

Revision of species of the ammonite genus *Pseudosubplanites* from the Berriasian of the Crimean mountains

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Abstract

Several species of the ammonite genus *Pseudosubplanites* in Berriasian deposits of the Crimean mountains have been established following revision. These are *P. ponticus* (Retowski), *P. grandis* (Mazenot), *P. lorioli* (Zittel), *P. subrichteri* (Retowski), *P. combesi* Le Hégarat, *P. crymensis* Bogdanova and Arkadiev sp. nov., *P. fasciculatus* Bogdanova and Arkadiev sp. nov. *Berriasella* (Hegaratella) *paramacilenta* (Mazenot) and *B. (H.) jauberti* (Mazenot) are also described. *P. euxinus* (Retowski) is considered to be a junior synonym of *P. lorioli* (Zittel). The species described allow a standard Jacobi Zone to be distinguished in the Berriasian section.

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1. Introduction

The position of the Jurassic/Cretaceous boundary in the Mediterranean region continues to be a debated topic. In France, according to solution of the Lyon-Neuchâtel symposium (1973), the lower boundary of the Berriasian was drawn at the base of the *Berriasella jacobi*-*Pseudosubplanites grandis* Zone or *P. grandis* s.l. (Colloque, 1975). This zone has been named by other palaeontologists as the *Pseudosubplanites ponticus*-*P. euxinus* Zone in Crimea (Drushchits, 1975), the Jacobi/Grandis Zone in Spain (Cordoba) (Enay and Geysant, 1975), and the Euxinus Zone in Spain (Murcia) (Wiedmann in Allemann et al., 1975). More recently, the International Workshop of the Lower Cretaceous Cephalopod Team proposed to name it the *B. jacobi*

Zone in their zonation of the Mediterranean region (Hoedemaeker and Bulot, 1990; Hoedemaeker et al., 2003).

In addition to the analogue of the Jacobi Zone in the Crimea (*Pseudosubplanites ponticus*-*P. euxinus* Zone; Drushchits, 1975), the local *Pseudosubplanites ponticus*-*Pseudosubplanites grandis* Zone has also been used (Bogdanova et al., 1981, 1984) and, more recently, the *B. jacobi*-*P. grandis* Zone (Bogdanova et al., 1999; Arkadiev, 2003a), which coincides with the name of the lower zone of the Berriasian in the Crimea proposed by Kvantaliani and Lysenko (1979). However, we are aware that the stratigraphic extent of this zone exceeds that of an average standard zone. The lower Berriasian zone can be well characterized in central (Tonas River Basin) and eastern (vicinity of Feodosiya) regions of the Crimea, where it is represented by clayey-carbonate flyschoid deposits several hundreds of metres thick. A recent investigation of the Feodosiya section on the St. Elias Cape provided us with the opportunity to

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propose a subdivision of Jacobi-Grandis Zone into Chomeracensis and Grandis subzones (Arkadiev, 2003a). However, in 2003 Arkadiev examined the deposits of this zone in the Tonas River Basin and showed that the species *Berriasella jacobi* Mazenot is present only in the lower part of the zone, and *Pseudosubplanites grandis* (Mazenot) only in the upper part. Hence, we name the lower zone of the Berriasian in the Crimea as the Jacobi Zone and divide it into a lower Jacobi Subzone and an upper Grandis Subzone. In 2002 and 2003 Arkadiev found *Oloriziceras schneidi* Tavera and *Paraulacosphinctes transitorius* (Oppel) in the Feodosiya section in beds under the Jacobi Zone. These ammonites characterize the Upper Tithonian (Arkadiev, 2004).

In the Crimea the ammonite association of the Jacobi Zone includes numerous representatives of the genus *Pseudosubplanites*. This guide-genus was recognised in Berriasian deposits of the Crimea long ago, but the species composition has remained uncertain hitherto. There have been no monographic treatments, only a brief description of *P. grandis* (Glushkov, 1997). The specimens are, as a rule, poorly preserved, and the morphology of their earlier whorls and suture lines are practically unknown. A uniform type of sculpture characterizes the adult whorls, particularly those with a body chamber, with little difference in whorl involution and thickness. All of these facts hamper their morphological interpretation and identification. We have studied

Crimean *Pseudosubplanites* at different times during the course of 20 years. Some of our specific identifications have remained the same, but sometimes they have differed. Recently we have arrived at a unified view of the scope of the species and their characteristics, which has instilled confidence that their definitions are correct.

2. Material

In this paper we describe a collection of specimens of *Pseudosubplanites* and *Berriasella* (*Hegaratella*) collected at different times by V.V. Drushchits, N.I. Lysenko, V.M. Nerodenko, T.N. Bogdanova, A.Yu. Glushkov and V.V. Arkadiev from Berriasian sections in central Crimea, in the Tonas River Basin and in the vicinity of the town of Feodosiya (Fig. 1). The collection, 13077, is housed at the CNIGR Museum (F.N. Chernyshev Central Research Geological Museum), St. Petersburg, Russia. During our work for the paper we examined Retowski's collection of ammonites from marls of the lower part of the Berriasian in the vicinity of Feodosiya, which is also housed in the museum (10916). Retowski (1893) described three new species, *Perisphinctes ponticus*, *P. subrichteri* and *P. euxinus*, which Le Hégarat (1971a) subsequently grouped into another genus *Pseudosubplanites*. The sizes of the specimens and their figures in Retowski's work are given in the paper for comparison.



Fig. 1. Location of the sections studied.

3. Systematic palaeontology

Family: Perisphinctidae Steinmann, 1890

Genus *Pseudosubplanites* Le Hégarat, 1971a

Type species. *Pseudosubplanites berriasensis* Le Hégarat, 1971a, p. 850, by original designation.

Diagnosis. Planulate shell evolute or moderately evolute. Whorl section high, rectangular-oval. Flanks wide, flattened or slightly convex, covered with thin, dense, mainly bifurcating ribs branching at one-third to two-thirds of the whorl height. Besides simple ribs (main and intercalate) there are trifurcate or polygyrate, fascicular and bidichotomous ribs (Fig. 2). Ribs characteristically thin and sharp at the umbilical margin and in most cases gradually become broader and rounder towards venter; they cross venter without interruption. Suture line (seen only on one poorly preserved specimen, 91/13077, identified as *Pseudosubplanites* sp. indet.; Fig. 3) represented by a deep lateral lobe (L) and bifid saddle V/L. Ventral lobe (V) not preserved, but appears to be very narrow.

Distinction. Differs from *Parapalasiceras* in the lack of a ventral interruption of the ribs; from *Berriasella* in having a more complicated sculpture and in the absence of ventral interruption of the ribs; and from *Delphinella* in the absence of tubercles and smoothing of the ribbing.

Species attributed. *Pseudosubplanites berriasensis* Le Hégarat, *P. combesi* Le Hégarat, *P. crymensis* Bogdanova and Arkadiev, sp. nov., *P. fasciculatus* Bogdanova and Arkadiev, sp. nov., *P. grandis* (Mazenot), *P. lorioli* (Zittel), *P. ponticus* (Retowski), *P. subrichteri* (Retowski).

Distribution. Lower Cretaceous, Berriasian.

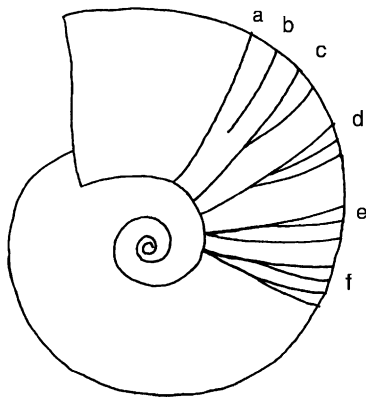


Fig. 2. Types of ribbing on conchs of *Pseudosubplanites*. a, b, simple (a, long simple, main; b, short simple, intercalate); c, d, single (c, dichotomous, bifurcated; d, trifurcated, polygyrate); e, fasciculated; f, bidichotomous.

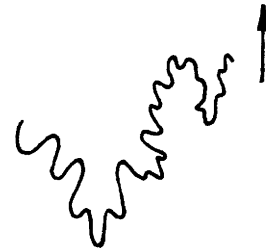


Fig. 3. Suture of *Pseudosubplanites* sp. indet., 91/13077, central Crimea, village of Krasnoselovka, Jacobi Zone; $\times 6.5$.

Remarks. Le Hégarat (1971a, b) stated that higher whorls, sloping rather than a vertical umbilical wall, and sigmoidal rather than straight ribs distinguished *Pseudosubplanites* from *Subplanites*. We, and other authors (e.g. Khimshiashvili, 1976), have pointed out the very close morphological similarity of the two genera. Our studies have shown that many specimens we have assigned to *Pseudosubplanites* have bidichotomous ribs, a feature not mentioned as characteristic for the genus when it was distinguished (Le Hégarat, 1971a, b). Nevertheless, as for other morphological features, the validity of our assignments to *Pseudosubplanites* is beyond question. The presence of the bidichotomous ribs makes the genus similar to *Delphinella*, which has such ribs. Retowski (1893) pointed out the presence of fasciculated ribs when he described *Perisphinctes euxinus*, later assigned to *Pseudosubplanites* by Le Hégarat. In this respect, *Pseudosubplanites* is similar to *Fauriella*. Hoedemaeker (pers. comm. 2003) considered, however, that the fasciculated ribs accompany shallow constrictions, whereas in *Fauriella* they are not related to constrictions. We have not observed any constrictions on our *Pseudosubplanites* shells, probably because we do not have any earliest whorls of specimens, where they may be seen.

