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Ammonites of Tethyan Origin from the Ryazanian of the Russian Platform: Genus *Subalpinites* Mazenot

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Abstract—The ammonite genus Subalpinites is known from the Berriasian of southern and central Europe, North Africa, Mangyshlak, and Ryazanian Stage of Central Russia. New species are described: *S. gruendeli* sp. nov., *S. faurieformis* sp. nov., *S. remaneiformis* sp. nov. These species and also *S. krischtafowitschi* Mitta characterize the lower subzone of the *Riasanites rjasanensis* Zone in the Moscow Region. The upper subzone of this zone in the Ryazan Region contained members of *Subalpinites* identified in open nomenclature.

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INTRODUCTION

The Russian Platform, especially its central part, is the most promising region to solve the problem of the Boreal-Tethyan correlation of the boundary Jurassic–Cretaceous beds. The basal Cretaceous beds in this region contain a mixed Boreal-Tethyan ammonite assemblage, in a narrow stratigraphic interval of the *Riasanites rjasanensis* Zone of the Ryazanian Stage (Central Russian equivalent of the Berriasian of the standard scale). In the previous publication (Mitta, 2008), I revised the genus *Riasanites*. The study of ammonites of Tethyan origin in the Ryazanian Stage is in progress, and in this paper I discuss the ammonite genus *Subalpinites*.

The genus *Subalpinites* was first described from the Tithonian–Berriasian of southeastern France (Mazenot, 1939), and representatives of the genus were subsequently described from other countries of the Sub-Mediterranean paleogeographic province, Algeria (Benest et al., 1977) and Bulgaria (Sapunov, 1979; Nikolov, 1982). The stratigraphic distribution of the genus has usually been given as the *jacobi* Zone of the Upper Tithonian to the *paramimounum* Subzone of the *boissieri* Zone (Berriasian), inclusive. At present the *jacobi* Zone (including the *jacobi* Subzone and *grandis* Subzone) is uniformly accepted as the basal zone of the Berriasian. Hence, the stratigraphic distribution of *Subalpinites* is restricted to the Berriasian Stage. However, representatives of the genus are known only from the lower Subzone of the *jacobi* Zone, Middle Subzone of the *occitanica* Zone and lower Subzone of the *boissieri* Zone (Le Hégarat, 1973).

Khimshiashvili (1976, p. 134, pl. 7, figs. 4, 5) described two ammonites from the "Berriasian basal calcareous sandstone" in the basin of the Belaya River, which he identified as *Subalpinites fauriensis* Mazenot. However, these specimens are poorly preserved and therefore can only be identified as *Subalpinites* ? sp., and the presence of *Subalpinites* in the Northern Caucasus is not confirmed. In subsequent summaries on ammonites and biostratigraphy of the Berriasian in this region (Sei and Kalacheva, 1997, 1999; Kolpenskaya et al., 2002), *Subalpinites* was not mentioned.

Papers on the Berriasian of the Crimea, which some workers have also considered promising for Boreal-Tethyan correlation, do not list *Subalpinites*.

The discovery of the *Subalpinites* fauna in Mangyshlak by Luppov et al. (1979) was totally unexpected. The monograph on the Berriasian in this region (Luppov et al., 1988) contains descriptions of three species of *Subalpinites*, recorded from the basal Berriasian zone of Mangyshlak, "*Neocosmoceras* Regional Zone and *Septaliphoria semenovi* Regional Zone".

Until recently no *Subalpinites* were recorded from the Russian Platform, with the possible exception of two ammonites figured from the basin of the Oka River a River, a region some workers also consider promising for Boreal-Tethyan correlations, in the classical work on the Ryazanian Stage (Bogoslovsky, 1896). The shape of the cross-section and, partly, the ornamentation suggest that these may belong to *Subalpinites*. These specimens are from the "Lower and Middle parts of the Ryazanian Horizon" from a section near the village of Shatrishchi on the Oka River, and are identified by Bogoslovsky (1896, pl. V, fig. 8; pl. VI, fig. 6) as *Hoplites* sp. indet. B and *Hoplites* sp. indet. E. However, the poor state of preservation of these ammonites, which are represented by small fragments does not allow positive identification.

Mitta (2002) described the first occurrence of *Subalpinites* from the Russian Platform, but only tentatively identified the generic affinity of *S. krischtafowitschi* Mitta. In addition, insufficient material prevented correct identification of microconchs of this species. Having examined Berriasian ammonite collections from southeastern France housed in the Université-Claude Bernard (Lyon) and Université Pierre et Marie Curie (Paris, Sorbonne collections) I was able to confirm that the generic assignment was correct. During subsequent fieldwork in the Moscow and Ryazan regions, I collected additional material of ammonites of the Ryazanian Stage including the genus under discussion.

Macroconchs of *Subalpinites krischtafowitschi* were described (Mitta, 2002, p. 31, pl. III, figs. 1–3) from the lower part of the *Riasanites rjasanensis* in the quarry no. 10 of the Lopatinsky phosphorite mine in the Voskresensk District of the Moscow Region (for a description of the section see Mitta, 2005). This taxon has a shell with a subtrapezoid cross-section, with developed umbilical nodes and indistinct lateral nodes. At the same time I suggested that ammonites of the "*Euthymiceras euthymi* (Pictet) group", found together with *Subalpinites* could be microconchs of the new species. Later I examined a small collection of R.R. Gabdullin (Moscow State University) from the same quarry, from the same beds (*rjasanensis* Subzone, *Riasanites rjasanensis* Faunal Horizon according to Mitta and Bogomolov, 2008). In addition to *Riasanites rjasanensis* (Nikitin) and *Pseudocraspedites bogomolovi* Mitta, commonly found in this locality, the collection contained one ammonite (Pl. IV, fig. 5), which has ornamentation similar to that of *Subalpinites krischtafowitschi*, but with a wider umbilicus and small shell diameter. This *Subalpinites* is probably a microconch of *S. krischtafowitschi.*

