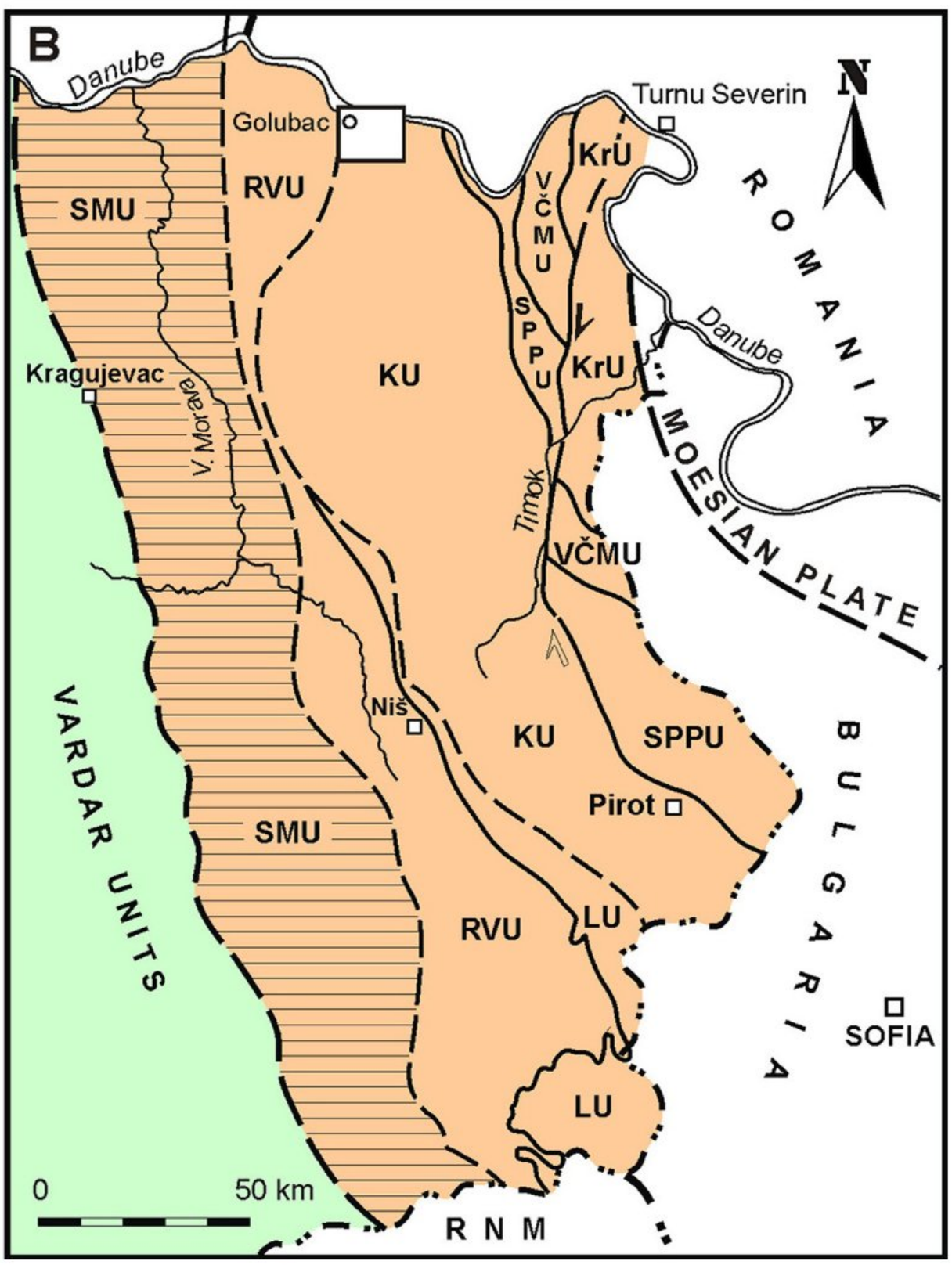
MNE
AL
RNM


B
Danube
Golubac
Turnu Severin
N
SMU
RVU
KU
VČMU
KrU
SPPU
Kragujevac
V. Morava
Timok
MOESIAN PLATE
VARDAR UNITS
Niš
Pirot
LU
SOFIA
ROMANIA
BULGARIA
RNM
0 50 km

Suborder Perisphinctina Steinmann, 1890
Superfamily Perisphinctoidea Steinmann, 1890
Family Ataxioceratidae Buckman, 1921
Subfamily Lithacoceratinae Zeiss, 1968

Genus *Pseudosubplanites* Le Hégarat, 1971
Type species. *Pseudosubplanites berriasensis* Le Hégarat, 1971

The systematic position of the genus *Pseudosubplanites* has been the subject of long-standing debate, beginning with the establishment of the genus in Le Hégarat (1971, 1973), through the analyses of Callomon (1981), Bogdanova and Arkadiev (2005), Arkadiev and Bogdanova (2012), and Hoedemaeker in Hoedemaeker et al. (2016). The genus *Pseudosubplanites* is characterised by polygyrate ribs, ribs crossing the ventral side without interruption, lacking tubercles and being semi-evolute whorled. On the basis of a detailed discussion by the abovementioned Russian authors Arkadiev and Bogdanova (2012), they consider the genus as representative of the family Neocomitidae Salfeld, 1921, subfamily Berriasellinae Spath, 1922. Hoedemaeker et al. (2016), relying on the views of Callomon (1981), considers the genus *Pseudosubplanites* as the terminal representative of the Jurassic family Ataxioceratidae Buckman, 1921, subfamily Lithacoceratinae Zeiss, 1968. Hoedemaeker et al. (2016) accepted Callomon's views. He does not consider the genus *Pseudosubplanites* as one of the starting elements of the newly emerging family Neocomitidae. This concept is also accepted here.

Species composition and their detailed characterisation have been recently mainly addressed by Arkadiev and Bogdanova (2012) and Hoedemaeker et al. (2016). The latter author also distinguishes microconchs and macroconchs in the genus *Pseudosubplanites*.

Pseudosubplanites lorioli (Zittel, 1868)
Fig. 4C–E

1868 *Ammonites Lorioli* Zitt.; Zittel, p. 103, pl. 20, figs. 6a–c (lectotype), 8, *non* fig. 7a, b (unidentifiable).
1939 *Berriasella Lorioli* (Zittel); Mazenot, p. 125, pl. 19, figs. 3a–d (refigured lectotype), 4a, b, 6a, b, 7a, b, *non* 5a, b (unidentifiable).
1973 *Pseudosubplanites lorioli* (Zittel); Le Hégarat, p. 40, pl. 1, fig. 3 (refigured lectotype), 4, 5; pl. 37?, figs. 3, 7, 8.
1979 *Peudosubplanites (Pseudosubplanites) lorioli* (Zittel); Sapunov, p. 189, pl. 40, figs. 4, 5.
1982 *Pseudosubplanites (Pseudosubplanites) lorioli* (Zittel); Nikolov, p. 42, pl. 2, fig. 3a, b (refigured lectotype); pl. 5, fig. 5; *non* pl. 2, Fig. 2 (= *Berriasella crymensis* Bogdanova and Arkadiev); *non* pl. 5, fig. 6 (= *Pseudosubplanites fasciculatus* Bogdanova and Arkadiev); non pl. 5, fig. 7 (= *Berriasella jacobi* Mazenot); *non* pl. 5, fig. 8 (= *Berriasella oppeli* Kilian).
1985 *Berriasella* (*Pseudosubplanites*) *lorioli* (Zittel); Tavera Benitez, p. 261, text-fig. 20/I, pl. 36, fig. 10.
2005 *Berriasella* (*Pseudosubplanites*) *lorioli* (Zittel); Klein, p. 158.
2005 *Pseudosubplanites lorioli* (Zittel); Bogdanova and Arkadiev, p. 493, figs. 4D, 5C, 6A, B, 7A–I.
2012 *Pseudosubplanites lorioli* (Zittel); Arkadiev et al., p. 168, pl. 12, figs. 3–7, text-figs. 63–3, 63–4.
?2013 *Pseudosubplanites lorioli* (Zittel); Szives and Főzy, p. 313, pl. 9, fig. 3.
2016 *Pseudosubplanites lorioli* (Zittel); Hoedemaeker et al., p. 120, pl. 2, figs. 12–17; pl. 3, figs. 1–9 (cum syn.).

Material. Small outer moulds with preserved last and parts of penultimate whorl (specimens S97/4, S98/1, S99/1 and specimen D5). The last specimen has an exposed venter.
Description. Semi-evolute specimens with whorls that are not very high and have a relatively narrow umbilicus. The low umbilical wall descends rather steeply to the line of coiling. The whorls are slightly arched with a relatively long stretch descending to the venter. The ventral side is narrow, flat, and rounded. The ribs on the penultimate whorl and at the beginning of the last whorl are densely spaced. On the penultimate whorl, the initial bifurcations of the primary ribs are inclined towards the peristome. Points of the bifurcation of ribs with a similarly small size of the specimens are still visible near the line of coiling. At the beginning of the last whorl, the ribs are somewhat S-shaped, with the splitting of ribs occurring below half the height of the whorl. In the final quarter of the whorl, the ribs are slightly concave and somewhat sparsely spaced. Inserted and polygyrate ribs are present.
Measurements. The 99/1 specimen has a Dmax = 28.5 mm, H = 11.6 (0.41) and U = 8.3 (0.29). There are approximately 19 primary ribs per half-whorl at the umbilicus and approximately 33 secondary plus intacalar ribs. The specimen D5 has measurements, at Dmax, of D = 26.5 mm, H = 11.5 (0.43), and U = 7.8 (0.29). At this D by the umbilicus, there are approximately 18 ribs per half-whorl and 42 ribs on the ventral side.
Remarks and relations. Adult microconchs reach only a small size (see the discussion in Hoedemaeker et al., 2016). Macroconchs are distinguished from microconchs, even in early stages, by more sparsely spaced ribs. This feature, with similar sizes of specimens, distinguishes *Ps. lorioli* from other representatives of the genus *Pseudosubplanites*.
Distribution. *Pseudoplanites lorioli* is known from lower Berriasian of Spain, France, Czech Republic, Bulgaria, Crimeria, Kaukasus, and Morocco. Frau et al. (2016b) reported *Pseudosubplanites* gr. *lorioli* from the Les Combes section in France from approximately the middle part of the Jacobi Zone.
Occurrence. Marlstones at layers 95, 97, 98, and 99.

Pseudosubplanites* cf. *ponticus (Retowski, 1893)
Fig. 4F

cf. 1893 *Perisphinctes ponticus* n. sp.; Retowski, p. 256, pl. 10, fig. 9 (holotype).
cf. 1938 *Berriasella pontica* Retowski; Roman, p. 325, pl. 32, fig. 307.
cf. 1960 *Berriasella pontica* Retowski; Drushchits, p. 277, pl. 21, fig. 2 (refigured holotype).
cf. 1973 *Pseudosubplanites ponticus* (Retowski); Le Hégarat, p. 42, pl. 1, figs. 6 (refigured holotype), 7; pl. 38, fig. 1.
cf. 1976 *Pseudosubplanites ponticus* (Retowski); Patrulius and Avram, p. 171, pl. 7, figs. 7, 8.
cf. 1982 *Pseudosubplanites (Pseudosubplanites) ponticus* (Retowski); Nikolov, p. 42, pl. 6, figs. 1, 2, non fig. 6 (= *Pseudosubplanites grandis* Mazenot).
cf. 2000 *Pseudosubplanites* cf. *ponticus* (Retowski); Boorová et al., p. 306, pl. 13, fig. 1.
cf. 2005 *Berriasella (Pseudosubplanites) pontica* (Retowski); Klein, p. 159 (cum syn.).