Many specialists have discussed the systematic position of *Pseudosubplanites*. Initially Le Hégarat (1971a, b) assigned it to the family Perisphinctidae and included species in it that were previously referred to *Perisphinctes* and *Berriasella* (Kilian, 1889; Retowski, 1893; Mazenot, 1939). Khimshiashvili (1976) accepted this systematic arrangement. Hoedemaeker (1981, 1982) and Tavera (1985) considered *Pseudosubplanites*, along with *Berriasella*, *Busnardoiceras*, and *Hegaratella*, to be subgenera of *Berriasella*. Tavera (1985) assigned it to the family Berriasellidae.

At present the differences between *Pseudosubplanites* and *Berriasella* are based on external morphological features. In contrast to *Berriasella*, *Pseudosubplanites* lacks a ventral break between ribs. It is characterized by complicated ribbing: there are simple (long simple or main and short simple, or intercalate), single (dichotomous or bifurcated and trifurcated, or polygyrate), bidichotomous and fasciculated ribs (Fig. 2). *Berriasella* has only simple and bifurcated (dichotomous) ribs.

Most of researchers have followed Le Hégarat (1971a, b) in assigning *Pseudosubplanites* to the Perisphinctidae (e.g. Patruilus and Avram, 1976). Callomon (in Donovan et al., 1981) placed it in the subfamily Lithacoceratinae of the family Ataxioceratidae. According to Wright et al. (1996), *Berriasella* belongs to the subfamily Berriasellinae of the family Neocomitidae. We also believe that the incorporation of these genera in the same family is not expedient, at least at present, because of insufficient data on the morphogenesis of the suture line and the inner structures of both genera. Hoedemaeker (pers. comm. 2003) noted that the suture line of the Perisphinctidae is not different from that of the Neocomitidae, but we have our doubts because there can be ontogenetic differences as in the Aptian families Deshayesitidae and Parahoplitiidae. The suture lines of adult whorls of the shells of these families are the same, but their ontogeny is quite different.

Thus, in accordance to views of many investigators of Berriasian ammonites, we consider *Pseudosubplanites* to be within the family Perisphinctidae.

Pseudosubplanites ponticus (Retowski, 1893)

Figs. 4B, 5A, 6E, 7L–N

1893 *Perisphinctes ponticus* Retowski, p. 51, pl. 2, fig. 9.

non 1899 *Hoplites ponticus* (Retowski); Simionescu, p. 3, pl. 1, fig. 1 (= new species in manuscript of Hoedemaeker, pers. comm. 2003).

1934 *Berriasella pontica* (Retowski); Stefanov, p. 217, pl. 7, fig. 3.

1939 *Berriasella pontica* (Retowski); Mazenot, p. 131, pl. 21, fig. 9.

1960 *Berriasella pontica* (Retowski); Drushchits, p. 277, pl. 21, fig. 2.

pars 1960 *Berriasella pontica* (Retowski); Nikolov, p. 167, pl. 8, fig. 4; pl. 9, figs. 1–3 (fig. 1 = *P. subrichteri*).

1971b *Pseudosubplanites ponticus* (Retowski); Le Hégarat, p. 43, pl. 1, figs. 6, 7; pl. 38, fig. 1.

1976 *Pseudosubplanites ponticus* (Retowski); Patruilus and Avram, p. 171, pl. 7, figs. 7, 8.

1982 *Pseudosubplanites* (*Pseudosubplanites*) *ponticus*; Nikolov, p. 42, pl. 2, fig. 6; pl. 6, figs. 1, 2.

Holotype. By monotypy, the specimen 30/10916 figured by Retowski (1893, pl. 2, fig. 9) from the Berriasian of the Crimea, Feodosiya.

Material. 19 specimens (1–17/13077, 94–95/13077) from the eastern Crimea (the settlements of Nanikovo, Sultanovka and in the Feodosiya area) and in the Tonas River Basin. One specimen (30/10916) is from Retowski's collection from the eastern Crimea (Feodosiya area, St. Elias Cape).

Shape. Shell discoidal, of medium size, semievolute. Flanks almost flat, venter narrow, rounded. Whorl section high-oval (Fig. 4B). Umbilicus wide, shallow; umbilical wall gentle, low; umbilical border smooth, indistinct.

Sculpture. Flanks covered with thin, dense ribs (ca. 100 ventral ribs per whorl). Ribs straight or slightly curved, begin at the umbilical seam; on umbilical wall of the earlier whorls (D = 10 mm) they are deflected backwards, but on flanks they are straight and radial. On mature whorls (D = 35–40 mm) ribs form a double sinus: near umbilicus they are deflected backwards, in the middle of the flanks they gently curve forwards, when approaching the venter they are again deflected backwards, and near the ventral side they bend slightly forward once more. On last whorl, ribs usually almost

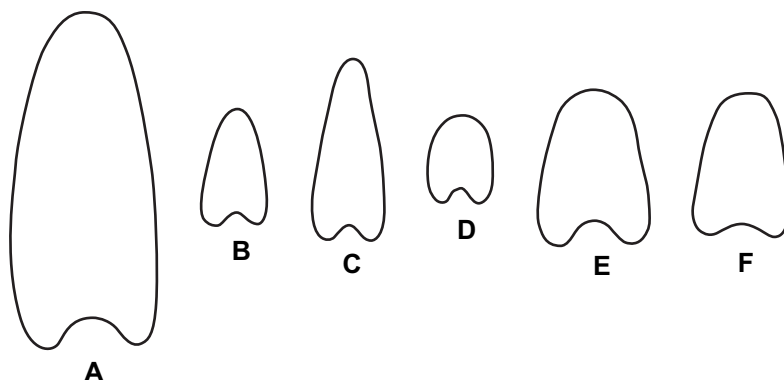


Fig. 4. Cross-sections of the shells of species of *Pseudosubplanites* and *Berriasella* (*Hegaratella*). A, *P. (P.) grandis* (Mazenot), 18/13077, eastern Crimea, Feodosiya, St. Elias Cape, Jacobi Zone. B, *P. (P.) ponticus* (Retowski), 1/13077, central Crimea, village of Blagodatnoe, Jacobi Zone. C, *P. (P.) subrichteri* (Retowski), 65/13077, eastern Crimea, village of Nanikovo, Jacobi Zone. D, *P. (P.) lorioli* (Zittel), 51/13077, central Crimea, Tonas River Basin, Jacobi Zone. E, *P. (P.) crymensis* Bogdanova and Arkadiev sp. nov., 73/13077, eastern Crimea, Karabi Yaila, Jacobi Zone. F, *B. (H.) jauberti* (Mazenot), 85/13077, central Crimea, Sary-Su River Basin, Boissieri Zone. All $\times 1$.

straight; they are sinuously bent forward only on the body chamber.

The ribbing is regular, but there are many kinds. Bifurcated ribs predominate. They start from the umbilical seam. Simple ribs begin from the seam and simple intercalated ribs begin in the middle of the flanks (3–10 per whorl). Sometimes there are intermediate bifurcating ribs (2–3 per whorl). Fasciculate or polygyrate ribs are rare on mature whorls. On some specimens there are ribs with double branching (bidichotomous) on earlier whorls. In these cases the rib first splits into two branches at the umbilical rim, then each branch again subdivides into two parts at one-third to two-thirds of the whorl height. After branching the bifurcated and bidichotomous ribs may be similar or different in appearance. The ribbing of earlier whorls is finer and denser than that of mature whorls. The interspaces on the umbilical wall (at $D = 35\text{--}40\text{ cm}$) ranges from 0.3 mm at the beginning of the whorl to 1.0 mm at the end. All the ribs cross the venter without any breaks.

Dimensions (in mm) and numbers of ribs per whorl. D, diameter of shell; H, height of whorl; W, width of shell; D_u , diameter of umbilicus.

Specimen	D	H	W	D_u	H/D	W/D	D_u/D	Number of ribs	
								Ventral	Umbilical
5/13077	29	10.5	—	9	0.36	—	0.31	80	40
4/13077	34	13.5	7.0	10.5	0.40	0.21	0.31	82	—
1/13077	37	15.5	5.0	11.5	0.42	0.14	0.31	97	50
2/13077	51	20	—	16.5	0.39	—	0.32	108	54
3/13077	65.5	24	—	20.5	0.37	—	0.31	100	50
	28.5	14.5	—	7.5	0.51	—	0.26	128	64
30/10916	97.5	35.0	16.0	36.5	0.36	0.16	0.37	115	58

Comparison. The morphologically closest species is *P. subrichteri* (Retowski) (1893, p. 60, pl. 2, fig. 8). When Luppov (in Luppov et al., 1949, p. 220) compared the two species, he noted that *P. ponticus* is characterized by the presence of trifurcating (polygyrate) ribs, which are