Later, fieldwork was continued in another quarry of the Lopatinsky Mine, no. 12-2, several km southwest of the aforementioned quarry. This quarry contains a section very similar in composition and lithology, but different in the composition of the ammonite assemblage of the *rjasanensis* Zone (Mitta, 2007a), referred to the *Riasanites swistowianus* Faunal Horizon. In addition to a few specimens of *S. krischtafowitschi*, which are, as usual, poorly preserved (Pl. 4, fig. 6), we also found other species of *Subalpinites*, differing in shape and ornamentation. One species (Fig. 1; pl. 4, figs. 1–4) resembles *S. fauriensis* Mazenot in early stages, and taking into account that only the umbilical row of nodes was developed, this species may be ancestral to *S. krischtafowitschi.* Another species (Fig. 2, 3), phragmocones of which resemble those of *S. remanei* Le Hégarat, in that at the adult stages they have well developed umbilical and lateral rows of nodes. At the same time, the Russian specimens are clearly different from the abovementioned French species in the more sparsely spaced ribs at the end of the phragmocone and on the body chamber. This character is also typical of the species *S. gruendeli* sp. nov. from Central Russia, which is distinguished by extremely weakly developed (or completely absent) nodes. In addition, unlike other *Subalpinites* from this locality, which usually retain the nacreous layer, specimens of the latter species are almost always represented by black phosphorite molds found in the lower, condensed layers of the *rjasanensis* Zone. The morphogenesis of ornamentation of this species is similar to that of species from the *Pseudosubplanites grandis* (Mazenot) group and taking into account the state of preservation, is likely to represent the earliest *Subalpinites* of Central Russia.

Le Hégarat (1973) suggested that *Subalpinites* evolved from an as yet undiscovered Late Tithonian (*transitorius* Zone) ancestor, common for that genus and *Dalmasiceras*. In my opinion it is possible that *Subalpinites* could have evolved from *Pseudosubplanites*. At the same time it is clear that *Subalpinites* is similar to *Malbosiceras* and *Mazenoticeras*, and other representatives of the Neocomitidae. It is evident that the evolution of *Subalpinites* from Central Russia proceeded separately from the ancestral taxa of Mediterranean origin, although the inherited program of their evolution was very similar. The distribution in the Sub-Mediterranean and Central Russian basins of similar, although not identical, species indicates that these seas were connected for a short timeand were subsequently separated for a longer period.

New species are not well suited for biostratigraphic correlations before they are discovered in other regions. However, the relatively high taxonomic diversity of *Subalpinites* in the Russian Platform and Mangyshlak, while there is no evidence of their presence in the Crimea or the Northern Caucasus, supports the hypothesis of a direct connection between the Sub-Mediterranean, Central Russian, and Mangyshlak marine basins at the beginning of the Berriasian (Ryazanian) (Mitta, 2007b).

Below is a redescription of the genus and descriptions of three new species.

SYSTEMATIC PALEONTOLOGY

Family Neocomitidae Salfeld, 1921

Genus *Subalpinites* Mazenot, 1939

Subalpinites: Mazenot, 1939, p. 224; Le Hégarat, 1973, p. 221; Sapunov, 1979, p. 186; Nikolov, 1982, p. 1982.

Type species. *Subalpinites fauriensis* Mazenot, 1939; Southeastern France, section near the village of La Faurie; Berriasian, unrecognized zone.

Diagnosis. Genus dimorphic. Dimorphic pairs recognized within species. Phragmocone of macroconchs up to 140 mm in diameter; adult shells with body chamber apparently exceeding 180 mm in diameter. Microconchs half the size and with more evolute shell. Shell compressed, with suboval cross-section and flattened venter in early whorls. Umbilicus wide or moderately wide. Complete length of body chamber and shape of aperture unknown. Ornamentation consisting of curved mainly bipartite, less commonly sim-