Fig. 1. Geological and geographical locations of the Dedina section in eastern Serbia (Kučaj Unit). **A**, Locality map of the investigated Upper Jurassic and Lower Cretaceous Dedina succession. The collection locality is indicated by the star and red curved line. Small right sketch: the positions of the Getic and Danubian nappes are shown; H, Hungary; RO, Romania; BG, Bulgaria; RNM, Republic of North Macedonia; AL, Albania: MNE, Montenegro; B and H, Bosnia and Herzegovina; CRO, Croatia. **B**, Units/terranes of the east Carpatho-Balkanides, Dacia Megaunit (Anđelković and Nikolić, 1974, 1980; Krstić et al., 1996): SMU, Serbo-Macedonian Unit (brownish with lines); East Serbian Carpatho-Balkanides (brownish): RVU, Ranovac–Vlasina Unit (Supragetic); LU, Lužnica Unit (Kraishte); KU, Kučaj Unit (Getic); SPPU, Stara Planina–Poreč Unit (Upper Danubian); VČMU, Vrška Čuka–Poreč Unit (Lower Danubian); KrU, Krajina Unit (Severin). The marked position of the Dedina section is indicated by a white rectangle.

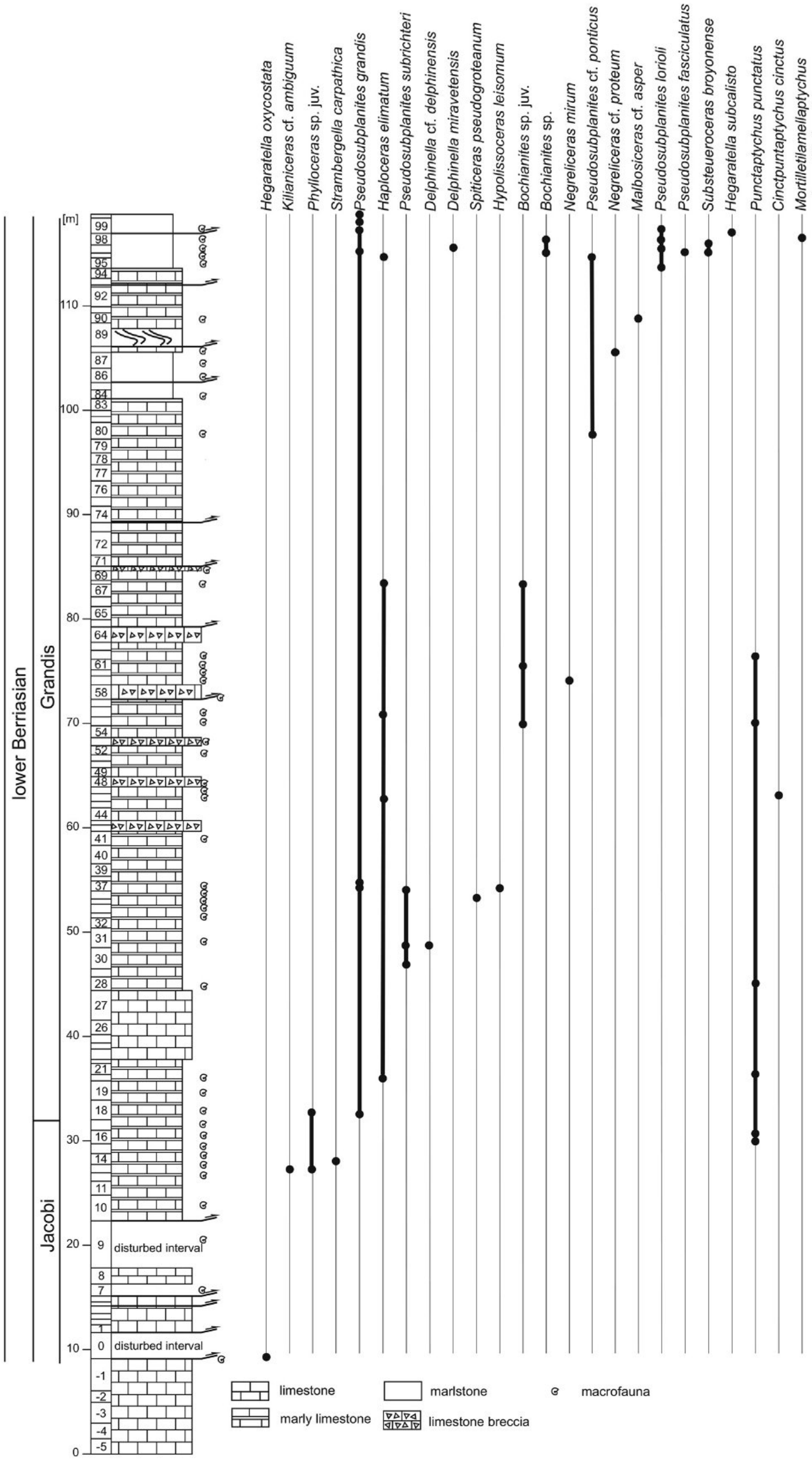


Fig. 2. Lithology and vertical distribution of ammonites and aptychi of the Dedina section.

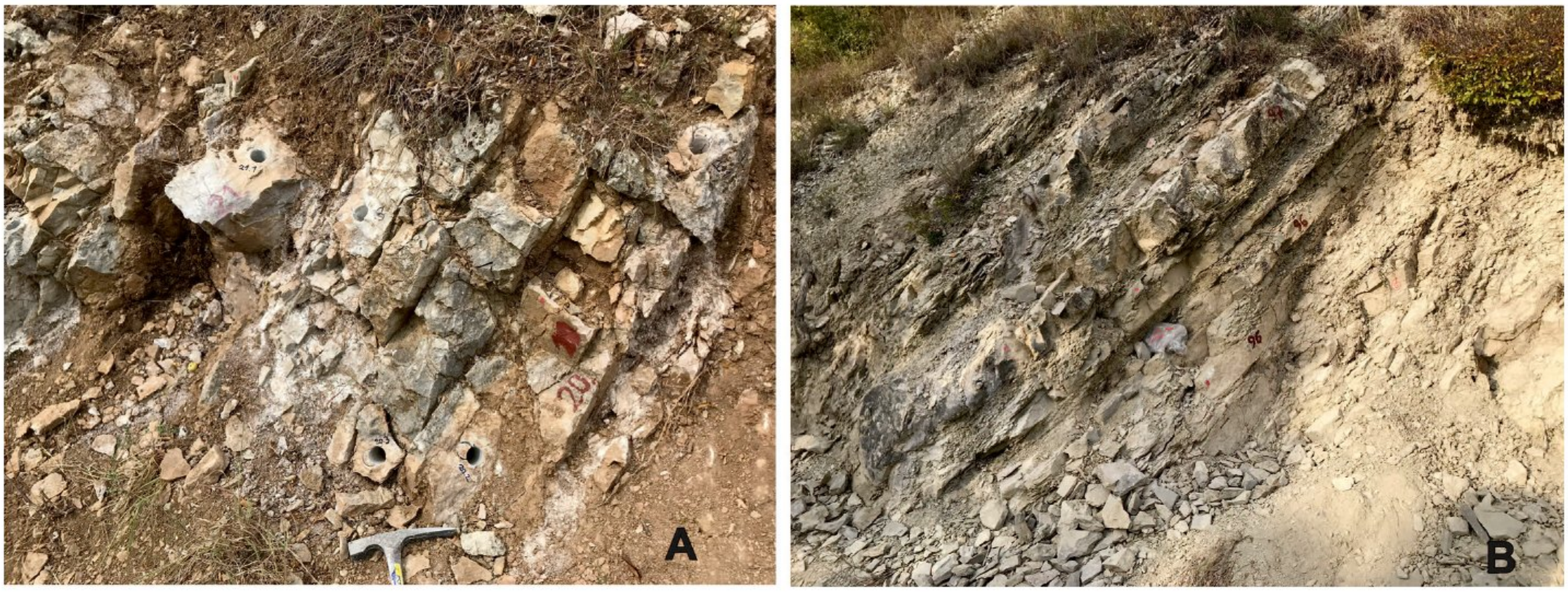


Fig. 3. Field photographs of section **A**, layers 20 and 21. Light grey to reddish, thinly bedded bioclastic limestones with ammonites in the lower part of the section; **B**, layers 95–97. Light grey marlstones with limestone layers and ammonites in the uppermost part of the section.

cf. 2005 *Pseudosubplanites ponticus* (Retowski); Bogdanova and Arkadiev, p. 491, figs. 5A, 6E, figs. 7L–N.
cf. 2012 *Pseudosubplanites ponticus* (Retowski); Arkadiev and Bogdanova, p. 172, pl. 13, figs, 1–4, 6, 7, 5?.
cf. ?2013 *Pseudosubplanites ponticus* (Retowski); Szives and Főzy, p. 314, pl. 8, fig. 1a, b.
cf. 2016 *Pseudosubplanites ponticus* (Retowski); Hoedemaeker et al., p. 123, pl. 4, figs. 1–7.

Material. One incomplete specimen S80/5a, b with almost the entire last whorl not very well preserved as an outer mould and its impression. The second specimen, SA 96/3, with an outer mould, has only the end quarter of the deformed half of the last whorl more favourably preserved.
Description. A semi-involute medium-sized specimens with slightly arched flanks, descending to the coiling line by an unbounded low rounded zone. The ventral side is narrow and slightly rounded. The greater part of the whorl of both specimens probably belongs to the phragmocone, and the terminal quarter of specimen S80/5 belongs to the body chamber. The phragmocone is covered by dense ribs, which are slightly S-shaped. First, they are concave in a short section, and then in a much longer section, they are convexly bent as primary ribs and slightly inclined towards the peristome. These bifurcate closely approximately halfway up the whorl. On the venter, they are slightly inclined towards the peristom. The ribs cross the ventral flank without interruption. On the body chamber at the end of the larger specimen S80/5, only the lower part of the primary ribs that is inclined towards the peristome is preserved. The ribs are somewhat thicker than those of the previous section. They are conspicuously sparse.
Measurements. Specimen S80/5 has measurements at D of ca. 55.5 mm H = 20.5 (0.37), and U = 17.2 (0.31). Due to incomplete preservation, the number of ribs is not countable. In specimen SA96/3, the entire (complete) diameter of the shell is not preserved. Estimated measurements at D are ca. 55 mm, H = 19.5 (0.35), and U of ca. 20.0 (0.36). There are approximately 30 ribs at the umbilicus on half of the whorl.
Remarks and relations. The inner whorls are densely ribbed. The contrast in the density of ribbing of the initial and terminal part of the whorl of the adult specimen is striking. The sparse ribbing of the living chamber is documented by Hoedemaeker et al. (2016, pl. 4, fig. 1).
Distribution. *Pseudosubplanites ponticus* should come from transitional deposits between the Tithonian and Berriasian and, according to Arkadiev and Bogdanova (2012), from the lower Berriasian (Jacobi Zone) of Crimea, Bulgaria, Romania, Austria, France, and Spain.
Occurrence. Light grey marlstones of layers 80 and 96.

Pseudosubplanites subrichteri (Retowski, 1893)
Fig. 4G

1893 *Perisphinctes subrichteri* n. sp.; Retowski, p. 255, pl. 10, fig. 8.
1979 *Pseudosubplanites (Hegaratella) subrichteri* (Retowski); Sapunov, p. 192, pl. 41, fig. 1.
1982 *Pseudosubplanites (Hegaratella) subrichteri* Retowski; Nikolov, p. 50, pl. 8, fig. 3, fig. 2?.
1999 *Berriasella (Berriasella) subrichteri* (Retowski); Kvantaliani, p. 90, pl. 11, figs. 1, 2.
2005 *Berriasella (Hegaratella) subrichteri* (Retowski); Klein, p. 161 (cum syn.).
2005 *Pseudosubplanites subrichteri* (Retowski); Bogdanova and Arkadiev, p. 497, figs. 4C, 5B, 6C, 8A–C.
2012 *Pseudosubplanites subrichteri* (Retowski); Arkadiev and Bogdanova, p. 173, pl. 13, figs. 9, 10, text-figs. 63:2, 64:3.