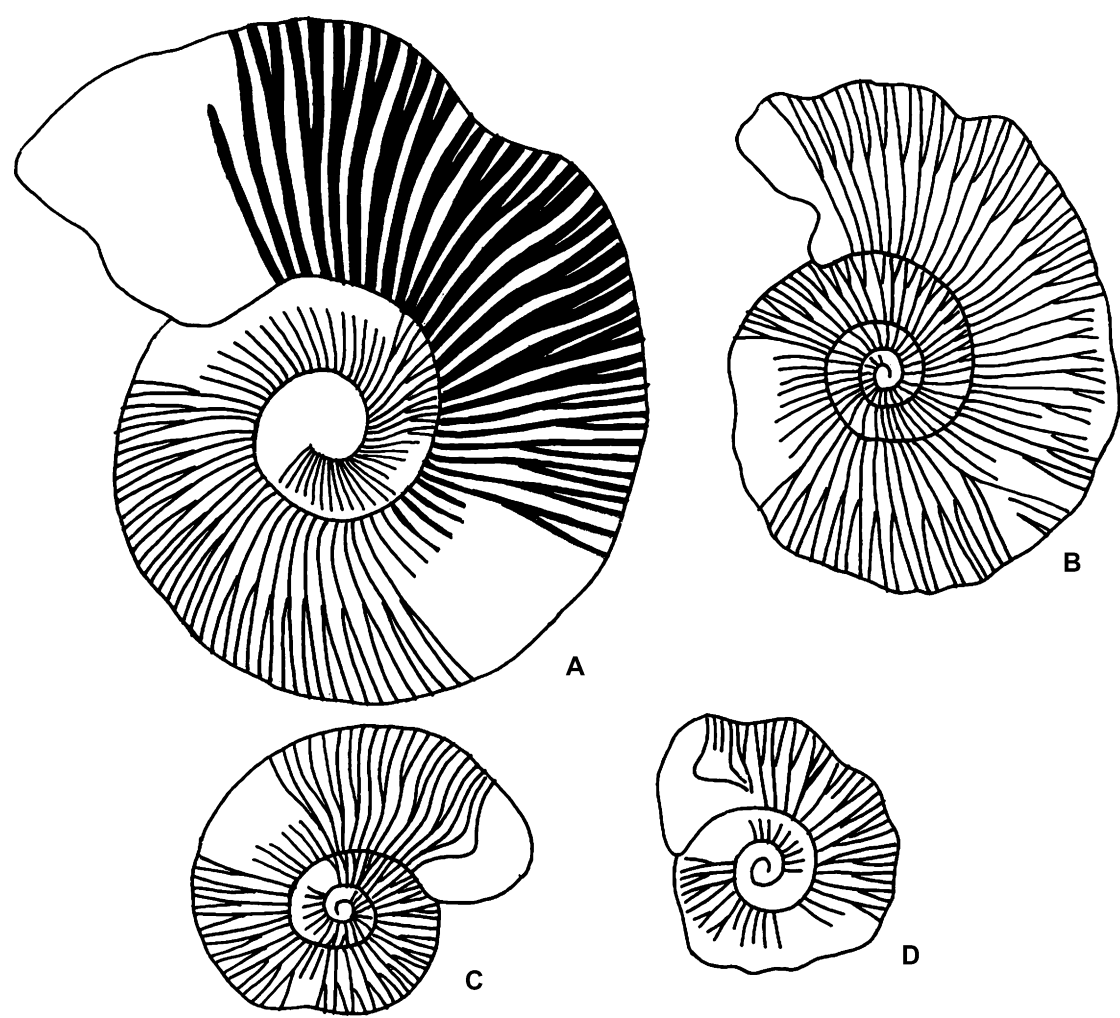


Fig. 5. Species of *Pseudosubplanites* (from Retowski, 1893). A, *P. ponticus* (Retowski, pl. 2, fig. 9). B, *P. subrichteri* (Retowski, pl. 2, fig. 8). C, *P. euxinus* (Retowski, pl. 2, fig. 5) (= *P. lorioli* herein). D, *P. euxinus* (Retowski, pl. 2, fig. 7) (= *P. fasciculatus* sp. nov. herein). All $\times 1$.

absent from *P. subrichteri*. The specimen of *P. ponticus* in Retowski's collection (1893, pl. 2, fig. 9), however, has only one trifurcating rib and this obviously cannot be considered as a basis for comparison of the two species. We think that the main characteristic is the very dense thin ribbing of early whorls of *P. ponticus* (over 100 ribs on the venter).

Geographic and stratigraphic distribution. The Crimea, southeast France, Spain, Berriasian, Jacobi Zone; northwest Caucasus, Poland, Bulgaria, Central Switzerland, Tunisia, Berriasian; Romania, transitional layers between the Tithonian and Berriasian.

Pseudosubplanites grandis (Mazenot, 1939)
Figs. 4A, 6F, 7J, K

- 1939 *Berriasella grandis* Mazenot, p. 133, pl. 22, figs. 3, 6.
1939 *Berriasella consanguinoides* Mazenot, p. 138, pl. 23, fig. 2a, b.
1967 *Berriasella grandis* Mazenot; Nikolov, p. 608, figs. 1, 2.
1968 *Berriasella grandis* Mazenot; Le Hégarat and Remane, p. 25, pl. 5, figs. 6, 7.
1971b *Pseudosubplanites grandis* (Mazenot); Le Hégarat, p. 38, pl. 2, figs. 3, 4; pl. 37, fig. 9.
1976 *Pseudosubplanites* cf. *grandis* (Mazenot); Khimshvili, p. 79, pl. 4, fig. 3.
1997 *Pseudosubplanites grandis* (Mazenot); Glushkov, p. 90, pl. 2, figs. 1, 2.
1982 *Pseudosubplanites* (*Pseudosubplanites*) *grandis* (Mazenot); Nikolov, p. 38, pl. 1, figs. 2, 3; pl. 2, fig. 5; pl. 3, figs. 1, 2; pl. 4, fig. 1.

Holotype. By original designation, the specimen figured by Mazenot (1939, pl. 22, fig. 6a,b), Berriasian, southeast France, Chevallon.

Material. Four specimens (18–19/13077, 91–92/13077) from the eastern Crimea (near the settlement of Sultanovka and in the Feodosiya area, St. Elias Cape).

Shape. Shell large, discoid, evolute. Flanks high, slightly convex, turning into the rounded venter. Umbilicus wide, shallow; umbilical wall almost vertical; umbilical border rounded. Whorl section high-oval, reaches maximum width near umbilicus (Fig. 4A).

Sculpture. Lateral sides covered with strong, mainly bifurcating ribs. Ribs of juvenile whorls fine and dense (ca. 50 umbilical ribs), begin at the umbilical seam; on the umbilical rim they slightly curve backwards. Higher on the flanks they are straight and cross the lateral side with a very slight forward curve. Ribs of the mature whorls thicker and their number decreases (ca. 40 umbilical ribs); on the flanks they are straight. Ribs branch

at about two-thirds of the whorl height, but sometimes near the middle of the flanks. Both branches are of similar strength; occasionally the anterior branch at the point of branching stands apart from the posterior one. On the last whorl (incomplete) there is only one simple rib. The ribs of the last whorl tend to thicken towards the aperture. They cross the venter perpendicular to the axis of coiling, without elevation or strengthening. On some specimens the anterior branch of the rib on one flank connects with the posterior branch on the other flank.

Dimensions (in mm)

Specimen	D	H	W	D _u	H/D	W/D	D _u /D
18/13077	122	46	21.5	50	0.38	0.18	0.41

Comparison. Our specimen differs from that depicted by Le Hégarat (1971b, pl. 2, figs. 3, 4) in the absence of polygyrate and intermediate simple ribs. It differs from other species in the dimensions and distinct thickening of ribs on the last whorl.

Geographic and stratigraphic distribution. The Crimea, southeast France, Berriasian, Jacobi Zone; the Caucasus, Berriasian, Ponticus-Grandis Zone; Bulgaria, Romania, Tunisia, Berriasian.

Pseudosubplanites lorioli (Zittel, 1868)
Figs. 4D, 5C, 6A, B, 7A–I

- 1868 *Ammonites lorioli* Zittel, p. 103, pl. 20, figs. 6–8.
non 1880 *Ammonites* (*Perisphinctes*) *lorioli* Zittel; Favre, p. 33, pl. 3, figs. 1, 2.
non 1889 *Perisphinctes lorioli* (Zittel); Kilian, p. 652, pl. 28, fig. 3.
1890 *Perisphinctes lorioli* (Zittel); Toucas, p. 598, pl. 16, fig. 2.
1893 *Perisphinctes euxinus* Retowski, p. 49, pl. 2, fig. 5 (non figs. 6, 7).
1939 *Berriasella lorioli* (Zittel); Mazenot, p. 125, pl. 19, figs. 3–7.
1939 *Berriasella richteri* (Zittel); Mazenot, p. 129, pl. 21, fig. 3.
1939 *Berriasella euxina* (Retowski); Mazenot, p. 125, pl. 20, fig. 5a,b.
1960 *Berriasella euxina* (Retowski); Drushchits, p. 277, pl. 20, fig. 4.
1960 *Berriasella lorioli* (Zittel); Nikolov, p. 166, pl. 3, fig. 4.
1967 *Berriasella lorioli* (Zittel); Dimitrova, p. 103, pl. 48, fig. 3.
1971b *Pseudosubplanites euxinus* (Retowski); Le Hégarat, p. 37, pl. 2, fig. 2; pl. 37, figs. 4–6.