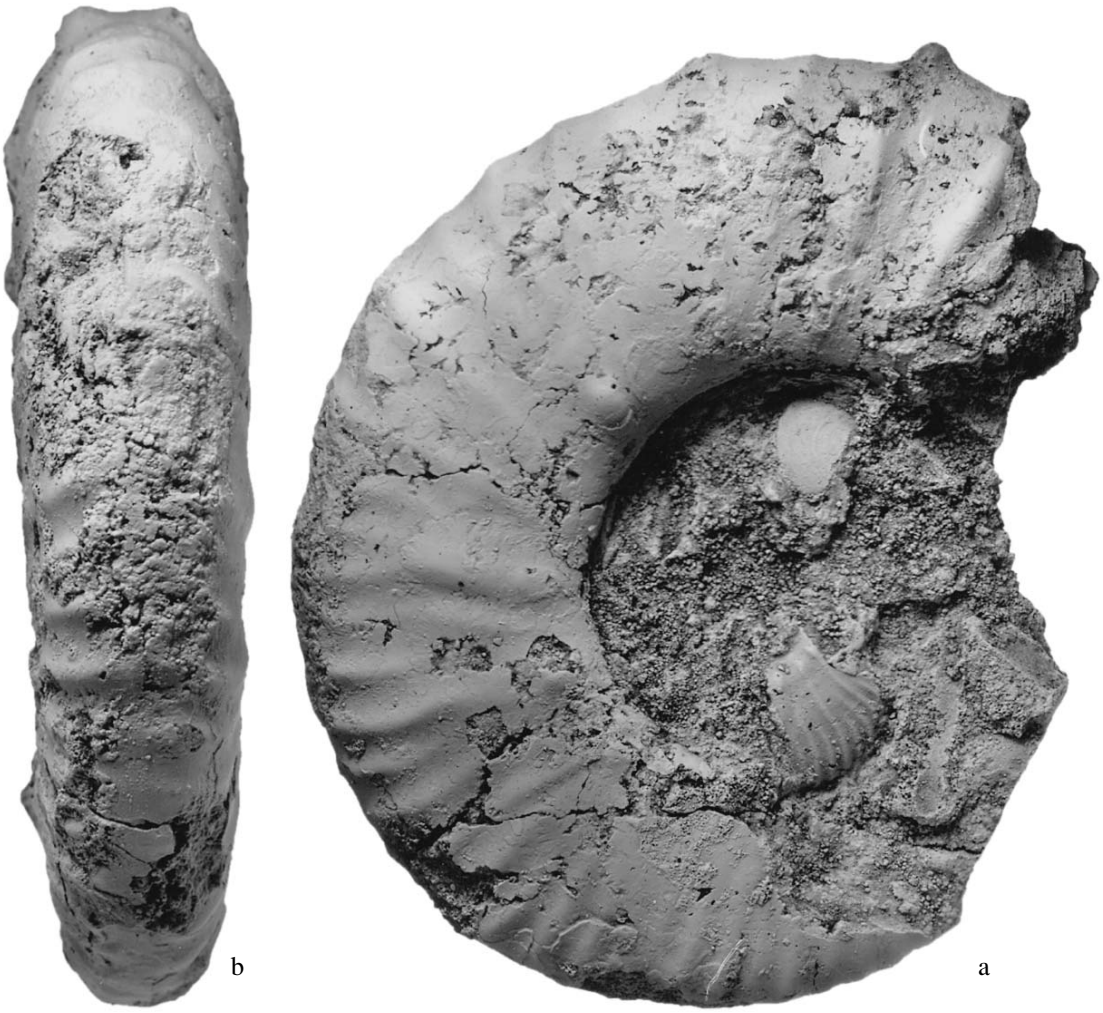


Fig. 1. *Subalpinites faurieformis* sp. nov., holotype no. 3990/328, macroconch (× 1); (a) phragmocone, lateral view; (b) ventral view. Collected by A.V. Stupachenko.

ple, intercalating, and tripartite ribs, sometimes lower in mid-venter. In umbilical region of ribs and in bifurcation point, near mid-flank, more or less pronounced inflations present. Body chamber possessing prominent simple ribs.

Species composition. *S. aristidis* (Kilian, 1896), *S. fauriensis* Mazenot, 1939, *S. mediterraneus* Mazenot, 1939, *S. remanei* Le Hégarat, 1973 (all from Western Europe); *S. bajarunasi* Luppov, 1988, *S. mangyschlakensis* Luppov, 1988 (Mangyschlak); *S. krischtafowitschi* Mitta and three new species, described below (Russian Platform).

Comparison. This genus is distinguished from the genera *Fauriella* Nikolov, *Jabronella* Nikolov and other necomitids with a similar whorl cross-section, members of *Subalpinites* have less frequently spaced and coarser ribs. It differs from *Mazenoticeras* Nikolov in the weakly developed umbilical and lateral inflations, and from *Dalmasiceras* Djanelidze in the absence of smoothening of the ornamentation in adult whorls. Compressed whorls with a high cross-section, narrower umbilicus, and different ornamentation, distinguish *Subalpinites* from *Malbosiceras* Grigorieva.

Remarks. Two small (up to 30 mm in diameter) ammonites were described by Mazenot (1939, pl. XXVI, fig. 2, holotype, and fig. 3, paratype) as "Incertae sedis: *Dalmasiceras* (?) Blondeti n. sp.". Later, Le Hégarat (1973), Nikolov (1982), and Klein (2005) included this species in the genus *Subalpinites*. However, taking into account the state of preservation of the holotype, this name is in fact *nomen dubium.* The paratype is a specimen with an almost complete body chamber and could be a microconch of *Subalpinites* (*Subalpinites* ? sp. indet., [m]), but it is hardly possible to identify more precisely.

In the basin of the Oka River in the Ryazan Region, in the near the village of Nikitino, beds of the *spasskensis* Subzone of the *rjasanensis* Zone (for the section