Material. One-third of the last and penultimate whorl is preserved as an outer mould (positive), with another quarter preserved as an incomplete impression (specimen S37/3), a poorly preserved positive of the outer mould of the last whorl with a small part of the penultimate whorl (specimen S30.4/1) and the juvenile specimen S31.2/4.
Description. Semi-involute specimens with medium-high whorls and relatively narrow umbilicus. The flanks of the whorls are slightly arched, almost abruptly following the coiling line. Ribbing on the whorls through ontogeny is visible in two parts. Only primary ribs are observed on the penultimate whorl, and they are slightly inclined towards the peristome. On the last whorl, the slightly S-shaped ribs diverge into two at approximately 2/3 of their height. In only one case, there is a single rib.
Measurements. Specimen S37/3 reaches a Dmax of approximately 48 mm. At D = 46.5 mm, H = 17.5 (0.38), and U = 17.0 (0.36). There are 23 ribs at the umbilicus per half-whorl at Dmax and 40 ribs on the ventral side. The juvenile specimen S31.2/4 has only 16 ribs at the umbilicus.
Remarks and relations. The specimen of *Pseudosubplanites subrichteri* illustrated by Bogdanova and Arkadiev (2005, Fig. 8B) demonstrates that the ribs cross the ventral side without

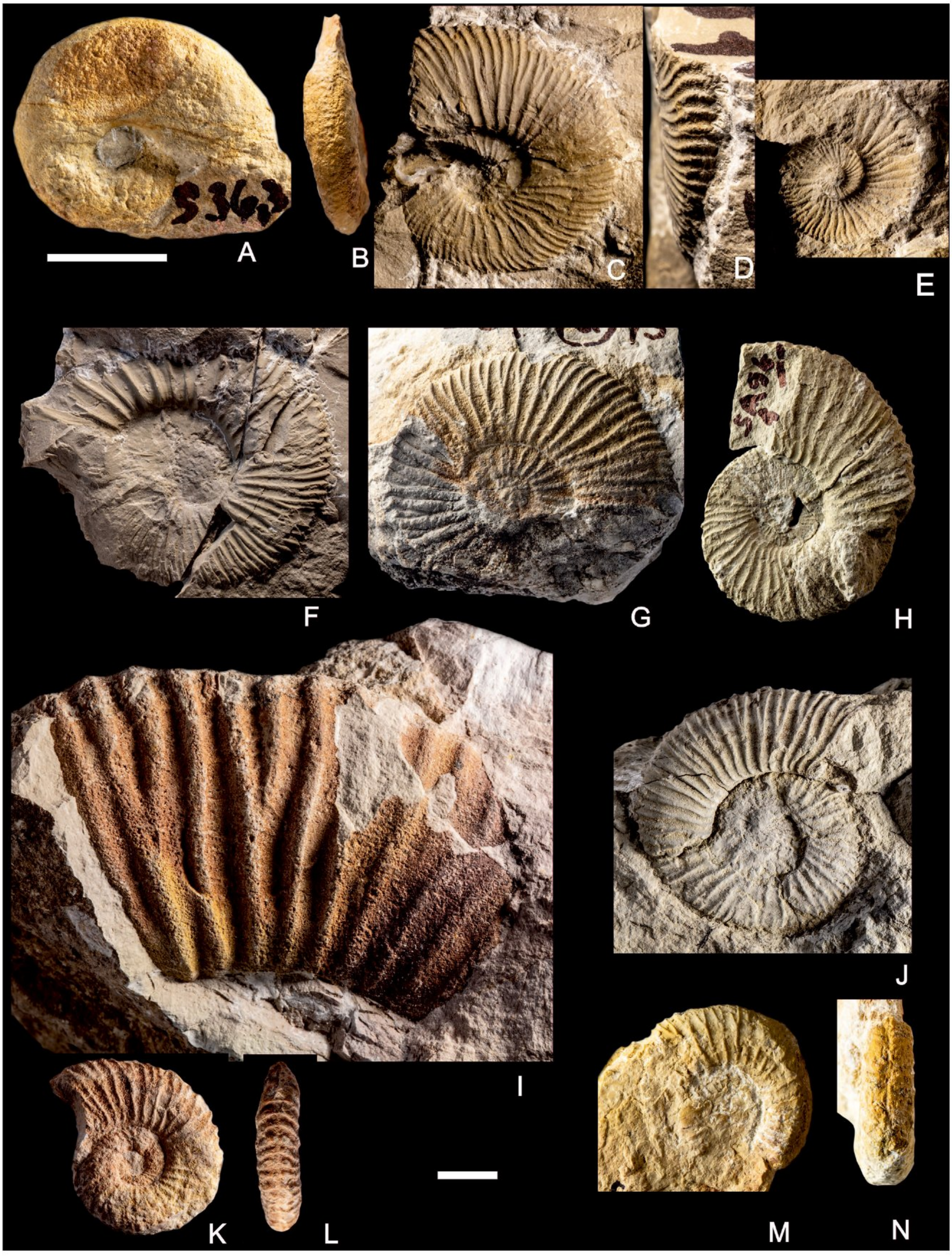


Fig. 4. **A**, **B**, *Hypolissoceras leiosoma* (Oppel, 1865), specimen S36.3/1; A, lateral view, B, ventral view with indistinct crenulation; layer 36. **C**, **D**, *Pseudosubplanites lorioli* (Zittel, 1869), specimen D5; C, lateral view, D, ventral view; layer 99. **E**, *Pseudosubplanites lorioli* (Zittel, 1869), specimen 99/1; layer 99. **F**, *Pseudosubplanites* cf. *ponticus* (Retowski, 1893), specimen S80/5 with sparse ribs at the beginning of the body chamber; layer 80. **G**, *Pseudosubplanites subrichteri* (Retowski, 1893), specimen S37/3; layer 37. **H**, *Pseudosubplanites fasciculatus* Bogdanova and Arkadiev, 2005, specimen SA96/1; layer 96. **I**, *Pseudosubplanites grandis* (Mazenot, 1939), specimen S37/2; layer 37. **J**, *Hegaratella subcalisto* (Toucas, 1890), specimen S99/2; layer 99. **K**, **L**, *Delphinella* cf. *delphinense* (Kilian, 1889) juv. specimen S31.2/5, K, lateral view, L, ventral view with the siphonal groove; layer 31. **M**, **N**, *Hegaratella oxycostata* (Mazenot, 1939), specimen SA/2 m; M, lateral view, N, ventral view; layer 2 m below the beginning of section. Scale bars: A, B, D, and E: 20 mm; C, F–N: 10 mm.

interruption. This circumstance favours generic placement in the genus *Pseudosubplanites*. On the other hand, unambiguous polygyrate ribs were not recorded in the Serbian material, similar as the specimens in Bogdanova and Arkadiev (2005, figs. 6C, 7A–C). A characteristic feature is the sparser distribution of the ribs on the inner whorls.

Distribution. *Pseudosubplanites subrichteri* is reported from the lower Berriasian (Jacobi Zone) from Crimea, Caucasus, and Bulgaria.

Occurrence. In reddish limestones in layer 30 (40 cm from the base) and layer 31 (40 cm from the base), and in light grey clayey limestones in layer 37.

Pseudosubplanites fasciculatus Bogdanova and Arkadiev, 2005
Fig. 4H

1893 *Perisphinctes euxinus* n. sp.; Retowski, p. 254, pl. 10, fig. 5, fig. 6, *non* fig. 7 (= *Psedosubplanites euxinus* Retowski).
1939 *Berriasella Richteri* (Opp. *in* Zitt.); Mazenot, p. 129, pl. 21, fig. 3a, b, *non* figs. 2, 4, 5 (= *Richterella richteri* (Zittel)).
1973 *Pseudosubplanites lorioli* (Zittel); Le Hégarat, p. 40, pl. 3, 7, 8.
1982 *Pseudosubplanites euxinus* (Retowski); Hoedemaeker, p. 10, pl. 1, fig. 1.
2005 *Pseudosubplanites fasciculatus* sp. nov.; Bogdanova and Arkadiev, p. 499, figs. 5D, 6G, 9A–C, 9D, E.
2012 *Psudosubplanites fasciculatus* Bogdanova et Arkadiev; Arkadiev and Bogdanova, p. 178, pl. 14, fig. 2a, b, text-fig. 64:7, figs. 3a, b, 4, text-fig. 63:4.
2016 *Pseudosubplanites fasciculatus* Bogdanova et Arkadiev; Hoedemaeker et al., p. 118, pl. 1, figs. 4–9.

Material. External crushed outer mould with the last and penultimate whorls (specimen SA96/1).

Description. Semi-evolute specimen, probably with slightly arched, moderately high whorls and with relatively broad umbilicus. The penultimate whorl bears thin, rather sparsely spaced, weakly axially curved simple ribs that are inclined towards the peristome. On the last whorl, the ribs are stouter, slightly S-shaped, and inclined towards the peristome. The ribs begin at the line of coiling with a very short concave section. Then, they continue only as simple ribs that are weakly convexly arched at the flanks towards the peristome. Approximately halfway up the whorl, the ribs diverge, with only a few exceptions. Exceptionally, there is a loose rib inserted in the upper part of the whorl, which disappears around the level of the bifurcation of the ribs, as well as a triple rib. From the point of bifurcation, the ribs are weakly concave towards the peristome. They pass through the narrow ventral side slightly convexly bent without interruption.

Measurements. At Dmax, D = 46.2 mm, H = 18.5 (0.40), and U = 15.7 (0.34). At Dmax, ca. 21 ribs at the umbilicus on the half-whorl.

Remarks and relations. Hoedemaeker et al. (2016) provide a detailed discussion of the synonymy of *Psudosubplanites fasciculatus*. They demonstrate that *Ps. fasciculatus* has denser ribs than *Ps. lorioli* because the ribs of the latter species have wider intercostal spaces. Among the dimensional parameters reported by Arkadiev and Bogdanova (2012), the lower H/D value differs somewhat from the Serbian specimen.

Distribution. Jacobi Zone of Crimea, France, Spain, lower Berriasian.

Occurrence. Light marlstones in layer 96.

Pseudosubplanites grandis (Mazenot, 1939)
Fig. 4I

1939 *Berriasella grandis* n. sp.; Mazenot, p. 133, pl. 22, figs. 3a, b, 6a, b.
1967 *Berriasella grandis* Mazenot; Nikolov, p. 608, figs. 1, 2.
1997 *Pseudosubplanites grandis* (Mazenot); Glushkov, p. 90, text-fig. 2:1, 2.
2005 Berriasella (Pseudosubplanites) grandis (Mazenot); Klein, p. 158.
2013 *Pseudosubplanites grandis* (Mazenot); Vašíček et al., p. 463, figs. 3, 4A, B (cum syn.).
2016 *Pseudosubplanites grandis* (Mazenot); Hoedemaeker et al., p. 127, pl. 7, figs. 5, 6.

Material. A few fragments of larger whorls, partly with the ventral side preserved (e.g., specimens S36.3/2, S37/2, SA96/2), and one fragment that is flatly deformed has approximately half of the last whorl lying in a crumbly argillaceous layer, which could not be removed from layer 96.

Description. Large, apparently semi-evolute specimens with relatively flat whorl flanks of greater height and with a broad umbilicus. The fullest specimen bears thick, sparsely spaced ribs. The ribs begin near the line of coiling as single ribs. At approximately half the height of the whorl, or slightly higher, the ribs bifurcate, with a few exceptions. The anterior of the bifurcated ribs continues in the direction of the primary rib, while the posterior rib deviates to the rear. One polygyrate rib is visible on fragment SA96/2. The ventral flank, if preserved, is relatively narrow and only weakly arched. The ribs cross the venter unchanged without interruption.