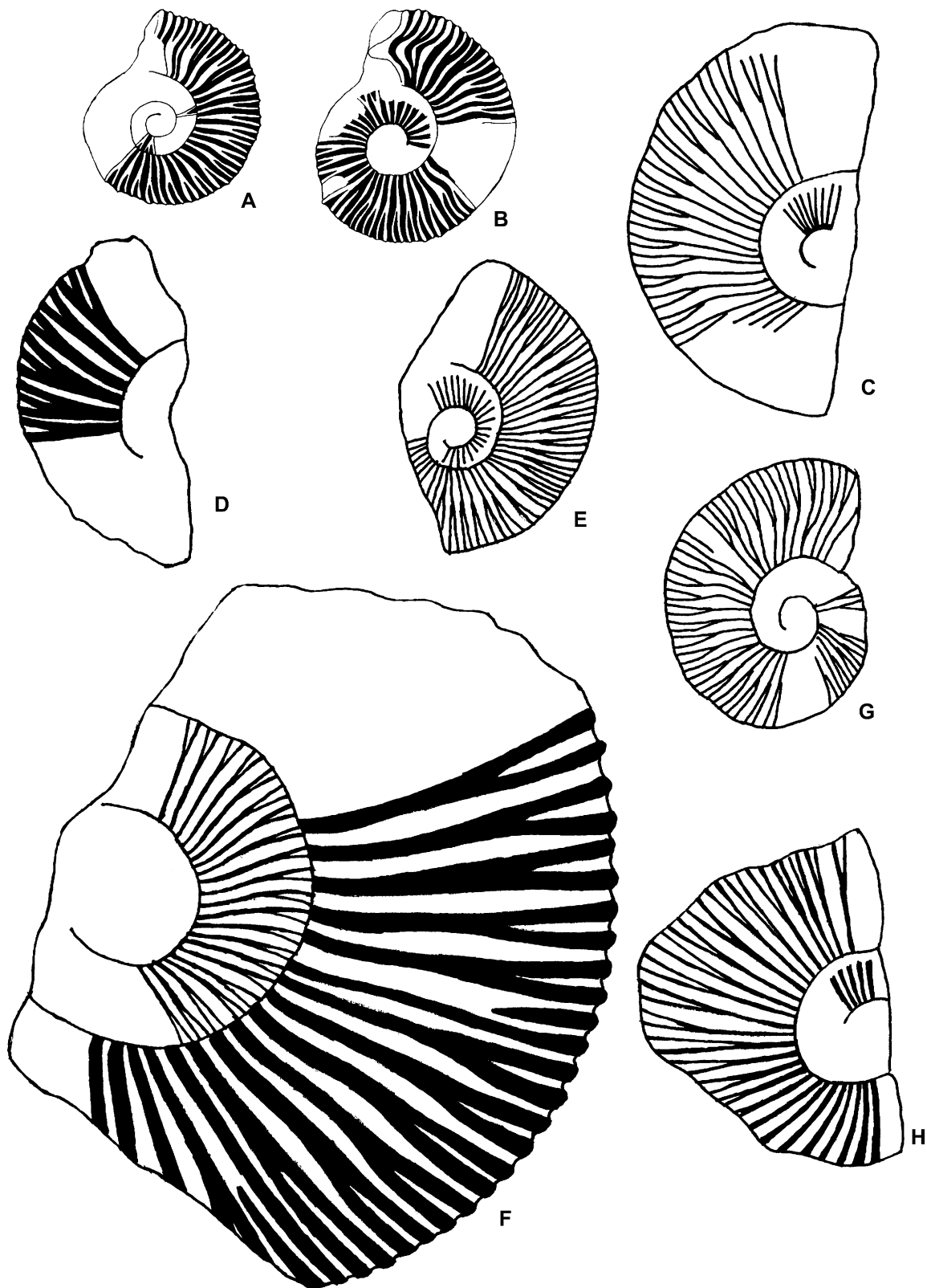


Fig. 6. Species of *Pseudosubplanites*. A, *P. (P.) lorioli* (Zittel), 28/13077, eastern Crimea, Feodosiya, St. Elias Cape, Jacobi Zone. B, *P. (P.) lorioli* (Zittel), 26/13077, central Crimea, Tonas River Basin, Jacobi Zone. C, *P. (P.) subrichteri* (Retowski), 67/13077, central Crimea, Tonas River Basin, Jacobi Zone. D, *P. (P.) combesi* Le Hégat, 97/13077, eastern Crimea, village of Sultanovka, Jacobi Zone. E, *P. (P.) ponticus* (Retowski), 9/13077, central Crimea, village of Krasnoselovka, Jacobi Zone. F, *P. (P.) grandis* (Mazenot), 18/13077, eastern Crimea, Feodosiya, St. Elias Cape, Jacobi Zone. G, *P. (P.) fasciculatus* Bogdanova and Arkadiev sp. nov., 61/13077, central Crimea, Sary-Su River Basin, Jacobi Zone. H, *P. (P.) crymensis* Bogdanova and Arkadiev sp. nov., 74/13077, eastern Crimea, Karabi Yaila, Jacobi Zone. All $\times 1$.

- 1971b *Pseudosubplanites lorioli* (Zittel); **Le Hégarat**, p. 40, pl. 1, figs. 3–5; pl. 37, figs. 3, 7, 8.
- 1976 *Pseudosubplanites lorioli* (Zittel); **Khimshiashvili**, p. 77, pl. 16, figs. 1–3.
- 1976 *Pseudosubplanites* cf. *lorioli* (Zittel); **Patrulus and Avram**, p. 171, pl. 7, figs. 5, 6.
- 1979 *Pseudosubplanites* (*Pseudosubplanites*) *lorioli* (Zittel); **Sapunov**, p. 189, pl. 40, figs. 4, 5.
- 1979 *Pseudosubplanites* (*Pseudosubplanites*) *euxinus* (Retowski); **Sapunov**, p. 188, pl. 40, fig. 3.
- 1982 *Pseudosubplanites* (*Pseudosubplanites*) *lorioli* (Zittel); **Nikolov**, p. 42, pl. 2, figs. 2, 3 (3, refigured lectotype); pl. 5, figs. 5–8.
- 1982 *Pseudosubplanites* (*Pseudosubplanites*) *euxinus* (Retowski); **Nikolov**, p. 36, pl. 2, fig. 4; pl. 5, figs. 1, 2.
- 1984 *Pseudosubplanites lorioli* (Zittel); **Bogdanova et al.**, pl. 3, figs. 2, 3.
- 1985 *Berriasella* (*Pseudosubplanites*) *lorioli* (Zittel); **Tavera**, p. 261, pl. 36, fig. 10, text-fig. 20/1.
- 1989 *Pseudosubplanites lorioli* (Zittel); **Khimshiashvili**, p. 8, pl. 5, fig. 4; pl. 6, figs. 5, 6.

Lectotype. The specimen figured by **Zittel** (1868, pl. 20, fig. 6), according to **Elias and Vašíček** (1995) from Berriasian of the Czech Republic, Konakov (formerly Koniakau). It was incorrectly designated by **Mazenot** (1939, p. 126) as the holotype.

Material. 40 specimens (20–35/13077, 37–60/13077) from the eastern Crimea (in the Feodosiya area, and near the settlements of Nanikovo and Sultanovka) and from the Tonas River Basin (near the settlement of Krasnoselovka). One specimen in Retowski's collection (26/10916) is from the eastern Crimea (Feodosiya area, St. Elias Cape).

Shape. Shell small, discoidal, with low flattened whorls, evolute to moderately evolute. Flanks weakly convex. Venter rounded, gradually passing into the flanks. Section of last whorl rounded-rectangular (Fig. 4D). Umbilicus wide, shallow, with a low, steep wall; umbilical border rounded.

Sculpture. Flanks covered with sharp, straight or slightly curved, mainly bifid ribs, which begin on umbilical wall near the umbilical seam. They bifurcate at one-half to two-thirds of the whorl height. Both branches are of equal strength; the anterior branch remains straight; the posterior branch is slightly inclined backwards. In addition to the bifurcated ribs there are simple ribs (one or two per whorl) and rarely, on juvenile whorls bidichotomous ribs. On the last whorl there may also be up to five polygyrate ribs. All ribs cross the venter in a straight line without weakening. Some of the specimens with a preserved body chamber show adoral convexity of

the ribs in the middle of the flanks. Conjunction of the ribs on the venter is symmetrical: the anterior and posterior branches of the right flank are also the anterior and posterior branches of the left flank respectively.

Dimensions (in mm)