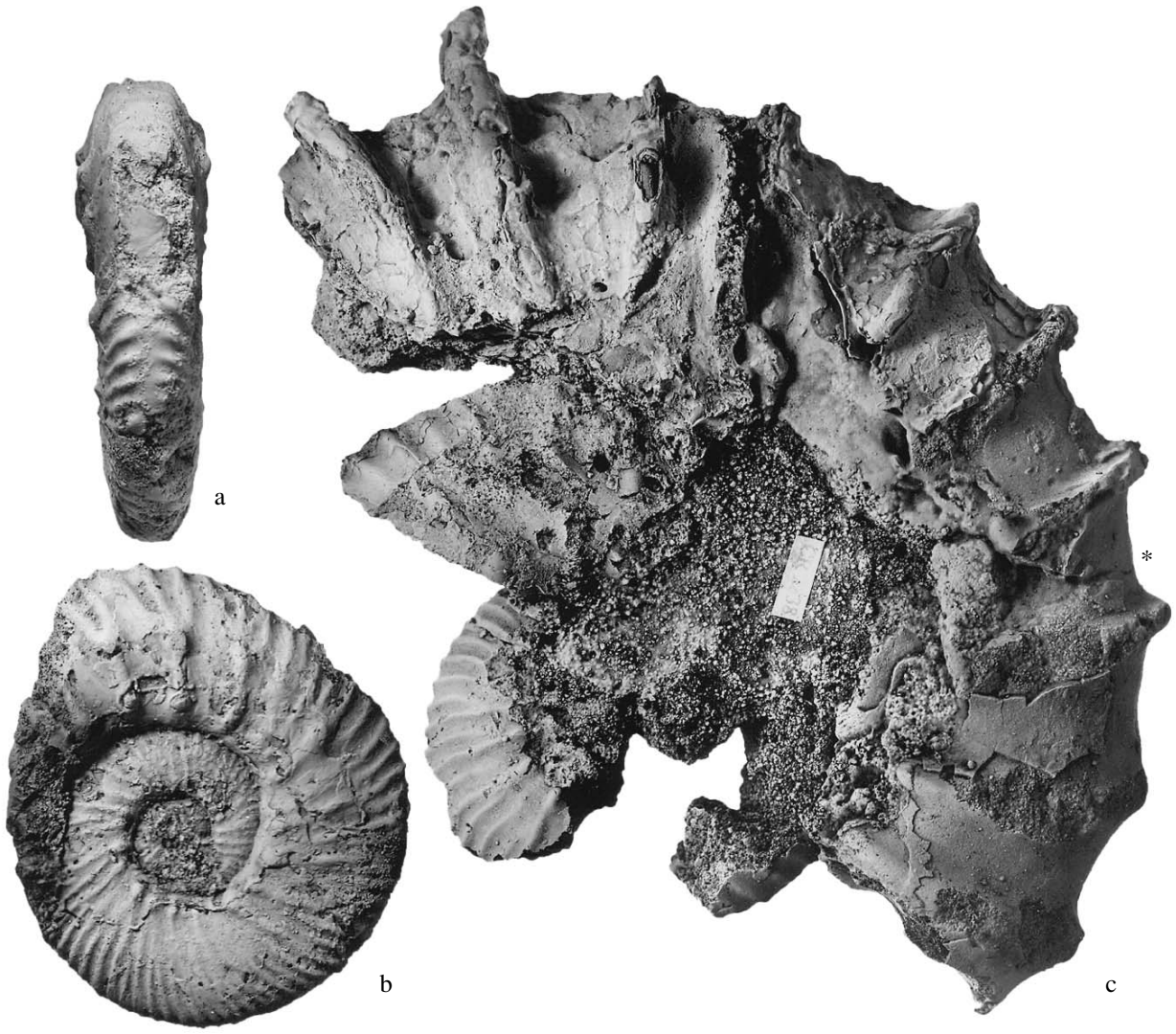


Fig. 2. *Subalpinites remaneiformis* sp. nov., × 1: (a) specimen no. ABC/1002, microconch ?, phragmocone, ventral view; (b) the same, lateral view; (c) holotype no. 3990/336, macroconch, phragmocone with a partly preserved body chamber, lateral view; asterisk (*) marks the beginning of the body chamber. Collected by A.V. Stupachenko.

description see Mitta, 2007a), contained specimens of another species of *Subalpinites*, similar to *S. krischtafowitschi* (Fig. 4).A fragment from here figured by Mitta (2007a, pl. II, fig. 5) as *Dalmasiceras* ? sp., may also belong to the same taxon. Poor preservation of material does not allow more precise identification.

My material from Central Russia is mainly represented by phragmocones. Consequently, the identification below as macro- and microconchs is based on size and degree of whorl overlap. The association of microconchs with particular macroconchs in the condensed beds is also provisional.

Explanation to Plate 3

All sizes are natural

Figs. 1–3, 5, 6. *Subalpinites gruendeli* sp. nov: (1) specimen no. 3990/319, juvenile, lateral view; (2) holotype no. 3990/318, macroconch: (2a) phragmocone, lateral view, (2b) ventral view, (2c) apertural view; (3) specimen no. 3990/320, macroconch: (3a) phragmocone, lateral view, (3b) apertural view; (5) specimen no. 3990/322, (5a) phragmocone, lateral view, (5b) ventral view; (6) specimen no. 3990/321, macroconch: (6a) phragmocone, lateral view, (6b) ventral view.

Fig. 4. *Subalpinites faurieformis* sp. nov., specimen no. 3990/333, microconch ?, phragmocone, lateral view.

All specimens from : Moscow Region, Lopatinsky phosphorite mine, quarry no. 12-2; Ryazanian Stage, *Riasanites rjasanensis* Zone, *rjasanensis* Subzone. Collected by V.V. Mitta and A.V. Stupachenko.