Measurements. The dimensional parameters listed below were measured on the specimen in the layered area only as a guide due to the less-than-perfect preservation. At D of ca. 158 mm, H = 50.0 (0.32), and U is ca. 67.0 (0.42). At the given almost maximum diameter per half-whorl, there are approximately 22 ribs in the umbilicus.

Remarks and relations. *Pseudosubplanites grandis* differs from most species of the genus by the considerably larger size of adult specimens with adequate strength of the mostly forked ribs.

Distribution. *Pseudosubplanites grandis* is recorded in the upper part of the lower Berriasian (former Grandis Subzone) of France, Crimea, Bulgaria, and the Czech Republic.

Occurrence. Fragments of large whorls occur over a stratal sequence from layer 18 to layer 100.

Family Neocomitidae Salfeld, 1921
Subfamily Berriasellinae Spath, 1922

The following genera, in accordance with other authors (e.g. Nikolov, 1982; Hoedemaeker et al., 2016), are viewed as representatives of the superfamily Perisphinctoidea Steinmann, 1890, and not of the superfamily Olcostephanoidea (Pavlow, 1892), as suggested by Kvantaliani (1999, p. 63), or of the superfamily Olcostephanaceae Pavlow, as stated by Arkadiev and Bogdanova (2012). The generic concept of the group included under the term berriasellid ammonites is extremely complex.

The genus *Berriasella* Uhlig, 1905, was and is also currently fragmented and conceived in several different concepts. The most common division of this genus is into two subgenera: the typical subgenus *Berriasella* and the subgenus *Hegaratella* Nikolov and Sapunov, 1977. The subgenus *Hegaratella*, according to Hoedemaeker et al. (2016), is supposedly restricted to the Jacobi Zone (lower Berriasian), while the typical subgenus *Berriasella* is restricted to the late Berriasian, which is not entirely correct from a theoretical taxonomic point of view. *Berriasella* (*Berriasella*) sensu Hoedemaeker (1982) supposedly differs from *Berriasella* (*Hegaratella*) sensu Hoedemaeker (1982) in that *Berriasella* (*B.*) bears straight prorsiradiate to radial ribs that more or less protrude in the upper parts of the whorls. They supposedly differ from *Berriasella* (*H.*) mainly by the convexity of the ribs in the middle of the whorl.

The type species of the subgenus *Hegaratella* is *Berriasella* (*H.*) *paramacilenta* Mazenot, 1939. The ribs of this species bear mid-ventral notches, which lead to the indication of only a ventral furrow or a spatial type of siphonal furrow (Hoedemaeker et al., 2016, p. 128). Originally, *B.* (*Hegaratella*) was a subgenus of the genus *Pseudosubplanites* (see Nikolov, 1982). However, *B.* (*Hegaratella*) cannot be part of this subgenus, as, among other things, representatives of the subgenus lack subvirgatotome ribs.

Hoedemaeker (1982) united all berriasellid species occurring in the Jacobi Zone into the subgenus *Berriasella* (*Hegaratella*). These were previously included by Mazenot (1939) in the category *Berriasella* without siphonal furrow. Subsequently, Le Hégarat (1973) placed them in the genus *Berriasella* Uhlig, 1905. *Berriasella* (*Hegaratella*) is considered the ancestor of *Berriasella* (*Berriasella*).

Very close to the above mentioned representatives of the genus *Berriasella* are the not-quite-conclusively-valid genera *Chapericeras* Hoedemaeker, 1982, *Fauriella* Nikolov, 1966 and *Picteticeras* Le Hégarat, 1973. Another problematic genus is *Strambergella* Nikolov, 1966. In the latter genus, Frau et al. (2016a) recently reassigned the index species *Berriasella jacobi* Mazenot, 1939. However, the aforementioned species does not correspond to the genus *Strambergella* in the character of its ribbing, as the type specimen of Zittel (*Strambergella carpathica*) bears both triple ribs and ribs that bifurcate at the umbilicus. Therefore, we consider this generic reassignment to be unjustified.

Due to the above mentioned problems with ambiguity, we have abandoned the division of the genus *Berriasella* into subgenera in the presented paper, considering, in accordance with Frau et al. (2016b) and Szives and Főzy (2022), the subgenus *Hegaratella* as a separate genus.

Genus *Hegaratella* Nikolov and Sapunov, 1977
Type species. *Berriasella paramacilenta* Mazenot, 1939

According to Hoedemaeker et al. (2016), the *Hegaratella* subgenus ambiguously defined in several versions is supposedly characterised primarily by the development of a siphonal furrow on the ventral side, but this may also disappear. The subvirgatotome (polygyrate) ribs are not developed. According to Frau et al. (2016a), the two species described subsequently here belong to the genus *Berriasella*.

Hegaratella subcalisto (Toucas, 1890)
Fig. 4J

1890 *Hoplites Calisto* d'Orb. sp. 1° Variété *subcalisto*; Toucas, p. 601, pl. 17, fig. 4A, B.
1939 *Berriasella subcalisto* (Toucas); Mazenot, p. 53, pl. 3, figs. 11a, b, 14a, b.
1968 *Berriasella subcalisto* (Toucas); Le Hégarat and Remane, pl. 5, fig. 4.
1973 *Berriasella (Berriasella) subcalisto* (Toucas); Le Hégarat, p. 66, pl. 6, figs. 3–6; *non* pl. 39, fig. 2 (= *Berriasella* (*Hegaratella*) *vasiceki* Hoedemaeker in Hoedemaeker et al., 2016).
1982 *Berriasella (Berriasella) subcalisto (Toucas)*; Nikolov, p. 56, pl. 10, fig. 2; *non* pl. 11, fig. 1 (= Le Hégarat, 1973, pl. 39, fig. 2 = *Berriasella* (*Hegaratella*) *vasiceki* Hoedemaeker et al., 2016).
1985 *Berriasella (Berriasella) subcalisto* (Toucas); Tavera Benitez, p. 245, pl. 34, fig. 3, text-fig. 19M.
2004 *Berriasella subcalisto* (Toucas); Arkadiev and Bogdanova, p. 373, pl. 1, figs. 10a, b, 11a, b.
2005 Berriasella (Berriasella) subcalisto (Toucas); Klein, p. 177.
2012 *Berriasella subcalisto* (Toucas); Arkadiev and Bogdanova, p. 146, pl. 5, figs. 6a, b, 7a, b.
2016 *Berriasella (Hegaratella) subcalisto* (Toucas); Hoedemaeker et al., p. 129, pl. 8, figs. 1–3.

Material. The last whorl of an external mould, specimen S99/2, slightly lateral deformed. The venter is not preserved.
Description. Evolute specimen with low, slightly arched whorls and a broad umbilicus. The ribs are equally strong on the entire whorl. Beginning at the umbilicus, the primary ribs are concave in a short section. Slightly convex, continuing to approximately half the height of the whorl. There, they bifurcate and end at the venter. Occasionally, there are simple insertion ribs running through the entire whorl.
Measurements. Dmax in the shortening axis reaches 39.5 mm. H = 14.5 (0.37), and U = 15.6 (0.39). At D = 36.5 mm (in the elongation axis), H = 12.7 (0.35), and U = 14.8 (0.405). At Dmax, there are 23 ribs at the umbilicus and 42 ribs at the ventral side per half-whorl. Between the main axes of deformation at D = 37 mm, H = 13.5 (0.36), and U = 15.9 (0.40).
Remarks and relations. *Beriasella subcalisto* is characterised by a broad umbilicus that is larger than the height of the whorl. The specimen designated *B. subcalisto*, illustrated by Le Hégarat (1973, pl. 39, fig. 2), is distinguished by thicker, more densely distributed ribs (according to Hoedemaeker et al., 2016). When the umbilicus is narrower than the height of the whorl, then Hoedemaeker (in Hoedemaeker et al., 2016) designated these specimens as *B.* (*Hegaratella*) *vasiceki*.
Distribution. The lower Berriasian (Jacobi Zone?) of Crimea, Bulgaria, France, Spain. Bulot et al. (2014) from the Le Chouet section in SE France reported *B. subcalisto* from the basal part of the Jacobi Zone.
Occurrence. Clayey limestones in layer 99.

Hegaratella oxycostata (Mazenot, 1939)
Fig. 4M, N

1939 *Berriasella oxycostata* (Jacob) in Breistroffer; Mazenot, p. 51, pl. 3 fig. 9a-j, *non* fig. 10a–c (= *Fauriella simplicostata* Mazenot).
1953 *Berriasella oxycostata* (Jacob) in Mazenot; Arnould-Saget, p. 29, pl. 3, figs. 5a–c, 6a–c.
1973 *Berriasella* (*Picteticeras*) *oxycostata* (Jacob); Le Hégarat, p. 78, pl. 8, figs. 4–6; pl. 40, figs. 2–4.
1979 *Berriasella* (*Picteticeras*) *oxycostata* (Mazenot); Sapunov, p. 176, pl. 56, figs. 3, 4.
1982 *Berriasella* (*Hegaratella*) *oxycostata* (Mazenot); Nikolov, p. 70, p. 15, fig. 2.
1985 *Berriasella* (*Picteticeras*) *oxycostata* (Mazenot); Cecca, p. 149, pl. 2, fig. 2.
1985 *Berriasella* (*Berriasella*) *oxycostata* (Mazenot); Tavera Benitez, p. 241, pl. 33, figs. 14, 15, text-fig. 19C.
1989 *Berriasella* (*Picteticeras*) *oxycostata* (Jacob)?; Khimshiashvili, p. 10, pl. 3, figs. 4, 5.
2005 *Berriasella* (*Berriasella*) *oxycostata* Mazenot; Klein, p. 174.
2016 *Berriasella* (*Hegaratella*) *oxycostata* Mazenot; Hoedemaeker et al., p. 131, pl. 8, figs. 7–9.

Material. Almost half of a small, mostly quite heavily corroded outer mould, which is perhaps only slightly deformed (specimen SA/ under 2 m).
Description. Semi-evolute specimen with low, equally wide whorls and a broad umbilicus. The flanks of the whorls are weakly arched, falling smoothly to the line of coiling; they fall more steeply to the ventral side. The venter is slightly arched or flat. The whorl bears rather sparsely spaced ribs, mostly of the same type. They start as simple, almost straight ribs that are slightly inclined towards the peristome. At two-thirds of the height of the whorl, the ribs diverge in a bifurcated manner. The posterior ribs of the resulting pair continue in the direction of the original single rib, while the anterior ribs deviate strongly towards the mouth. Lateral tubercles are indicated where the ribs fork. A narrow siphonal furrow is visible

on the venter at the beginning of the last whorl, which is less distinct in the further continuation of the whorl. The ribs cross the venter without interruption.
Measurements. At Dmax, D = 30.5 mm, H = 10.0 (0.33), U = 12.5 (0.41), and B = 10.0 (0.33). At Dmax, there are approximately 21 ribs per half-whorl at the umbilicus.
Remarks and relations. The specimen is characterised by an evolute coiling when the umbilicus is wider than the height of the whorls. Ribs are weakly prorsiradiate, straight, thin and sparsely spaced. Only bifurcated ribs are visible on the last whorl. The single ribs are not detectable. *Berriasella* (*Hegaratella*) *oxycostata* somewhat resembles *B*. (*H.*) *chomeracensis* (Toucas, 1890). *H. oxycostata* has a particularly broad umbilicus and few single ribs.
Distribution. According to Nikolov (1982), the species is more abundant in the upper Tithonian and less abundant in the lower Berriasian of France, Spain, Tunisia, and Bulgaria. Hoedemaeker et al. (2016) state that they are present in the higher part of the Jacobi Zone (calpionellid Ferasini Subzone).
Occurrence. This single find comes from a position approximately 2 m into the bedrock at the level of the start of the studied section (layer 0).