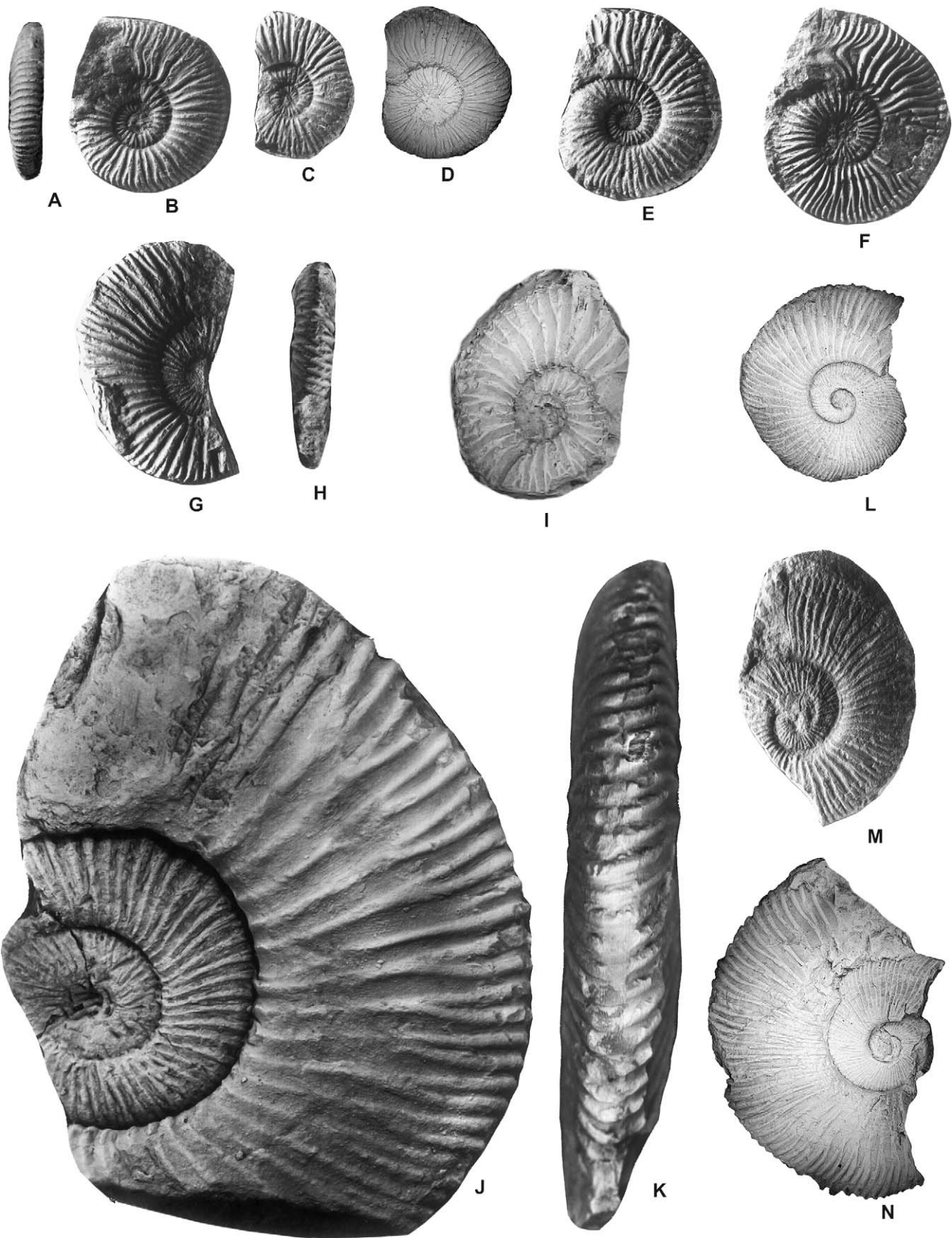
Specimen	D	H	W	D _u	H/D	W/D	D _u /D
24/13077	14.5	6.2	—	5.5	0.43	—	0.38
22/13077	25.5	9.8	—	10.0	0.38	—	0.39
23/13077	26.5	9.5	7.5	9.3	0.36	0.28	0.35
27/13077	28	10.5	—	9.0	0.38	—	0.32
20/13077	30?	12.5	—	10.5	0.42?	—	0.35?
31/13077	30.5	10.8	—	12.3	0.35	—	0.40
32/13077	30.6	13.3	—	10.5	0.43	—	0.34
28/13077	31	11.5	6.6?	12.5	0.37	0.21?	0.40
21/13077	31.5	12.5	9.8	11.0	0.40	0.31	0.35
30/13077	32.5	13.2	—	10.7	0.40	—	0.32
33/13077	34.5	12.5	10.5?	12.4	0.36	0.30?	0.36
29/13077	35?	—	—	—	—	—	—
26/13077	36.5	13.5	—	13.0	0.37	—	0.36
25/13077	37.5	15	—	13.5	0.40	—	0.36
26/10916	38.5	16.0	—	14.5	0.42	—	0.38

Characteristics of ribbing

Specimen	Diameter (mm)	Number of ribs		Number of polygyrate ribs on the last whorl
		Ventral	Umbilical	
24/13077	14.5	54	27	2
22/13077	25.5	62	31	2
23/13077	26.5	76	38	2
27/13077	28.0	—	—	1
20/13077	30?	68	34	5
31/13077	30.5	70	35	1
32/13077	30.6	84	42	—
28/13077	31.0	70	35	—
21/13077	31.5	66	32	3
30/13077	32.5	68	34	1
33/13077	34.5	72	36	1
29/13077	35?	74	37	—
26/13077	36.5	76	38	1
25/13077	37.5	84	42	3
26/10916	38.5	—	38	1

Comparison. Differs from other small species of *Pseudosubplanites* in the smaller number of ribs and in the presence of weakly flexuous ribs.

Remarks. When comparing the species *P. lorioli* and *P. euxinus*, most authors (**Le Hégarat**, 1971b; **Sapunov**, 1979; **Nikolov**, 1982) have noted that they differ only in the amount of polygyrate ribs on the last whorl, but **Retowski** (1893, p. 50) pointed out that there are transitional forms between these species. Our investigations showed that between the extreme members of the *P. lorioli* (forms free of polygyrate ribs) to *P. euxinus* (forms with 4–5 polygyrate ribs on the last whorl) group there are numerous transitional forms with 1–3



polygyrate ribs. Taking into account that other features of these species are similar, it is practically impossible to separate them; hence, it is necessary that they are integrated. *P. euxinus*, erected by Retowski (1893) is a younger synonym of *P. lorioli*, described by Zittel (1868).

Ammonites assigned to *P. lorioli* in the papers of Favre (1880, p. 33, pl. 3, figs. 1, 2) and Kilian (1889, p. 652, pl. 28, fig. 3) are characterized by large shells, contradicting Le Hégarat's conclusion (1971b, p. 41) and our observation that *P. lorioli* is a microconch of the dimorphous pair *P. lorioli*-*P. combesi*. Besides, the specimen depicted in Kilian's paper shows a distinct S-shaped curvature of the ribs.

Our examination of the specimens in Retowski's collection assigned to *Perisphinctes euxinus* revealed that all are characterized by different features. Specimen 28/10916 (Retowski, 1893, pl. 2, fig. 7) shows distinct polygyrate and fasciculated ribs. It differs from the other specimens he described (his pl. 2, figs. 5, 6) and from other species of *Pseudosubplanites* in the presence of fasciculated ribs. Specimen 108/10916, identified by Retowski as *Perisphinctes* aff. *euxinus* but not depicted in his work, shows similar ribbing. The fasciculated ribs are an important feature, which in our opinion allows us to consider that these specimens belong to a new species. Specimen 27/10916, identified as *Perisphinctes euxinus* by Retowski (1893, pl. 2, fig. 6) shows a distinct break in the ventral ribs at the beginning of the last whorl. It cannot, therefore, be assigned to *Pseudosubplanites*. Thus we include only specimen 26/10916 in Retowski's collection (1893, pl. 2, fig. 5) in the synonymy of *P. lorioli*.

Geographic and stratigraphic distribution. The Crimea, southeast France, Spain, Berriasian, Jacobi Zone; the Caucasus, Berriasian, Ponticus-Grandis Zone; Poland, Bulgaria, Czech Republic, Austria, Tunisia, Berriasian; Romania, transitional layers between the Tithonian and Berriasian.

Pseudosubplanites subrichteri (Retowski, 1893)

Figs. 4C, 5B, 6C, 8A–C

1893 *Perisphinctes subrichteri* Retowski, p. 50, pl. 2, fig. 8.

1899 *Hoplites ponticus* Retowski; Simionescu, p. 3, pl. 1, fig. 1.

non 1939 *Berriasella subrichteri* (Retowski); Mazenot, p. 130, pl. 21, fig. 10 (= *Berriasella paramacilenta*)

1960 *Berriasella subrichteri* (Retowski); Drushchits, p. 277, pl. 21, fig. 3.

pars 1982 *Pseudosubplanites (Hegaratella) subrichteri* (Retowski); Nikolov, p. 50, pl. 8, fig. 3.

Lectotype. Designated herein, specimen 29/10916, figured by Retowski (1893, pl. 2, fig. 8) from the Berriasian of the Crimea, Feodosiya.

Material. Four specimens (65–68/13077) from the eastern Crimea (the settlement of Nanikovo in the Feodosiya area) and the Tonas River Basin, and two specimens (29/10916, 109/10916) from the Feodosiya area in Retowski's collection.

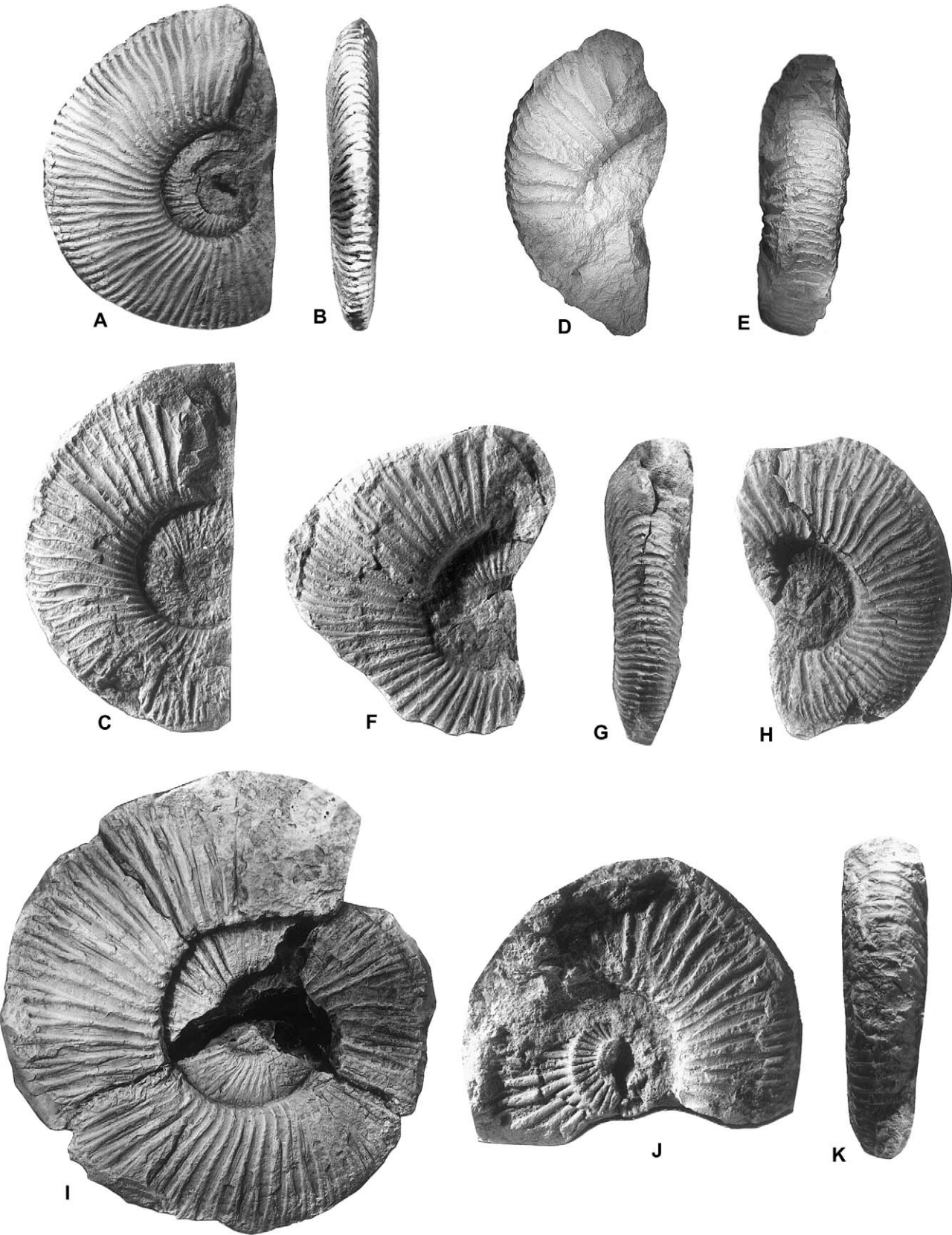
Shape. Shell discoid, strongly compressed, semi-evolute with wide, almost parallel flanks. Venter narrowly rounded. Umbilicus wide, shallow, stepped, with a steep wall and rounded umbilical rim. Cross-section of last whorl narrow, high-oval (Fig. 4C).