Plate 3

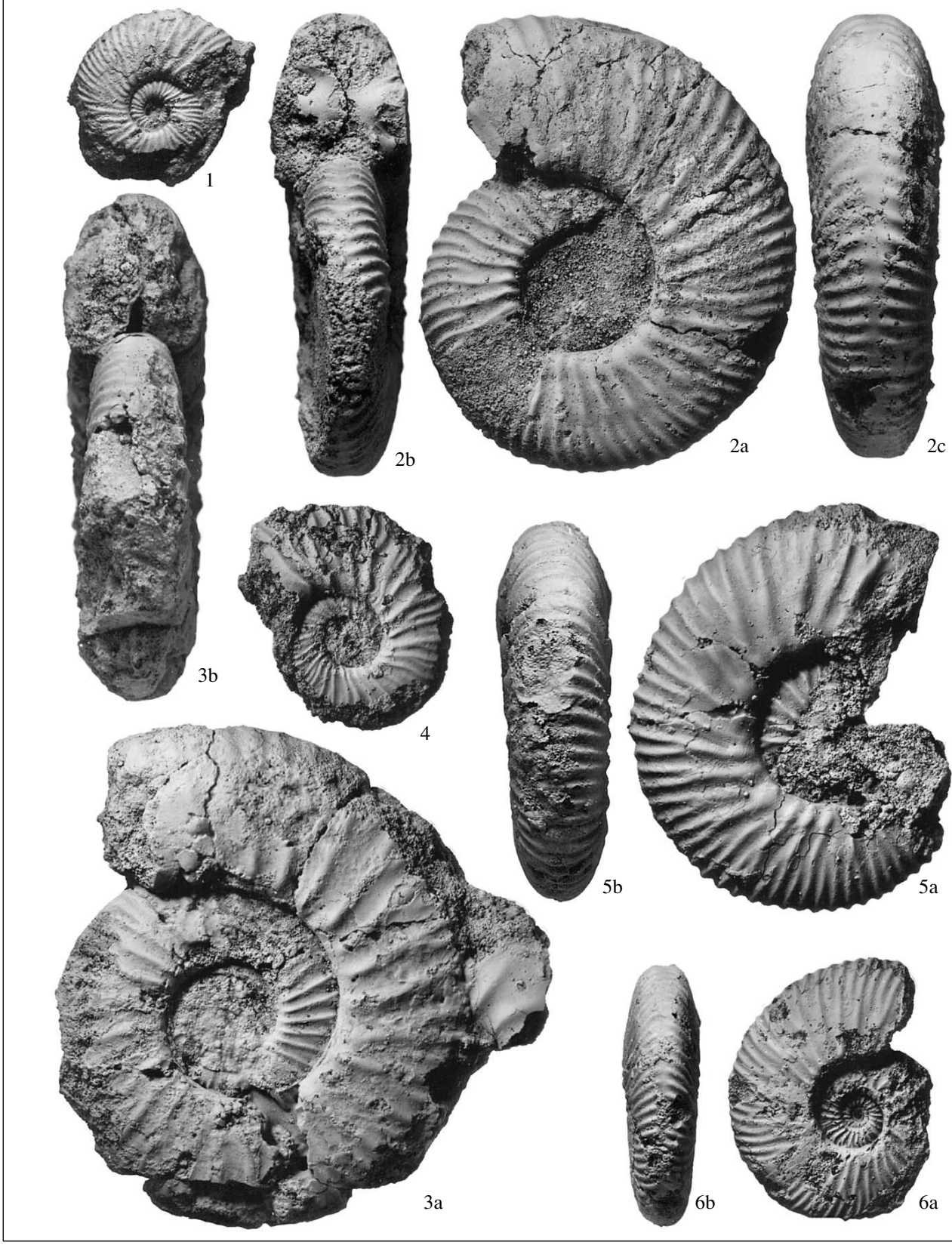
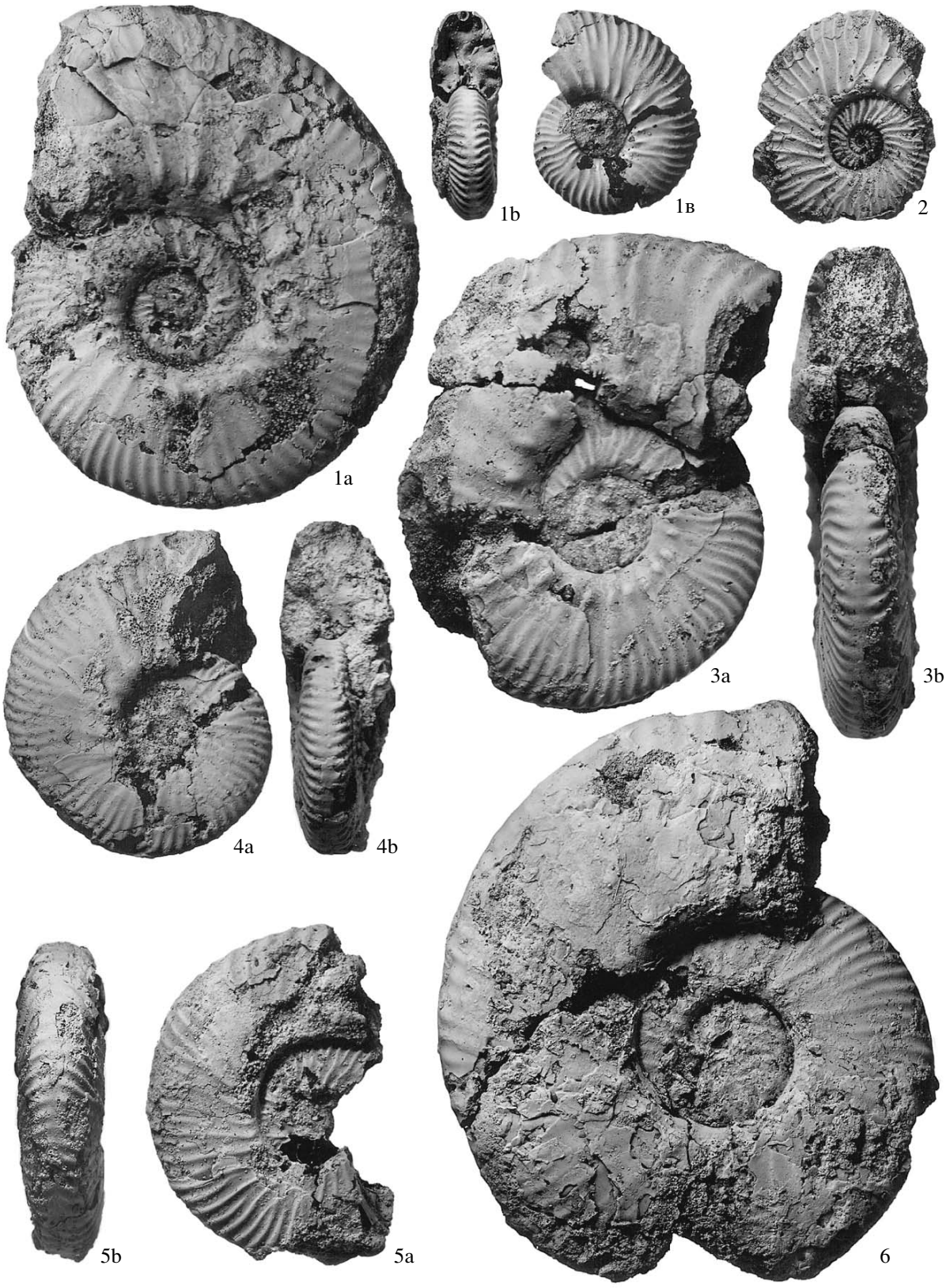