Genus *Delphinella* Le Hégarat, 1971
Type species. *Hoplites delphinensis* Kilian, 1889

Remarks. Semi-evolute specimens with trapezoidal whorl cross-sections. On adult whorls, lateral tubercles may form when the ribs bifurcate or trifurcate. The ribs are interrupted on the venter. However, according to Hoedemaeker et al. (2016, p. 146), in some species, the ventral furrow is lost during growth. Adult whorls may be accompanied by the disappearance of sculpture on the flanks of the whorl.

Delphinella* cf. *delphinense (Kilian, 1889)

Fig. 4K, L

cf. 1889 *Hoplites delphinensis* n. sp.; Kilian, p. 662, text-fig. 1.
cf. 1939 *Berriasella delphinensis* (Kilian); Mazenot, p. 67, pl. 6, figs. 14a, b, 15a–c.
cf. 1953 *Berriasella delphinensis* (Kilian) Mazenot; Arnould-Saget, p. 45, pl. 4, figs. 10a—c, 11a–c.
cf. 1973 *Delphinella delphinensis* (Kilian); Le Hégarat, p. 104, pl. 13, figs. 7, 8; pl. 42, figs. 3, 9.
cf. 1982 *Delphinella delphinensis* (Kilian); Nikolov, p. 86, pl. 20, figs. 2a, b, 3, 4.
cf. 2005 *Delphinella delphinensis* (Kilian); Arkadiev and Bogdanova, p. 494, pl. 6, fig. 5.
cf. 2005 *Delphinella delphinensis* (Kilian); Klein, p. 185.
cf. 2012 *Delphinella delphinensis* (Kilian); Arkadiev and Bogdanova, p. 164, pl. 10, fig. 4.
cf. 2013 *Delphinella delphinensis* (Kilian); Szives and Főzy, p. 311, pl. 7, fig. 3.
cf. 2016 *Delphinella delphinensis* (Kilian); Hoedemaeker et al., p. 144, pl. 10, fig. 10.
cf. 2016b *Delphinella delphinense* (Kilian, 1889) nom. correct; Frau et al., p. 175, text-figs. 3K–O.

Material. Two slightly flatly deformed juvenile outer moulds. The first, which is better preserved (specimen S31.2/3), forms less than half of the shell, and in the second (specimen S31.2/5), the last and penultimate whorl are preserved.
Description. Semi-evolute whorls with relatively low whorls and a wide umbilicus. The slightly arched flanks of the whorl descend gradually to the line of coiling. The flanks of the whorl in the ventral region edge into a narrow and flat ventral side. The ribs start as primary at the umbilicus. On the smaller specimen (S31.2/3), most ribs bifurcate quite high at approximately 3/5 of the whorl height. Slight lateral tubercles are visible at the bifurcation sites. In addition to bifurcated ribs, simple ribs are occasionally present. All ribs bear small ventrolateral tubercles on the edge, separating the flanks from the ventral side. The ventral ribs point obliquely towards the peristom. Their course is interrupted by a siphonal groove. On the fuller specimen (specimen S31.2/5), the penultimate whorl bears thin, dense, simple ribs. They are slightly concave and inclined towards the peristome. On the last whorl, the simple ribs are somewhat more numerous. The last two ribs project from the umbilicus together.
Measurements. Specimen 31.2/5 reaches a Dmax = 27.5 mm. At D = 24.1 mm, H = 8.4 (0.35), and U = 8.5 (0.35). B is ca. 6.2 (0.26). There are 21 ribs per half-whorl at Dmax.
Remarks. The size of specimens and unclear crossing in to small adult whorls makes unambiguous identification difficult. The dimensional parameters of the Serbian specimens correspond to the holotype when H/D and U/D are the same. Frau et al. (2016a) corrected the species name *delphinensis* to *Delphinella delphinense*.
Distribution. Lower Berriasian (middle part of the Jacobi Zone?) of Crimea, Bulgaria, Hungary, France, Spain, and Tunisia. Frau et al. (2016b) reported *Delphinella delphinense* from the Le Chouet section in France from the upper part of the Jacobi Zone; then, for *D.* gr. *delphinense* (Frau et al., 2016b) from perhaps the same profile, it was reported from the middle part of the Jacobi Zone.
Occurrence. A reddish marly limestone in layer 31 (20 cm from the base).

Delphinella miravetensis Hoedemaeker in Hoedemaeker et al., 2016
Fig. 5A
2016 *Delphinella (Delphinella) miravetensis* sp. nov.; Hoedemaeker in Hoedemaeker et al., p. 143, pl. 10, fig. 9.

Material. The last whorl of the outer mould cast deformed by lateral pressure (specimen S97/1).
Description. Specimen with evolute coiling, with flat flanks rising more steeply to the umbilicus than to the venter. The flanks smoothly transition to the line of coiling. The umbilicus is broad. The sculpture is different in two parts of the whorl. The initial part of the last whorl is covered by thin and dense ribs. They start as primary ribs on the line of coiling without tubercles. They are distinctly proverse. Around the lower third of the height of the whorl, they bend with a knee shape and bifurcate in the form of thin and densely spaced ribs. In one case, a triple rib is evident. In the remaining part of the whorl, the ribs are concave and inclined towards the peristome. At the likely end of the phragmocone, there is an abrupt change in ribbing. On the presumed body chamber, the ribs are more robust and sparsely spaced. Around the line of coiling, the primary ribs are concave in a short section. In the next part, the ribs are clearly inclined towards the peristome. At approximately half the height of the whorl, or slightly below, the ribs bend with a knee shape (less conspicuously than in the previous section) and bifurcate. At least in some places, there are faint bullate lateral tubercles at the point of the bifurcation of the ribs. The narrowly bifurcated ribs continue as slightly concave to the venter. A single rib inserted between the paired ribs appears in a few cases.
Measurements. Dmax = 39.5 mm. At D = 38.8 mm (between the main axes of deformation), H = 15.0 (0.39) and U = 14.2 (0.365). At Dmax, there are 15 ribs per half-whorl at the umbilicus.
Remarks. With the same diameter of the specimens, *Delphinella miravetensis* differs from *D. consanguinea* (Retowski, 1893) by lower whorls (H/D of the former = 0.35, of the latter = 0.37). On the flank of the whorl with spoon-shaped ribs, there are peculiar gaps caused by the short length of the secondary ribs.
Distribution. To date, the recently established *D. miravetensis* has been known only from the Jacobi Subzone (lower Berriasian) in Spain.
Occurrence. Marlstones in layer 97.

Genus *Substeueroceras* Spath, 1923
Type species. *Odontoceras koeneni* Steuer, 1897.

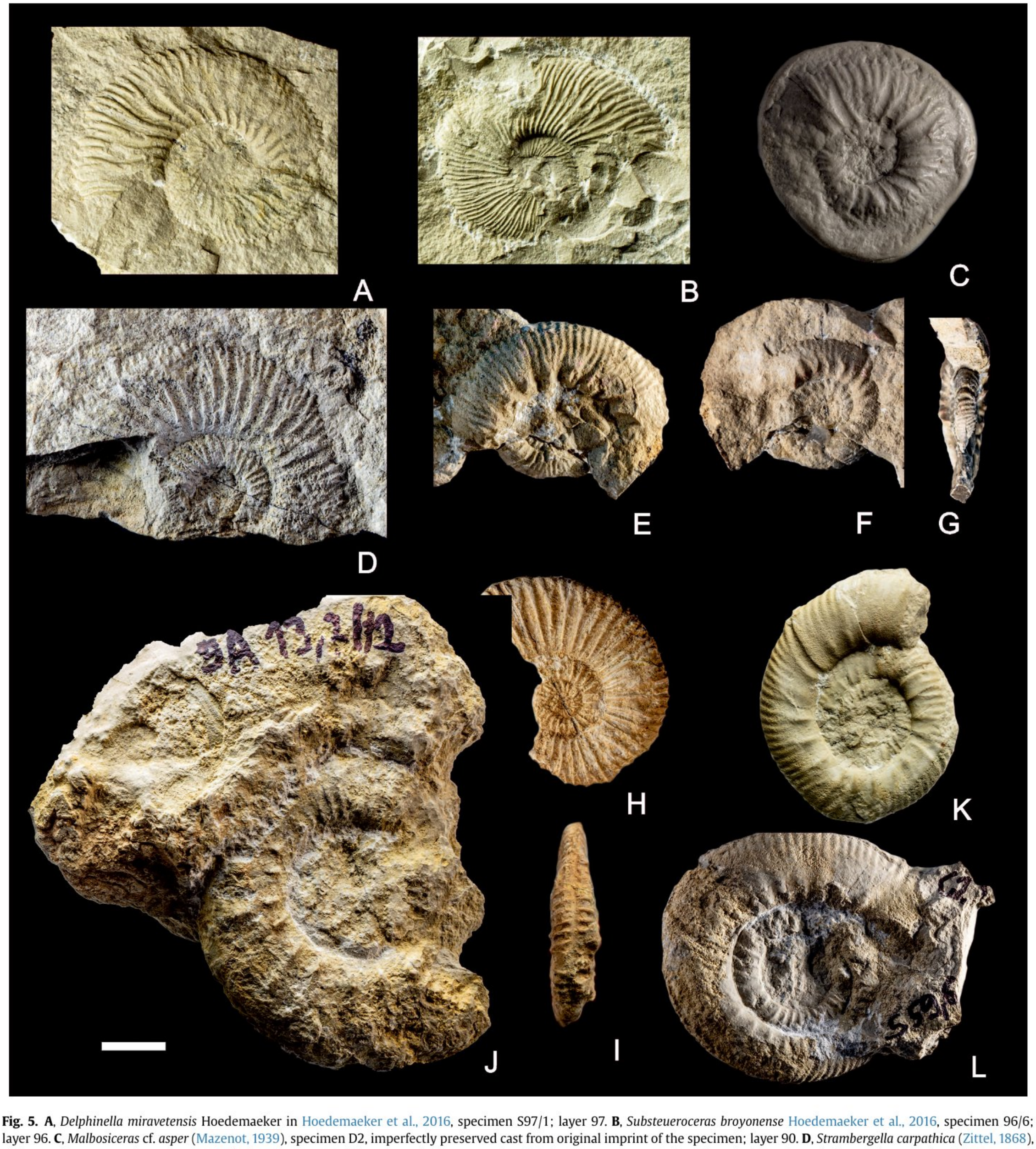


Fig. 5. **A**, *Delphinella miravetensis* Hoedemaeker in Hoedemaeker et al., 2016, specimen S97/1; layer 97. **B**, *Substeueroceras broyonense* Hoedemaeker et al., 2016, specimen 96/6; layer 96. **C**, *Malbosiceras* cf. *asper* (Mazenot, 1939), specimen D2, imperfectly preserved cast from original imprint of the specimen; layer 90. **D**, *Strambergella carpathica* (Zittel, 1868), unfavourable preserved specimen S14.2/2; layer 14. **E–G**, *Spiticeras pseudogroteanum* Djanélidzé, 1922, specimen S35/1, E, lateral view, F, lateral view of the opposite side, G, ventral view; layer 35. **H**, **I,** *Kilianiceras* cf. *ambiguum* (Djanélidzé, 1922), juvenile specimen SA 13.2/3, H – lateral view, I – ventral view; layer 13; J. *Kilianiceras* cf. *ambiguum* (Djanélidzé, 1922): strongly corroded adult specimen SA 13.2/12, layer 13. **K**, **L**, *Negreliceras mirum* (Retowski, 1893), K, spec. 59.6/1; L, specimen 59.6/2 with an initial part of the peristome; layer 59. Scale bar equals 10 mm.

Substeueroceras is a well defined genus, endemic of the Andean basins. The independence from the other Andean genus *Parodontoceras* was discussed in Parent et al. (2011, 2015), much more seriously and informed, based on described, illustrated and published material, complete ammonites. Some confusion may arise from the poor definition by Spath in 1923.