Sculpture. Flanks covered with fine, mainly bifurcated ribs. They begin near the umbilical seam, are slightly inclined backwards on the umbilical rim and cross the flanks with a slight forward curve. At one-half to two-thirds of the whorl height, the ribs split into two branches, the posterior branch being slightly inclined backwards. Both secondary ribs are of similar strength. Besides bifurcated ribs there are a few simple ribs (3–5 per whorl). The ribs cross the venter in a straight manner, without weakening. On some specimens the ribs connect, the anterior branch on the right flank corresponding to the posterior branch of the left flank. The density of ribbing in juvenile is similar to that in mature whorls (50–55 umbilical ribs per whorl).

Dimensions (mm) and number of ribs

Specimen	D	H	W	D _u	H/D	W/D	D _u /D	Number of ribs	
								Ventral	Umbilical
66/13077	52.5	19.2	—	19.0	0.37	—	0.36	97	50
65/13077	55.5	21.3	9.5	17.8	0.38	0.17	0.32	106	55
109/10916	57.0	22.0	9.5	19.5	0.39	0.16	0.34	96	50
								75	40
67/13077	64.0	24.5	10.0	21.5	0.38	0.16	0.34	100	52
29/10916	71.5	25.0	—	22.5	0.35	—	0.31	108	56
								77	40
								50	27

Fig. 7. A–I, *Pseudosubplanites* (*P.* *lorioli*) (Zittel). A, B, 28/13077 in ventral and side views, eastern Crimea, Feodosiya, St. Elias Cape. C, 23/13077, side view, eastern Crimea, village of Sultanovka. D, 20/13077, side view, eastern Crimea, village of Sultanovka. E, 33/13077, side view, eastern Crimea, Feodosiya, St. Elias Cape. F, 26/13077, side view, central Crimea, Tonas River Basin. G, H, 37/13077 in side and ventral views, eastern Crimea, village of Sultanovka. I, 24/13077, side view, central Crimea, village of Krasnoselovka; × 3. J, K, *Pseudosubplanites* (*P.* *grandis*) (Mazenot), 18/13077 in side and ventral views, eastern Crimea, Feodosiya, St. Elias Cape. L–N, *Pseudosubplanites* (*P.* *ponticus*) (Retowski). L, 1/13077, side view, central Crimea, village of Blagodatnoe. M, 9/13077, side view, central Crimea, Tonas River Basin. N, 3/13077, eastern Crimea. All Berriasian, Jacobi Zone and all × 1 except where indicated.



Comparison. The Crimean specimens in our collections, particularly 65/13077, are almost identical to specimens of this species depicted by Retowski (1893, pl. 2, fig. 8). It differs from closely similar *P. combesi* in having a more compressed shell and more flexuous ribs, and from *P. ponticus* in the absence of polygyrate ribs and the equal density of ribs on juvenile and mature whorls. It differs from species of *Lemencia*, first distinguished by Donze and Enay (1961), in the absence of a ventral break and polygyrate ribs.

Remarks. The specimen depicted by Mazonot (1939, pl. 21, fig. 10) has distinct ribbing that becomes lower on the venter. It must, therefore, be referred to *Berriasella paramacilentia*. The specimen described by Nikolov (1982, pl. 8, fig. 2) as *Pseudosubplanites (Hegarotella) subrichteri* cannot be satisfactorily identified because of its poor preservation but it is not this species; it was recorded from the Upper Berriasian.

Geographic and stratigraphic distribution. The Crimea, Caucasus, Bulgaria, France, Berriasian, Jacobi Zone.

Pseudosubplanites combesi Le Hégarat, 1971
Figs. 6D, 8D, E

1934 *Hoplites ponticus* Stefanov, p. 217, pl. 7, fig. 3.
1971b *Pseudosubplanites combesi* Le Hégarat, p. 36, pl. 1, fig. 2; pl. 37, fig. 1.
1982 *Pseudosubplanites (Pseudosubplanites) combesi* Le Hégarat; Nikolov, p. 38, pl. 4, fig. 2; pl. 5, figs 3, 4 (3, refigured paratype).

Holotype. By original designation, the specimen FSL 129367 figured by Le Hégarat (1971b, pl. 1, fig. 2) from the Berriasian (Grandis Zone) of southeast France, les Combes.

Material. One specimen, 97/13077, from the eastern Crimea (settlement of Sultanovka).

Shape. As far as we could observe: adult shell discoidal, evolute, rather swollen with convex flanks. Venter broad and slightly rounded. Umbilicus wide, shallow, with a steep, almost perpendicular umbilical wall.

Sculpture. Flanks adorned with mainly bifurcating, almost straight ribs. Branching of ribs is approximately at the middle of the flanks or a little higher. Both

branches are equal in length; posterior branch slightly inclined backwards. In addition to the bifurcated ribs there are four polygyrate ribs on the preserved half-whorl of the specimen. All ribs cross the venter in a straight line without becoming weak.

Dimensions (in mm)

Specimen	D	H	W	D _u	H/D	W/D	D _u /D
97/13077	55?	19	16	—	0.35?	0.29?	—

Comparison. Among the microconchs, *Pseudosubplanites lorioli* is morphologically closest to *P. combesi*, which differs in size and in having thicker whorls and straight ribs.

Geographic and stratigraphic distribution. The Crimea, southeast France, Bulgaria, Berriasian, Jacobi Zone.

Pseudosubplanites fasciculatus Bogdanova and Arkadiev, sp. nov.
Figs. 5D, 6G, 9A–E

1893 *Perisphinctes euxinus* Retowski, p. 49, pl. 2, fig. 7.

Derivation of name. Latin, *fasciculatus*, bundle-like.

Holotype. Specimen 61/13077, CNIGR Museum, St. Petersburg, Russia, from the Berriasian, Jacobi Zone, of central Crimea, Sary-Su River Basin.

Material. Six specimens (36/13077, 61–64/13077, 90/13077) from eastern Crimea (the settlement of Sultanovka in the Feodosiya area) and from the Tonas River Basin (the settlement of Krasnoselovka); two specimens (28/10916, 108/10916) from the eastern Crimea (Feodosiya, St. Elias Cape) in Retowski's (1893) collection.

Shape. Shell discoidal, semievolute with high, slightly convex flanks and rounded venter. Cross-section of last whorl moderately compressed, high-oval. Umbilicus wide, shallow, with an abrupt wall.

Sculpture. Flanks covered with fine, slightly curved, mainly bifurcating ribs. Ribs begin on the umbilical wall near the umbilical seam. On the juvenile whorls they are almost straight; on the last whorl they begin to curve slightly towards the aperture in the middle of the flanks. The curvature of the ribs is greatest near the aperture.

Fig. 8. A–C, *Pseudosubplanites (P.) subrichteri* (Retowski). A, B, 65/13077 in side and ventral views, eastern Crimea, village of Nanikovo. C, 67/13077, side view, central Crimea, Tonas River Basin. D, E, *Pseudosubplanites (P.) combesi* Le Hégarat, 97/13077 in side and ventral views, eastern Crimea, village of Sultanovka. F–K, *Pseudosubplanites (P.) crymensis* Bogdanova and Arkadiev, sp. nov. F, 74/13077, side view, eastern Crimea, Karabi Yaila. G, H, 70/13077, holotype in ventral and side views, eastern Crimea, Feodosiya, St. Elias Cape. I, 69/13077, side view, eastern Crimea, Feodosiya, St. Elias Cape. J, K, 73/13077 in side and ventral views, eastern Crimea, Karabi Yaila. All Berriasian, Jacobi Zone, and $\times 1$.

They bifurcate at one-third to two-thirds of the whorl height; the height of the bifurcation point of two neighbouring ribs can differ. Apart from the bifurcated ribs there are a few (3–5 per whorl) simple, bidichotomous and fasciculated (2–3 per whorl) ribs. According to Hoedemaeker (pers. comm. 2003) these fasciculated ribs seem to occur only alongside shallow constrictions. They divide into two branches at the umbilical rim. The anterior branch curves forward near the venter. The posterior branch again subdivides into two branches approximately in the middle of the flanks or slightly higher. All branches are of similar strength. Rib density is the same on juvenile and mature whorls.