Plate 4



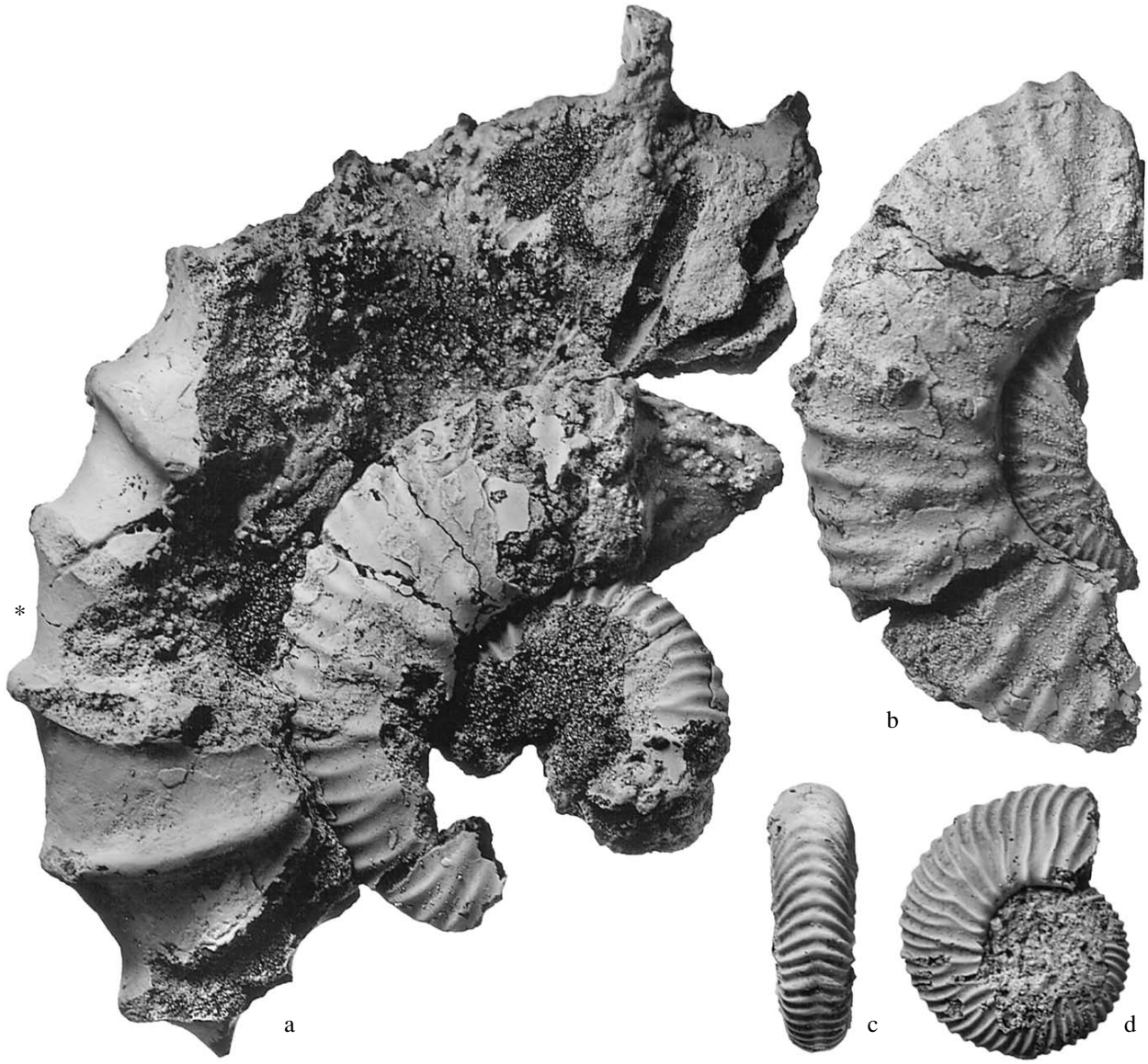


Fig. 3. *Subalpinites remaneiformis* sp. nov. (×1): (a) holotype no. 3990/336, macroconch, phragmocone with a partly preserved body chamber, lateral view; (b) specimens no. 3990/338, microconch ?, phragmocone, lateral view; (c) specimens no. 3990/340, internal whorls of the phragmocone, ventral view; (d) the same, lateral view; asterisk (*) marks the beginning of the body chamber. Collected by A.V. Stupachenko and V.V. Mitta.

***Subalpinites gruendeli* Mitta sp. nov.**

Plate 3, figs. 1–3, 5, 6

Etymology. In honor of the German paleontologist Joachim Gründel.

Holotype. PIN, no. 3990/318; Moscow Region, Lopatinsky phosphorite mine, quarry no. 12-2; Ryazanian Stage, *Riasanites rjasanensis* Zone, *rjasanensis* Subzone, *Riasanites swistowianus* Faunal Horizon.

Explanation to Plate 4

All sizes are natural

Figs. 1–4. *Subalpinites faurieformis* sp. nov: (1) specimen no. 3990/329, macroconch: (1a) phragmocone, lateral view; (1b) juvenile whorls from the apertural side, (1c) the same, lateral view; (2) specimen no. 3990/332, microconch ?, phragmocone, lateral view; (3) specimen no. 3990/330, macroconch: (3a) phragmocone, lateral view, (3b) apertural view; (4) specimen no. 3990/331, macroconch: (4a) phragmocone, lateral view, (4b) apertural view.

Figs. 5 and 6. *Subalpinites krischtafowitschi* Mitta: (5) specimen no. 3990/327, microconch: (5a) phragmocone, lateral view, (5b) ventral view; (6) specimen no. 3990/326, macroconch, phragmocone, lateral view.