Substeueroceras broyonense Hoedemaeker et al., 2016
Fig. 5B

1939 *Neocomites beneckei* (Jacob) in Roman and Mazenot; Mazenot, p. 208, pl. 32, fig. 10a, b, non figs. 11a, b, 12a–c, 13, 14 (= *Substeuroceras beneckei* Mazenot, 1939), non fig. 8a,

b (= *Lemencia mazenoti* Donze and Enay, 1961), non fig. 9a, b (= *Tirnovella allobrogensis* Mazenot, 1939).
1968 *Neocomites (?) beneckei* (Jac.); Le Hégarat and Remane, p. 20, pl. 5, fig. 3.
1985 *Tirnovella allobrogensis* (Mazenot); Tavera Benitez, p. 296, pl. 45, fig. 1.
2013 *Tirnovella allobrogensis* (Mazenot); Vašíček and Skupien, p. 337, figs. 5K–M.
2016 *Substeueroceras broyonense* sp. nov.; Hoedemaeker et al., p. 150, pl. 12, figs. 3–6.
2018 *Substeueroceras broyonense* Hoedemaeker; Vašíček et al., p. 197.

Material. An almost complete flatly deformed last whorl of the outer mould. The ventral side is not exposed (specimen S96/6); further, the impression and the cast made from it with the last and part of the penultimate whorl is preserved (juv. specimen S97/4).
Description. Semi-involute specimens with relatively high whorls and a moderately narrow umbilicus. The flanks of the whorl are only slightly arched. Around the line of coiling, the whorl descends roundly to the umbilicus in a short section. The very thin and very dense ribs begin with the simple primary ribs at the line of coiling. Near the line of coiling, they are slightly concave in a short section. In the juvenile region, ribs are sporadically found projecting from the umbilicus in pairs. With slight exceptions, the ribs bifurcate very narrowly, approximately halfway up the whorl. Single ribs are slightly more frequent at the end of the whorl than at the beginning. Occasionally, trifurcate ribs occur on the penultimate whorl. At the end of specimen S96.6, the last rib is trifurcated. All ribs are slightly axially curved. On the flanks of the whorl, the ribs with a convex curvature are inclined towards the peristome in the longer section. From the bifurcation area, the ribs are slightly concave, inclined towards the peristome in the ventral region, and are without constrictions, thicker ribs and tubercles.
Measurements. Specimen 96/6, at Dmax = 37.5 mm, has H = 16.0 (0.43) and U = 10.5 (0.28). The 28 ribs at the umbilicus lie at half of the whorl. In spec. 97/4 at D = 27 mm, H = 12.5 (0.46), and U = 6.6 (0.24). There are 17–18 ribs per half-whorl at the umbilicus and 34–36 ribs in the ventral region.
Remarks. The genus *Pseudargentiniceras* Spath, 1925, to which the very closely related species Substeueroceras *beneckei* and *S. broyonense* have sometimes been assigned, is probably foregoing to the genus *Substeueroceras*. However, *Pseudargentiniceras* is characterised by a semi-evolute to evolute coiling, whereas the species of *Substeueroceras* are more involute. According to Hoedemaeker et al. (2016), the ribs of *S. beneckei* are interrupted by a furrow on the venter. Compared to *S. broyonense* Hoedemaeker et al., 2016, *S. beneckei* lacks fasciculation of the ribs.
Distribution. Spain, France, and the Czech Republic in the Jacobi Zone.
Occurrence. Marlstones in layers 96 and 97.

Genus *Malbosiceras* Grigorieva, 1938
Type species. Ammonites Malbosi Pictet 1867.
The genus concept here is in agreement with that presented by Arkadiev and Bogdanova (2012).

Malbosiceras* cf. *asper (Mazenot, 1939)
Fig. 5C

cf. 1939 *Berriasella aspera* n. sp.; Mazenot, p. 84, pl. 9, figs. 2a–c, 3a, b.
cf. 1973 *Malbosiceras asper* (Mazenot); Le Hégarat, p. 84, pl. 9, figs. 1, 2; pl. 40, fig. 9.
cf. 1979 *Malbosiceras asper* (Mazenot); Sapunov, p. 183, pl. 57, fig. 1a, b.
cf. 1982 *Malbosiceras asper* (Mazenot); Nikolov, p. 126, pl. 47, fig. 3 (= Mazenot, 1939, pl. 9, fig. 2b), fig. 4a (= Sapunov, 1979, pl. 57, figs. 1a, b).
cf. 2005 *Malbosiceras asper* (Mazenot); Klein, p. 207.

Material. Impression and cast of the last whorl of a small specimen (spec. D2). The ventral area of this specimen is probably not complete.
Description. Semi-involute specimen with an arched last whorl. The whorl is most arched in the lower third of the height. At its base, there is a low and steep umbilical wall that is not separated from the flanks. The outer part of the whorl inclines smoothly towards the venter. The whorls are of medium height with a narrower umbilicus. The specimen is distinctly and relatively sparsely ribbed. There are slightly retroverse primary ribs on its terminal half in the lower part. At the very end of the whorl, the last ribs appear to protrude from a weak umbilical tubercle. Two ribs protrude from another tubercle, which is accompanied by a third shorter rib wedged between the primary ribs. With the exception of the terminal part, there are distinct lateral tubercles in the middle of the height of the whorl. Sometimes two or three clamped secondary ribs protrude from them. They are concave and proverse in the ventral region. The intercostal spaces between the ribs are unequally wide. The triple ribs on the anterior side are accompanied by wider gaps resembling constrictions.
Measurements. Due to the imperfectly preserved circumference of the specimen, the values of D and H are not unambiguous. At a D of ca. 27 mm, H is ca. 11.0 (0.41), and U = 9.0 (0.33). At the given D per half-whorl, there are 10–11 ribs at the umbilicus and 24 ribs secondary plus intacalar ribs.
Remarks. The small size and degree of preservation do not allow unambiguous species identification.
Distribution. *Malbosiceras asper* is mainly known in France, Spain and Bulgaria. According to Nikolov (1982), it is in the terminal Tithonian (?).
Occurrence. Light grey claystones in layer 90.

Genus *Strambergella* Nikolov, 1966
Type species. Ammonites carpathicus Zittel, 1868.

Strambergella carpathica (Zittel, 1868)
Fig. 5D

1868 *Ammonites carpathicus* Zitt.; Zittel, p. 107, pl. 18, fig. 4a–d, fig. 5?.
1939 *Berriasella carpathica* (Zittel); Mazenot, p. 103, pl. 13, fig. 4a–d.
1973 *Fauriella (Strambergella)* aff. *carpathica* (Zittel); Le Hégarat, p. 152, pl. 21, figs. 5, 6 (= Zittel, 1868, pl. 18, Figs. 4b, 5), non pl. 21, fig. 4, non pl. 46, figs. 2, 3.
1979 *Berriasella (Strambergella) carpathica* (Zittel); Sapunov, p. 179, pl. 56, fig. 6.
2005 *Strambergella carpathica* (Zittel); Klein, p. 264.
2011 *Fauriella* aff. *carpathica* (Zittel); Arkadiev, p. 9, pl. 3, figs. 6, 7.
2013 *Fauriella floquinensis* Le Hégarat; Szives and Főzy, p. 308, pl. 9, fig. 1.
2016a *Strambergella carpathica* (Zittel); Frau et al. p. 99, figs. 4A–G (cum syn).

Material. Almost half of a poor quality, flatly deformed outer mould with the preserved part of the last and adjacent part of the penultimate whorl (specimen S14.2/2). The ventral side is not visible.
Description. Semi-evolute specimen with only slightly arched flanks of whorls falling smoothly to the coiling line. The penultimate whorl is dominated by simple ribs that are slightly concave towards the peristome. On the penultimate whorl, at approximately one-third of the height of the whorl, the ribs split sporadically. In the

favourably preserved section of the last whorl, in its lower half, there are relatively sparse ribs, which are slightly concave towards the peristome. The ribs that bifurcate approximately halfway up the whorl are more frequent, with occasional ribs that are triarticulate. Faint lateral tubercles are indicated at the point of rib division (not in Zittel, 1868, but in Frau et al., 2016a, pl. 4 in some specimens). In a single case on the last whorl, a bifurcated rib can be seen running out from the umbilicus. The presence of faint bullate umbilical tubercles cannot be excluded.

Measurements. Incompletely preserved specimens do not allow the accurate measurement of dimensional parameters. At a Dmax of ca. 46.0 mm, H is ca. 16.5 (0.36), and U = 17.5 (0.38). At Dmax, there are ca. 18 umbilical ribs per half-whorl.

Remarks and relations. *Ammonites carpathicus* is a well-defined species. However, its systematic affiliation is highly disputed. The placement of the above species in the genus *Strambergella* has recently been discussed in detail by Frau et al. (2016a). In contrast to Frau et al. (2016a, p. 139), Hoedemaeker et al. (2016) concluded that the name *Strambergella* should be reserved only for *Strambergella carpathica*. Arkadiev (2011) notes that the Crimean specimens of his *Fauriella* aff. *carpathica* differ from the type material of Zittel (1868) by the absence of bidichotomous ribs. The same is probably true for the specimens illustrated by Le Hégarat (1973) under the designation *Fauriella* (*Strambergella*) aff. *carpathica*. However, it can be assumed that the above specimens show the morphological variability of *Strambergella carpathica*.

Distribution. *Strambergella carpathica* occurs in the higher part of the Jacobi Zone. Frau et al. (2016a, p. 104) report that at Les Combes, France; it is also reported in Crimea, Hungary, Bulgaria, Spain and Tunisia.

Occurrence. Light limestones in layer 14 (20 cm from the base).

Suborder Olcostephanina Haug, 1910
Superfamily Olcostephanoidea Haug, 1910
Family Olcostephanidae Haug, 1910
Subfamily Spiticeratinae Spath, 1924

The basic concept of the suborder Olcostephanina and its further subdivisions follows Kvantaliani et al. (1999) and Kvantaliani (1999, p. 78).

Genus *Spiticeras* Uhlig, 1903

Type species. *Ammonites spitiensis* Blanford, 1863.
Semi-evolute shells, initially on primary ribs with lateral tubercles, and later with umbilical tubercles.

Spiticeras pseudogroteanum Djanélidzé, 1922

Fig. 5E–G

1922 *Spiticeras* (s. str.) *pseudogroteanum* n. sp.; Djanélidzé, p. 93, pl. 3, figs. 2a–c, 3a, b.
1953 *Spiticeras (Spiticeras) pseudogroteanum* Djanélidzé; Arnould-Saget, p. 98, pl. 8, figs. 6a–c.
1967 *Spiticeras (Negreliceras) negreli* (Matheron); Dimitrova, 89, pl. 43, fig. 4.
1979 *Spiticeras (Spiticeras) pseudogroteanum* Dianélidzé; Sapunov, p. 170, pl. 54, fig. 3.
2005 *Spiticeras pseudogroteanum* Djanélidzé; Klein, p. 58.
2013 *Spiticeras pseudogroteanum* Djanélidzé; Szives and Főzy, p. 303, pl. 3, fig. 5a, b.

Material. Only one external mould (specimen S35/1) is preserved differently on both flanks. One side retains half of the last whorl, including part of the ventral side. On the opposite side, a larger part of the penultimate whorl is exposed (specimen S35/1).

Description. Evolute to semi-evolute whorled specimen with low, relatively broad whorls and a broad umbilicus. The flanks of the whorl are significantly arched. The inner half of the whorl descends rather steeply but smoothly to the line of coiling; the outer, larger half descends more slightly to the venter. On the penultimate whorl, on its inner half, there are slightly concave, sparsely spaced ribs, which bear weak lateral tubercles approximately halfway up. Three ribs that arcuately inclined towards the peristome protrude from the tubercles. The last part that is eventually more favourably exposed shows strong lateral tubercles from which 3–4 equally strong but thinner ribs protrude. They are slightly concave and inclined towards the peristom. All equally strong ribs continuously pass the ventral side with a hint of a chevron form. There are approximately three constrictions per whorl. There is usually one simple inserted rib between the bunched ribs.