Dimensions (in mm) and number of ribs

Specimen	D	H	W	D _u	H/D	W/D	D _u /D	Number of ribs	
								Ventral	Umbilical
28/10916	34.0	11.5	—	13.0	0.34	—	0.38	—	38
62/13077	44.5	17.0	10.0	15.5	0.38	0.22	0.35	102	55
61/13077	45.0	16.2	9.8	16.0	0.36	0.22	0.36	87	45
108/13077	81.5	29.5	21?	31.0	0.36	0.26	0.38	101	50

Comparison. *P. fasciculatus* differs from the other species of *Pseudosubplanites* in the presence of frequent fasciculated ribs. In this respect, specimen 28/10916, described by Retowski as *P. euxinus* (Retowski, 1893, pl. 2, fig. 7), differs markedly from the other specimens of the species; hence we distinguish it as a new species. We observed two fasciculated ribs on the last whorl of the specimen. The species is closest in morphology to representatives of *Fauriella* in having fasciculated ribs, but *Fauriella* has many fasciculate ribs that are not related to constrictions. In addition, it has no features that are typical of *Fauriella*, such as umbilical tubercles and an attenuating sculpture on the body chamber.

Geographic and stratigraphic distribution. The Crimea, Berriasian, Jacobi Zone.

Pseudosubplanites crymensis Bogdanova and Arkadiev, sp. nov.

Figs. 4E, 6H, 8F–K

Derivation of name. Latin, after Crimea.

Holotype. Specimen 70/13077, CNIGR Museum, St. Petersburg, Russia, from the Berriasian, Jacobi Zone, eastern Crimea, Feodosiya, St. Elias Cape.

Material. 12 specimens (69–79/13077, 93/13077) from the eastern Crimea (in the Feodosiya area, St. Elias Cape and the settlement of Sultanovka) and from Karabi Yaila.

Shape. Mature shell discoidal, evolute, with almost flat or slightly convex flanks. Ventral side broad, flattened or slightly rounded. Cross-section of last whorl oval-rectangular, high, elongated (Fig. 3E). Umbilicus wide, shallow, with a steep, almost vertical umbilical wall and rounded umbilical border.

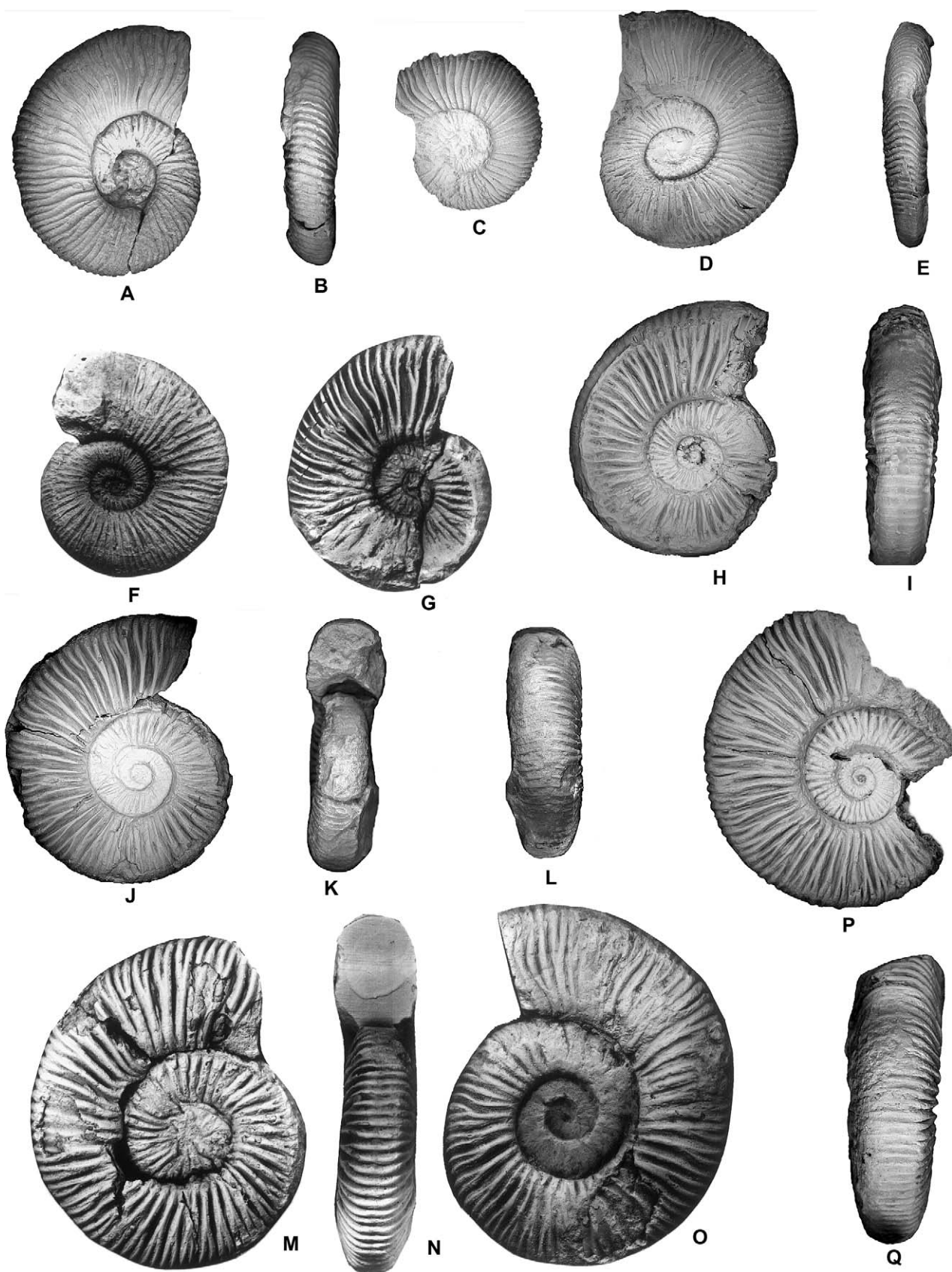
Sculpture. Flanks covered with dense (up to 100 ventral ribs per a whorl), straight or slightly flexuous, mainly bifurcated ribs. Most ribs originate approximately in the middle of the umbilical wall, curve slightly backwards at the umbilical rim, and are straight or curve slightly forwards on the flanks. The secondary ribs are of equal strength; the posterior branch is slightly inclined backwards. Apart from bifurcating ribs there are a few simple ribs (1–2 per whorl), which appear on the umbilical wall or higher. They occur alongside shallow constrictions where the direction of ribbing abruptly changes a little. All ribs cross the venter in a straight manner, without weakening. The junction of the ribs is symmetrical or zigzag, i.e. the posterior branches of the ribs on one flank may correspond to anterior branches on the other flank.

The sculpture of juvenile whorls can be determined only from specimen 69/13077, of which there is an imprint of the lateral side ca. 20 mm in diameter. This imprint shows fine ribbing, which is denser than on the mature whorls and mainly consists of bifurcating ribs.

Dimensions (in mm) and number of ribs

Specimen	D	H	W	D _u	H/D	W/D	D _u /D	Number of ribs	
								Ventral	Umbilical
70/13077	57	21	13.5	18.5	0.37	0.24	0.32	102	52
71/13077	62	23.5	14	23.5	0.38	0.23	0.38	97	50
69/13077	83	31	—	32.5	0.37	—	0.39	98	50

Fig. 9. A–E, *Pseudosubplanites* (*P.*) *fasciculatus* Bogdanova and Arkadiev sp. nov. A, B, 61/13077, holotype in side and ventral views, eastern Crimea, Feodosiya, St. Elias Cape. C, 90/13077, side view, eastern Crimea, village of Sultanovka. D, E, 62/13077 in side and ventral views, eastern Crimea, village of Sultanovka. F, *Berriasella* (*Hegaratella*) *paramacilenta* (Mazenot), 80/13077, side view, central Crimea, Sary-Su River Basin. G–Q, *Berriasella* (*Hegaratella*) *jauberti* (Mazenot). G, 89/13077, side view, central Crimea, Sary-Su River Basin. H, I, 85/13077 in side and ventral views, central Crimea, Sary-Su River Basin. J–L, 86/13077 in side, oral and ventral views, central Crimea, Sary-Su River Basin. M, 88/13077, side view, central Crimea, Sary-Su River Basin. N, O, 84/13077 in oral and side views, central Crimea, village of Balki. P, Q, 87/13077 in side and ventral views, central Crimea, Sary-Su River Basin. A–F, Berriasian, Jacobi Zone; G–Q, Berriasian, Boissieri Zone. All $\times 1$.



Comparison. *P. crymensis* differs from *P. combesi* in the lack of polygyrate ribs. Among microconchs, *P. lorioli* is closest to *P. crymensis*, which differs from *P. lorioli* in having a larger diameter, in being thicker, and in lacking bidichotomous ribs.

Geographic and stratigraphic distribution. The Crimea, Berriasian, Jacobi Zone.

Genus *Berriasella* Uhlig, 1905

Subgenus *Hegaratella* Nikolov and Sapunov, 1977

Type species. By original designation, *Berriasella paramacilenta* Mazenot, 1939, from southeast France, Berriasian.

Comparison. Differs from the closely related *Berriasella* (*Berriasella*) in the presence of an indistinct furrow or lowering of ribs on the venter.

Remarks. Nikolov and Sapunov (1977) introduced the subgenus *Hegaratella* within *Pseudosubplanites*. According to them, this differs from *Pseudosubplanites* (*Pseudosubplanites*) in lacking polygyrate ribs and in having an indistinct ventral groove. However, most palaeontologists now consider *Hegaratella* to be a subgenus *Berriasella*. Hoedemaeker has stated (pers. comm. 2003) that *Pseudosubplanites* never shows a mid-ventral notch or indentation.