All: Moscow Region, Lopatinsky phosphorite mine, Ryazanian Stage, *Riasanites rjasanensis* Zone, *rjasanensis* Subzone. (1–4, 6) quarry no. 12-2, collected by V.V. Mitta and A.V. Stupachenko; (5) quarry no. 10, collected by R.R. Gabdullin.

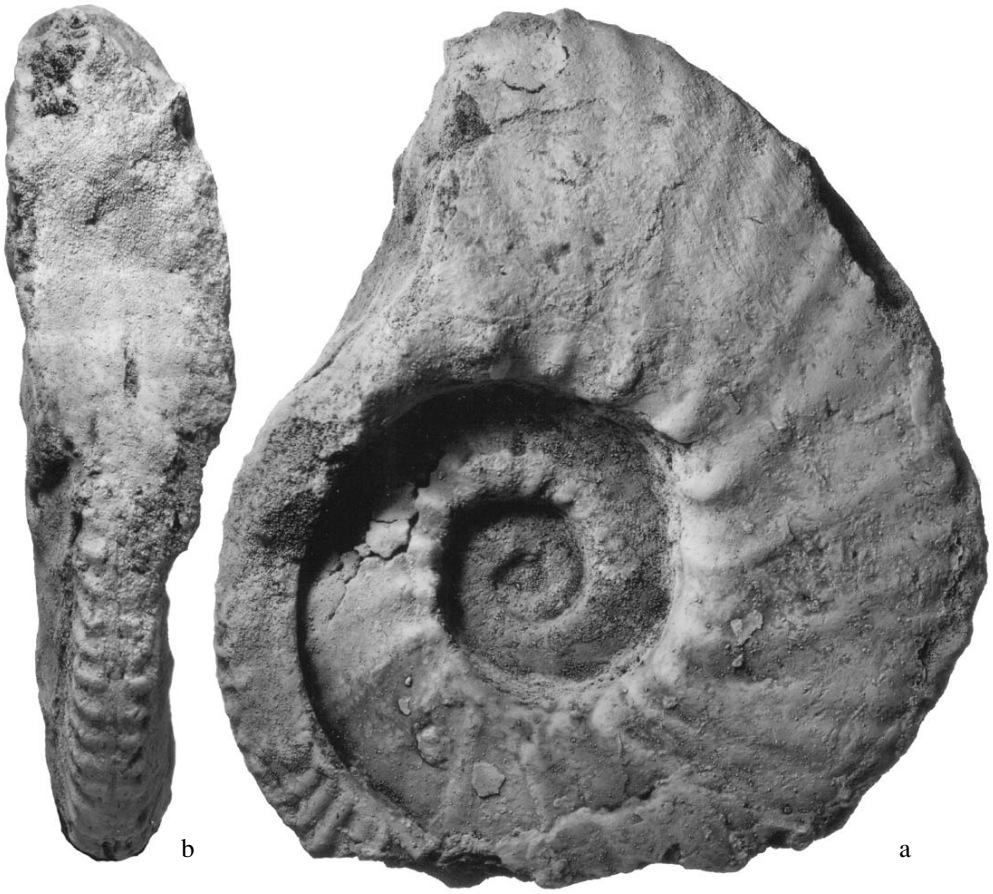


Fig. 4. *Subalpinites* aff. *krischtafowitschi* Mitta, specimen no. 3990/334, macroconch, ×1: (a) phragmocone, lateral view; (b) apertural view, Ryazanian Region, Spasskii District, right bank of the Oka River, downstream of the village of Nikitino; Ryazanian Stage, *Riasanites rjasanensis* Zone, *Surites spasskensis* Subzone. Collected by V.V. Mitta.

Description. The phragmocone of the macroconchs is up to 120 mm in diameter, and of the supposed microconchs up to 50 mm; the body chamber is unknown. Shell is laterally compressed, with whorls suboval in cross-section, with maximum width in the lower third if flanks. The venter is flattened up to a diameter of 75 mm, becoming rounded with growth. The umbilicus is wide. The umbilical wall is steep. The umbilical ridge is rounded.

The ornamentation in most of the phragmocone is represented by prominent mainly bipartite, less commonly simple, tripartite, and intercalating ribs. The division of ribs usually occurs slightly below the mid-flank. The umbilical ribs are subradial; the posterior branches of the ribs are slightly bent backwards, especially in early whorls. The umbilical parts of the ribs are noticeably widened, and a similar widening is also observed at the bifurcation point. At the end of the phragmocone in macroconchs, these widened areas are modified small node-like inflations; simple ribs predominate. In the mid-venter, the ribs are interrupted or more often flattened to form a ventral groove; by the end of the phragmocone this groove is weakly developed, or is completely absent.

Dimensions in mm and ratios:

Specimen no.	Du	WH	WW	UW	WH/Du	WW/Du	WU/Du
3990/335	114	35	31	48	0.30	0.27	0.42
	87	32	26	34	0.37	0.30	0.39
3990/320	96	30	25	38	0.31	0.26	0.40
Holotype 3990/318	95	32	26	33	0.34	0.27	0.35
3990/323	77	28	24	30	0.36	0.31	0.39
3990/322	72	26	20	27	0.36	0.28	0.38
3990/325	59	25	18	22	0.42	0.31	0.37
3990/321	48	20	14	16	0.42	0.29	0.33
3990/319	32	13	10	10	0.41	0.31	0.31
3990/324	31	13	10	11	0.42	0.32	0.35

Variability. Variability is primarily observed in the degree of expression of the umbilical and lateral nodes, in the timing of the disappearance of the ventral flattened zone. The specimen in Pl. 3, fig. 5 shows adult characters appearing very early, but with bipartite ribs predominating.