Measurements. On the penultimate whorl at D = 17.8 mm, H = 6.6 (0.37), and U = 8.0 (0.45). Dmax is approximately 35 mm. At Dmax, there are 11–12 lateral tubercles per half-whorl and approximately 45–50 secondary plus intacalar ribs. When H = 11 mm, B = 12 mm, so the threads are slightly wider than their height.

Remarks and relations. The Hungarian specimen (Szives and Főzy, 2013) belongs to the macroconch category.

Distribution. The species *Spiticeras pseudogroteanum* is described from the deposits of France, Tunisia, Hungary, and Bulgaria. Bulot et al. (2014) mentioned the occurrence of the species in the Le Chouet section in the higher part of the Jacobi Zone.

Occurrence. Light clayey limestone in layer 35.

Genus *Kilianiceras* Djanélidzé, 1922

Type species. *Stephanoceras damesi* Steuer, 1897.

This genus is characterised by an evolute coiling and a pair of tubercles on the primary ribs (sometimes only faintly indicated), whose representatives reach a larger size in adulthood.

Kilianiceras* cf. *ambiguum (Djanélidzé, 1922)

cf. 1922 *Spiticeras (Kilianiceras) ambiguum* n. sp.; Djanélidzé, p. 87, pl. 4, fig. 9a, b, text-fig. 18.
cf. 2005 *Kilianiceras ambiguum* (Djanélidzé); Klein, p. 63.

Fig. 5H–J

Material. Four specimens: two juvenile (SA13.2/2 and 13.2/3) and two adult (SA13.2/10 and 13.2/12). The outer mould of half of a juvenile specimen (SA13.2/3) with three whorls preserves partly highly and partly slightly less flatly deformed whorls. The terminal half of the last whorl of the adult specimen (SA13.2/10) belongs to the body chamber, and the rest belongs to the phragmocone. The end part of the phragmocone that is preserved as an internal mould is evidenced by indistinct suture lines (specimen SA13.2/12). It has a heavily corroded, flatly deformed first quarter of the last whorl and part of the third quarter of the last whorl, with a more favourable preservation of a less corroded outer mould. The unfavourably preserved opposite side shows a small segment of development of the significant ornamentation on the penultimate whorl.

Description. Juvenile semi-evolute specimens with medium to high whorls and a broad umbilicus. The flanks of the last whorl are slightly arched, sloping smoothly to a very low, obliquely angled umbilical wall. This feature is similar to that on the ventral side. The last whorl of juvenile specimens bears moderately dense, rather sharp triple-type ribs. Most often, there are bifurcated ribs at two-thirds of the height of the whorl (in one case, the bifurcation occurs below half the height of the whorl), isolated single ribs, and in one case, a bifurcated rib at the umbilicus when the posterior rib bifurcates once more. The ribs are straight till slightly concave. The

anterior of the bifurcated ribs follows the course of the primary ribs smoothly, and the posterior ribs are diverted. The last bifurcated ribs bear faint lateral tubercles at the place of bifurcation. The ribs are interrupted on the venter by a slight siphonal groove. Only simple, slightly convexly bent, slightly proverbial ribs are visible on the preceding whorls. The bifurcation of the ribs here probably occurs at the level of the coiling line. Adult specimens have low whorls and a broad umbilicus. The last whorl is weakly arched. It transitions rather abruptly into a narrow ventral side. The whorl at the base falls off with a not-very high, but clearly defined, oblique umbilical wall. The body chamber is separated from the phragmocone by a distinct constriction. The juvenile sculpture changes at a diameter of approximately 22 mm. The following ribs are more sparsely spaced. Umbilical tubercles appear at the base of the ribs. At a diameter of approximately 50 mm, in one case, the ribs split above the umbilicus. There is a slight lateral tubercle at the place of bifurcation. The last whorl bears sparsely spaced main ribs, which are weakly inclined towards the peristome. On these ribs, there are bullate umbilical tubercles at the base and fainter lateral tubercles of a somewhat bullate shape around half the height of the whorl. Two ribs probably protrude from the umbilical tubercles. Additional ribs protrude from lateral tubercles. Due to imperfect preservation, there are visible 4 to 5 ribs on the ventral area at intervals defined by two main ribs. Behind some of the main ribs, shallow and short constrictions inclined towards the peristome can be seen in the ventral area. Their continuation to the flanks of the whorl is suppressed by the corrosion of the whorl. The ribs probably cross the venter on the body chamber without interruption, with a hint of a chevron form.

Measurements. Juvenile specimen SA13.2/3 at a Dmax of ca. 36.5 mm has about 19 ribs per half-whorl at the umbilicus and 31 ribs on the outer side. On specimen SA13.2/12 at a D of approximately 82 mm, H = 29.0 (0.35), and U is approximately 34.0 (0,41). There are approximately 13 ribs per half-whorl at the umbilicus. On specimen SA13.2/10, at almost a Dmax of 94.5 mm, H = 32.0 (0.34) and U = 40.3 (0.43). At approximately D 89 mm, there are 13 umbilical ribs or umbilical tubercles per half-whorl. The sparsely spaced main ribs start at approximately 45–50 mm in diameter. The phragmocone ends at approximately 71 mm in diameter. The largest specimen reaches a diameter of approximately 95 mm.

Remarks and relations. The considerable imperfection of preservation, especially the considerable corrosion of the adult whorls, does not permit unambiguous determination of species. On the inner whorls of the specimen illustrated in Djanélidzé, only the lower uncovered parts of the simple ribs are visible. On the Serbian juvenile specimens, the course of the entire ribs is visible. These originally simple ribs bifurcate at 2/3 of the whorl height. A siphonal groove is indicated on the venter. The ribbing of adult whorls on the material from Serbia can be deduced from the combination of two better preserved sections; when on one side the lower parts of the sparsely spaced ribs with tubercles are clearly visible (see fig. 5 J), and on the opposite side the ribbing at the circumference of the whorl. In the area between the two main ribs, there are 4–5 uniform weaker ribs that extend to the level of the lateral tubercles. A specimen from Djanélidzé (1922, pl. 4, fig. 9) shows a similar morphology.

Distribution. K. ambiguum occurred probably only in France, in the department of Isère. The author of species mentions the Tithonian age.

Occurrence. Light clayey limestone in layer 13 (20 cm from the base).

Genus *Negreliceras* Djanélidzé, 1922

Type species, *Ammonites negreli* Matheron, 1880.

Negreliceras mirum (Retowski, 1893)

Fig. 5K, L

1893 *Holcostephanus mirus* n. sp.; Retowski, p. 251, pl. 10, fig. 2.
1922 *Spiticeras mirum* Retowski sp.; Djanélidzé, p. 188.
1976 *Spiticeras* (*Spiticeras*) aff. *mirum* (Retowski)?; Patrulius and Avram, p. 185, pl. 8, fig. 9a, b.
2005 *Spiticeras mirum* (Retowski); Klein, p. 55.
2012 *Negreliceras mirum* (Retowski); Arkadiev and Bogdanova, p. 211, pl. 35, figs. 5, 6, 9.

Material. Two outer moulds deformed by surface and lateral pressure (specimen S59.6/1, 2). On specimen S59.6/1, the last and penultimate whorls are preserved on both flanks. The somewhat corroded specimen S59.6/2 has on only one side a somewhat corroded last whorl, including the ventral side with part of the lappet and part of the penultimate whorl.

Description. Evolute whorls with low whorls and a wide umbilicus. The flanks of the whorls are only slightly arched, with the greatest arching near the umbilicus, from which the whorl descends smoothly to the narrow ventral side. On the penultimate whorl, only simple ribs inclined towards the peristome are visible at first and then are slightly concave. The beginning of their bifurcation is visible at the end of this whorl. There are two constrictions on this whorl. On the last whorl, the ribs begin as thick, sparsely spaced primary ribs extending to approximately one-third to one-half the height of the whorl. Their density increases near the peristome. They are variably straight to slightly concave. The primary ribs show an umbilical tubercle above the coiling line, with a more distinct bullate lateral tubercle at the opposite end. Usually, two, or possibly three, thinner ribs protrude from the lateral tubercles. Between the paired ribs, usually one or two ribs are inserted, which disappear around the level of the mid-flank. All these ribs are concave and inclined towards the peristome. The ventral side passes unbroken in the form of a chevron. On the last whorl, there are two concave constrictions. The last (third) convex constriction separates the whorl from the lappet in the zone of the peristome.

Measurements. The S59.6/1 specimen reaches a maximum diameter (on the axis of extension) of approximately 40 mm. At D = 29.4 mm (on the shortening axis), H = 9.6 (0.33), and U = 14.0 (0.48). There are approximately 14 ribs per half-whorl at the umbilicus and approximately 40 ribs at the circumference. Spec. S59.6/2 reaches a Dmax of approximately 41 mm in the area around the peristome. At D = 39.0 mm, H = 12.0 (0.31), and U = 19.5 (0.50). Approximately 15 ribs are by the umbilicus and approximately 50 ribs are on the ventral area on the half-whorl.

Remarks and relations. Dimensional quantities are somewhat affected by deformation. The width of the umbilicus is noticeable. The faint umbilical tubercles on the primary ribs are significant.

Distribution. *Negreliceras mirum* is known from Crimea, Romania, and France. According to Arkadiev and Bogdanova (2012), it is in the Berriasian (Jacobi and Boissieri Zones) in Crimea.

Occurrence. Light grey marlstones in layer 59 (60 cm from the base).

Negreliceras* cf. *proteum (Retowski, 1893)

Fig. 6A

cf. 1893 *Holcostephanus (?) proteus* n. sp.; Retowski, p. 252, pl. 10, figs. 3a, b, 4.
cf. 1922 *Spiticeras (Negreliceras) paranegreli* n. sp. échantillon C.; Djanélidzé, pl. 6, fig. 2.
cf. 1999 *Spiticeras (Spiticeras)* cf. *proteus* (Retowski); Kvantaliani, p. 81, pl. 8, fig. 2a, b, v; pl. 9, fig. 2a, b, v.
cf. 1999 *Spiticeras (Spiticeras) kiliani* Djanelidze; Kvantaliani, p. 82, pl. 9, figs. 1a, b, v, 2a, b, v.
cf. 2012 *Negreliceras proteum* (Retowski); Arkadiev and Bogdanova, p. 209, pl. 35, figs. 1–4, 7.
cf. 2016 *Negreliceras proteum* (Retowski); Hoedemaeker et al., p. 158, pl. 14, figs. 1, 2.

Material. Fragment of less than half of a whorl preserved as an outer mould (specimen S88/2).
Description. Not very tall, slightly arched whorl with an unpreserved venter, probably with a wide umbilicus. The whorl bears numerous, rather weak ribs. In the lower half of the whorl, there are sparsely spaced single thicker ribs with umbilical tubercles at the base. The whole of this area is indistinctly preserved, but it is partly evident that there is a bifurcation of the ribs. Around the mid-height of the whorl, the thicker ribs split into thin and dense ribs accompanied by more equally thick inset ribs. In the interval defined by the two main ribs, there are between 5 and 7 ribs on the circumference. There are 3 shallow constrictions on the preserved section of the whorl. The ribs are generally slightly proverse. The maximum height of the whorl is approximately 15 mm.
Remarks and relations. The incomplete preservation of the specimen does not allow unambiguous identification.
Distribution. Representatives of the type species have been recorded from the lower Berriasian (Jacobi Zone) of Crimea, and further specimens are known from France and Spain.
Occurrence. Light clayey limestone in layer 88.