Nikolov (1982) described four species, *kaffae*, *jauberti*, *paramacilenta* and *subrichteri*, within *Pseudosubplanites* (*Hegaratella*). Our study of specimens in Retowski's (1893) collection showed that the *subrichteri* has no furrow on the venter; therefore, it should be assigned to *Pseudosubplanites*. Most authors (Mazenot, 1939; Le Hégarat, 1971b; Patruilus and Avram, 1976; Hoedemaeker, 1982; Tavera, 1985) consider *paramacilenta* and *jauberti* to belong to the subgenus *Hegaratella*, but not to *Berriasella*. However, specimens of “*B.*” *jauberti* and “*B.*” *paramacilenta* with a distinct ventral break on inner whorls typical of *Berriasella* are not depicted in any publications. We have noted that some specimens of *paramacilenta* in Mazenot's monograph (1939; pl. 20, figs. 2b, 4b; pl. 21, figs. 7b, 10a) have lower ribs in the middle of the venter. Furthermore, Arkadiev's study of the morphogenesis of *jauberti* showed that its inner whorls probably have no real ventral break, only a wide, shallow hollow (Arkadiev, 2003b, p. 92). Hoedemaeker has written (pers. comm. 2003): “In my view the presence of a mid-ventral notch or indentation in many specimens of *paramacilenta*, regardless of whether it is visible or not, is a strong argument to separate this species from *Pseudosubplanites*, which never shows a notch or indentation, not even an indistinct one.”

There is no example of the species *kaffae* in our collection.

The description of *Berriasella* (*Hegaratella*) *paramacilenta* and redescription of *B. (H.) jauberti* below are given in order to provide some information on the Crimean specimens of these species.

Berriasella (*Hegaratella*) *paramacilenta* (Mazenot, 1939)
Fig. 9F

- 1939 *Berriasella subrichteri* (Retowski) Mazenot, p. 130, pl. 21, fig. 10.
pars 1939 *Berriasella paramacilenta* Mazenot, p. 127, pl. 20, figs. 1, 2, 4 (pl. 20, fig. 3 = *Berriasella evoluta* Le Hégarat; pl. 21, fig. 1 = *Berriasella evoluta* Le Hégarat).
1968 *Berriasella paramacilenta* Mazenot; Le Hégarat and Remane, pl. 4, fig. 5.
1971b *Berriasella* (*Berriasella*) *paramacilenta* Mazenot; Le Hégarat, p. 60, pl. 6, fig. 8; pl. 38, fig. 8; pl. 39, fig. 1.
1976 *Berriasella* (*Berriasella*?) *paramacilenta* Mazenot; Patruilus and Avram, p. 175, pl. 6, fig. 5.
pars 1982 *Pseudosubplanites* (*Hegaratella*) *paramacilentus* (Mazenot); Nikolov, p. 44, pl. 7, figs. 1–3; pl. 8, fig. 9.
1985 *Berriasella* (*Hegaratella*) *paramacilenta* Mazenot; Tavera, p. 259, pl. 36, figs. 3–9, text-fig. 20/H.

Holotype. By original designation, the specimen figured by Mazenot (1939, pl. 20, fig. 1) from the Berriasian of southeast France, Noyarey.

Material. Five specimens (80–83/13077, 96/13077) from eastern (Feodosiya area) and central (Sary-Su River Basin) Crimea.

Shape. Shell discoid, moderately evolute. Flanks slightly convex. Venter broad and flattened. Cross-section of last whorl oval-rectangular. Umbilicus wide, shallow, with a steep wall.

Sculpture. Flanks covered with fine, dense, mainly bifurcating ribs (80–100 ventral ribs per whorl) starting on the umbilical wall. Apart from the bifid ribs, there are simple ribs (2–3 per whorl). Ribs straight or weakly flexuous; at one-half to two-thirds of the flanks they divide into two branches of equal strength. On early whorls the point of branching is situated closer to the ventral side than in later whorls. The ribs cross the venter in a straight manner, without interruption (at least on the whorls of the specimens examined), but they are slightly weakened in the middle, becoming wide, shallow and lower.

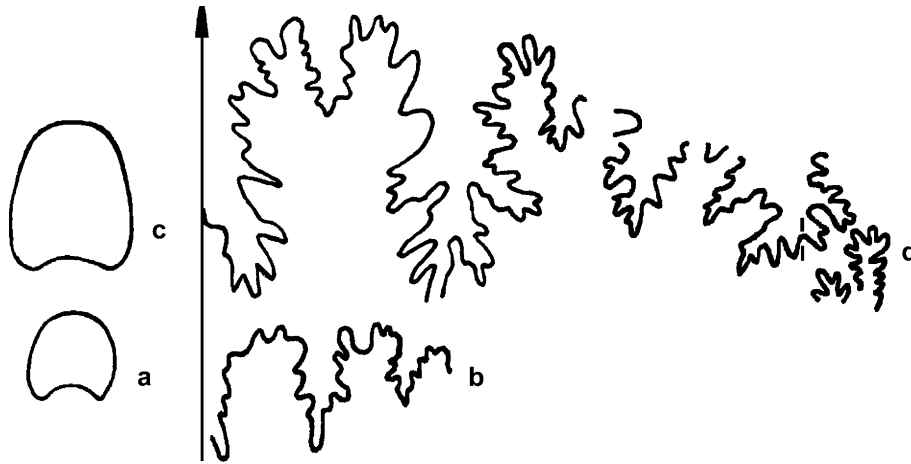


Fig. 11. Cross-sections and suture lines of the shell of *Berriasella (Hegaratella) jauberti* (Mazenot); specimen 87/13077, central Crimea, Sary-Su River Basin, Berriasian, Occitanica Zone. a, b, H = 5.8 mm and W = 5.0 mm (a, $\times 2$; b, $\times 5$); c, d, H = 18.4 mm and W = 16.0 mm (c, $\times 1$; d, $\times 3.3$).

Suture line. This is strongly dissected, with a deep, narrow, two-branched ventral lobe (Fig. 11). The lateral lobe is the same depth. The umbilical lobes, which are half as long as the lateral lobe, gradually decrease in depth in the direction of the suture where they form several denticles. The tops of the main saddles are deeply dissected. The dorsal lobe is narrow and deep with strongly notched walls.

The inner structure has been examined in one specimen (86/13077), which was polished in the median plane. The protoconch is spherical, large ($D_1 = D_2 = 0.5$ mm). The primary varix is well expressed at the end of the first whorl. The angle of the primary varix is ca. 300° . The siphon on the first whorl is apparently central, by the end of the second whorl (beginning of the third whorl) it becomes ventral. The phragmocone has six whorls. The body chamber is not preserved.

Comparison. Differs from *B. (Hegaratella) paramacilentia* in its coarser and less dense ribbing. The most similar species is *B. (Hegaratella) picteti* (Jacob). *B. (H.) jauberti* differs from it in being larger and in having more dense ribbing. Le Hégarat (1971b, p. 80) considered that they were extreme forms of the same species.

Remarks. Le Hégarat (1971a) distinguished the subgenus *Picteticeras* within the genus *Berriasella*, and assigned the following species to it: *B. (P.) chomeracensis* (Toucas), *B. (P.) evoluta* (Le Hégarat), *B. (P.) jauberti* (Mazenot), *B. (P.) moesica* (Nikolov and Mandov), *B. (P.) oxycostata* (Jacob) and *B. (P.) picteti* (Jacob). Later he (Le Hégarat, 1971b) provided descriptions and photographs of these species and distinguished several others. Judging from the photographs and figures in his monograph, species both with a pronounced ventral furrow and without it as well as species with fascicular ribs were assigned to the subgenus *Picteticeras*. There

are fasciculated ribs on the specimen of *B. (P.) jauberti* figured by Mazenot (1939, pl. 21, fig. 6, holotype) and refigured by Le Hégarat (1971b, pl. 8, fig. 9).

Nikolov (1982) supported the erection of the subgenus *Picteticeras* and described several new species, but assigned the species *jauberti* to *Pseudosubplanites (Hegaratella)*. Hoedemaeker (1982, p. 68, point 2), Tavera (1985) and Wright et al. (1996, p. 50) considered *Picteticeras* to be a synonym of *Berriasella (Berriasella)*. We partially agree with these authors. Some of the species with a distinct ventral furrow assigned by Le Hégarat and Nikolov to *Picteticeras* are apparently true *Berriasella*. We assign *jauberti* to *Berriasella (Hegaratella)* because it lacks a pronounced ventral furrow and develops fasciculated ribs only alongside constrictions, which are not diagnostic.

The specimen described by Dimitrova (1967, p. 102, pl. 48, fig. 5) as *Berriasella paramacilentia* shows very coarse distal ribbing (38 ventral ribs at $D = 43$ mm) and should be assigned to *Berriasella (Hegaratella) jauberti*.

Geographic and stratigraphic distribution. The Crimea, Bulgaria, France, Berriasian, Boissieri Zone.

4. Conclusion

The species of *Pseudosubplanites* described allow the standard Jacobi Zone to be distinguished with confidence in the Berriasian of mountainous Crimea and allow a correlation with the same zone in southeast France and Spain (Le Hégarat, 1971a, b; Allemann et al., 1975; Tavera, 1985; Hoedemaeker and Bulot, 1990; Hoedemaeker and Company, 1993). The presence of the subzonal index species *Pseudosubplanites grandis* (Mazenot) has been confirmed by our sampling in the Berriasian section in various parts of the Crimea.

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