Comparison. This species is distinguished from *S. krischtafowitschi* Mitta in the wider umbilicus, in the suboval and lower cross-section of less compressed whorls, and the more densely spaced ribs.

Remarks. This species is apparently, the earliest of the Central Russian members of the genus. In its shell shape and morphogenesis of ornamentation it resembles macroconchs of *Pseudosubplanites* from the Berriasian *jacobi* Zone. Perhaps this similarity can shed some light on the origin of *Subalpinites*.

Material. Sixteen specimens, including four specimens from the collection A.V. Stupachenko. All from the type locality.

***Subalpinites faurieformis* Mitta sp. nov.**

Plate 4, figs. 1–4

Etymology. Named for its similarity to *S. fauriensis* Mazenot.

Holotype. PIN, no. 3990/328; Moscow Region, Lopatinsky phosphorite mine, quarry no. 12-2; Ryazanian Stage, *Riasanites rjasanensis* Zone, *rjasanensis* Subzone, *Riasanites swistowianus* Faunal Horizon.

Description (Fig. 1). Phragmocone up to 135 mm in diameter. The shell is compressed at all stages. The whorl cross-section is high, suboval and subtrapezoid, with its maximum width in the lower third of the flanks. The venter is flattened at early stages, to become rounded as the shell grows. The umbilicus is moderately wide and shallow. The umbilical wall is relatively gently sloping.

The ornamentation consists of bi-and tripartite and intercalating ribs with strongly bent branches, often lacking a connection with the main rib. The ribs usually bifurcate in the mid-flank, but some ribs bifurcate in the umbilical zone to form a bidichotomous bunch. The umbilical shoulder possesses prominent nodes, which become inflations as the shell grows. The inflations in the mid-flanks are usually not pronounced, but occasionally occur at later stages. At the early whorls in the mid-venter, the ribs become lower. As the shell grows, some branches become raised on the ventrolateral shoulder to form inflations. On the single specimen with a preserved fragment of the body chamber, it can be observed that the body chamber is covered by simple ribs.

Dimensions in mm and ratios:

Specimen no.	Du	WH	WW	UW	WH/Du	WW/Du	WU/Du
Holotype 3990/328	132	46	31	55	0.35	0.23	0.42
3990/329	90	36	26	28	0.40	0.29	0.31
3990/330	87	34	23	28	0.39	0.26	0.32
3990/331	58	26	16	16	0.45	0.28	0.28
3990/333	44	18	13	15	0.40	0.30	0.34
3990/332	32	14	10	10	0.44	0.31	0.31

Variability. Variability is mainly observed in the degree of the rib curvature and in the development of the umbilical and lateral nodes.

Comparison. This species is distinguished from *S. fauriensis* in the trapezoid whorl cross-section, more gently sloping umbilical wall, and apparently, in the larger size. This species is distinguished from the Central Russian representatives of the genus by the strongly bent secondary ribs at early stages, well pronounced umbilical nodes and the absence of nodes at the point of rib bifurcation.

Material. 12 specimens, including 1 specimen from the collection of A.V. Stupachenko. In addition, there are another 7 specimens too poorly preserved for positive identification, but which are likely to belong to this species. All from the type locality.

***Subalpinites remaneiformis* Mitta sp. nov.**

Plate 3, figs. 1–4, 6–9

Etymology. Named for its similarity to *S. remanei* Le Hégarat.

Holotype. PIN, no. 3990/336; Moscow Region, Lopatinsky phosphorite mine, quarry no. 12-2; Ryazanian Stage, *Riasanites rjasanensis* Zone, *rjasanensis* Subzone, *Riasanites swistowianus* Faunal Horizon.

Description (Figs. 2, 3). The phragmocone of the macroconchs may reach 110 mm in diameter. The shell is compressed, with a high oval whorl cross-section. The maximum width is in the lower third of the flanks. The flattened venter in early whorls becomes rounded by the end of the phragmocone and on the living chamber. The umbilicus is wide and shallow. The umbilical wall is low, usually relatively gently sloping. The complete length of the body chamber and the shape of the aperture are unknown.

The ornamentation in early whorls (diameter up to 40 mm) is represented mainly by densely spaced bi-tripartite, bidichtotomous, simple and intercalating ribs, directed forward. Small widening areas are observed on the ribs on the umbilical shoulder and in the ventrolateral zone; the ribs become lower in the mid-venter. At later stages, the ribs are mostly bipartite and intercalating, less commonly tripartite. As the shell grows, the ribs become less densely spaced, and inflations appear

in the mid-flank (at the bifurcation point), while the umbilical inflations become more prominent. At the end of the phragmocone and on the body chamber simple, sparsely spaced ribs-folds are present.

Dimensions in mm and ratios:

Specimen no.	Du	WH	WW	UW	WH/Du	WW/Du	WU/Du
3990/339	100	32	25	40	0.32	0.25	0.40
3990/338	97	31	25	40	0.32	0.26	0.41
Holotype 3990/336	85	35	26	30	0.41	0.31	0.35
3990/337	81	31	23	29	0.38	0.28	0.36
	58	23	15	20	0.40	0.26	0.34
ABC/1002	64	23	16	25	0.36	0.25	0.39
3990/340	38	15	13	15	0.39	0.34	0.39

Comparison. This species is distinguished from other Central Russian *Subalpinites* by prominent lateral nodes, higher and coarser ribs on the body chamber. It differs from *S. remanei* in the less densely spaced and coarser ribs in adult whorls; in addition, the lateral row of nodes in the Russian species is much more prominent.

Remarks. This species is much closer to *Mazenoticeras* or *Malbosiceras* than to *Subalpinites* in its ornamentation morphogenesis in adult whorls. However, the morphology for the early whorls indicates that this species in fact belongs to *Subalpinites*.

Material. 10 specimens, including 3 specimens from the collection of A.V. Stupachenko. All from the type locality.

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