5. Aptychi

Lower Cretaceous ammonites can be found together with calcareous valves ribbed aptychi. The valves of aptychi are determined according to artificial taxonomy published in Měchová et al. (2010). Four genera were determined, and from each genera, only one species was identified. In the lower part of the section, the thick-walled *Punctaptychus punctatus* (Zittel, 1868) is quite common, reaching sizes from juvenile to adult valves up to 37 mm in length (Fig. 6C). A single small valve of *Cinctpunctaptychus cinctus* (Trauth, 1935) was also found in layer 47 (Fig. 6E). In the uppermost part of the section, juvenile thin-walled valves reaching 10–13 mm in length sporadically occur: *Beyrichilamellaptychus beyrichi* (Oppel, 1865) – Fig. 6F – and *Mortilletilamellaptychus submortilleti noricus* Měchová et al., 2010 (Fig. 6D). According to Měchová et al. (2010), all of these species occur in the Tithonian to Berriasian.

6. Discussion

The studied stratigraphic sequence in the Dedina section belongs to the biancone facies in terms of lithology. Light-coloured marlstones and clayey limestones predominate in this sequence.

The ammonites of the Dedina section belong to the suborders Haploceratina, Perisphinctina, Olcostephanina, and Ancyloceratina. Specimens of the later suborder are mainly represented by juvenile shells of one genus. No representatives of the suborder Lytoceratina were found, and only two juvenile representatives of the suborder Phylloceratina were discovered. The distribution of determined ammonites in the section is shown in Fig. 2. The collection also includes several findings of ribbed calcareous aptychi. Other cephalopods, i.e., belemnites, are scarce, currently being processed by colleagues from Prague.

Specifically, ribbed representatives of perisphinctid ammonites are the most abundant in the deformed ammonite material. They belong to six genera: *Pseudosubplanites, Hegaratella, Delphinella, Substeueroceras, Malbosiceras*, and *Strambergella,* represented by 12 species. The only strongly ribbed specimens with large adult whorls belong to *Pseudosubplanites grandis.* A somewhat controversial point in terms of taxonomy here is the classification of the species designated as e. g. *Berriasella (B.) subcalisto* and *Berriasella (Pictéticeras) oxycostata* in the genus *Hegaratella,* which, in agreement with some other authors, we consider to be a separate genus. Frau et al. (2016a), however, place both species in the genus *Berriasella.*

Haploceratid ammonites in the studied collection are represented by two genera (*Haploceras* and *Hypolissoceras*) – one species of each. Taxonomically interesting is the rare occurrence of the little-known *Hypolissoceras leiosoma.* In contrast, *Haploceras elimatum* is quite common throughout the succession.

Ammonites of the suborder Ancyloceratina include only straight-line fragments of very juvenile specimens (see Fig. 6B), together with some small adult fragments of the genus *Bochianites.* The suborder Olcostephanina includes three sparsely occurring genera (*Spiticeras, Kilianiceras*, and *Negreliceras*).

In terms of the modern ammonite stratigraphy of the Lower Cretaceous Kilian Group (see Reboulet et al., 2018), we support the Jacobi Zone for the basal Berriasian. The discussion above suggests that the Jacobi Zone is not divided into two subzones, i.e., the lower Jacobi and the upper Grandis. Frau et al. (2016a) somewhat earlier revised the existing zonal species of the lower Berriasian *Berriasella jacobi* to *Strambergella jacobi.* We disagree with this generic placement (see discussion of the subfamily Berriasselinae).

Arkadiev et al. (2018) reported on the ammonite zonation of the deposits around the J/K boundary in Crimea. The basal Berriasian belongs to the Jacobi Zone, which is subdivided into two subzones: Jacobi and Grandis. Recently, Szives and Főzy (2022) presented an account of the ammonite stratigraphy of deposits around the Jurassic–Cretaceous boundary based on the study of ammonites occurring at Hungarian localities. These latter authors conclude with the proposal of a new zonation. Their proposal in Fig. 2 suggests that the lower Berriasian sequence is topped by the Grandis Zone.

The following succession characterises the studied section, Dedina, in terms of ammonite species composition. At the beginning of the section, in its lowest part, there is a single specimen of *Hegaratella oxycostata.* The first 12 following layers contain only usually heavily corroded fragments of indeterminate whorls. Layer 13 contains heavily corroded, species-indeterminate, relatively large and very interesting specimens of the *Kilianiceras* cf. *ambiguum.* They are accompanied by other ammonite relicts, including juvenile *Phylloceras* sp. and small brachiopods. *Strambergella carpatica* was found in layer 14. In layer 18, the first unambiguously identifiable *Pseudosubplanites grandis* can be found; it occurs several times up to the highest part of the section. The same is true of *Haploceras elimatum.* A more species-rich ammonite spectrum is found in layers 30 to 37. *Pseudosubplanites subrichteri*, *Delphinella* cf. *delphinense*, *Spiticeras pseudogroteanum*, and *Haploceras leiosoma* are identified there. From layer 55 to the highest part of the section, juvenile fragments of *Bochianites* occur, partly also with fragments of poorly preserved adults. There is a single specimen of *Negreliceras mirum* in layer 59, *Pseudosubplanites* cf. *ponticus* in layer 80, and *Negreliceras* cf. *proteum* in layer 88. A rich ammonite association was found in the section of layers 95 to 99: again, *Pseudosubplanites* cf. *ponticus*, followed by *Pseudosubplanites lorioli*, *Pseudosubplanites fasciculatus*, *Malbosiceras* cf. *asper*, *Substeueroceras broyonense*, *Delphinella miravatensis*, and *Hegaratella subcalisto*, together with the species listed below, which occur in almost the entire length of the section; this is also true for the *Punctaptychus punctatus* valves. The accompanying association still includes several favourably preserved bivalves.

Based on the above ammonite association in the Dedina section, it is evident that *Pseudosubplanites grandis* and the stratigraphically insignificant *Haploceras elimatum* occur in almost the entire studied succession. There is no a single Tithonian species or a species from the underlying Jacobi Zone. The only exception is perhaps *Hegaratella oxycostata* from the tight bedrock at the very beginning of the section. Stratigraphically, it is the oldest finding and may not belong to the Grandis Subzone.

From the above chronostratigraphy, it can be concluded that the ammonite association corresponds to the Grandis Subzone, i.e., the upper part of lower Berriasian. From the point of view of

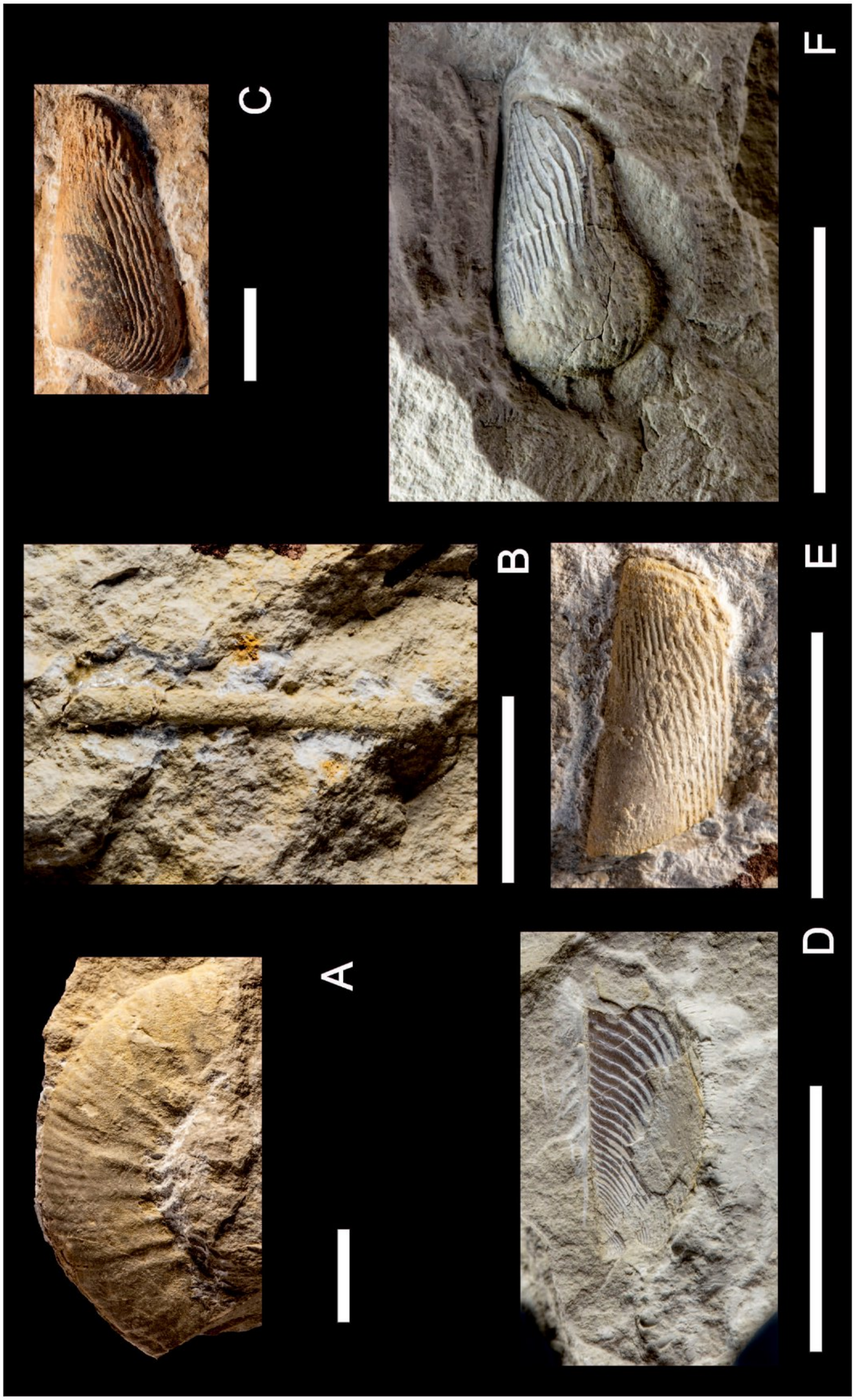


Fig. 6. **A**, *Negreliceras* cf. *proteum* (Retowski, 1893), specimen S88/2; layer 88. **B**, *Bochianites* sp. juv., specimen 55.3/1; layer 55. **C**, *Punctaptychus punctatus* (Zittel, 1868); specimen 28.8; layer 28. **D**, *Mortilletilamellaptychus submortilleti noricus* Měchová et al., 2010, specimen 99.2/6; layer 99. **E**, *Cinctpunctaptychus cinctus* (Trauth, 1935), specimen S47.1 characterised by discordant ribs at the outer end of the valve; layer 47. **F**, *Beyrichilamellaptychus beyrichi* (Oppel, 1865), specimen 99/1; layer 99. Scale bar equals: A, C 10 mm; B, 20 mm; D–F 30 mm.

the genera and species composition of ammonites, the association described here appears to be close to the ammonite association in Crimea.

7. Conclusion

According to a preliminary study of the section Dedina, it was suggested that the section includes the sediments around the J/K boundary. The continuing Dedina section is favourable for studying the lithology and magnetostratigraphy, as well as sample collection for micropalaeontology and macrofossil collection. The paper presents the results of the detailed taxonomical and stratigraphical study of the ammonite association found in the Dedina section. In brief, the section is characterised by the essentially continuous occurrence of *Pseudosubplanites grandis*. From this point of view, the currently studied section can be considered belongs to the ammonite subzone of the upper part of the lower Berriasian, e.g., the Grandis Subzone, which is interpreted, as defined by Arkadiev and Bogdanova (2012), Arkadiev et al. (2018) and Szives and Főzy (2022). The J/K boundary is not evident from the collected ammonite association. The following detailed integrated studies will be dedicated to magnetostratigraphy, studies of micropalaeontology, etc.

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