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Camille Frau, William A.P. Wimbledon, Christina Ifrim, Luc Bulot, Alexandre Pohl. Berriasian ammonites of supposed Tethyan origin from the type 'Ryazanian', Russia: a systematic re-interpretation.. Palaeoworld, 2021, 30 (3), pp.515-537. 10.1016/j.palwor.2020.07.004 . hal-03341891

HAL Id: hal-03341891

<https://hal.science/hal-03341891>

Submitted on 11 Oct 2021

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Berriasian ammonites of supposed Tethyan origin from the type ‘Ryazanian’, Russia: a systematic re-interpretation

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Abstract

For more than a century, a number of ammonite taxa of supposed Tethyan origin or affinity have been reported from the Berriasian condensed deposits of Russia (referred to as ‘Ryazanian’). These occurrences have been used to constrain long-distance correlation and palaeobiogeographic interpretation of the Russian Platform during the earliest Cretaceous. We revise these taxa herein. To accommodate the systematic issues, we introduce a new ammonite genus: *Mittaites* n. gen. (type species: *Mazenoticerias ceccai*). We also provide re-assessment for the genera *Tauricoceras* (= *Subriasanites*), *Riasanella*, *Riasanites*, *Prorjasanites*, and *Karasyazites*. Considering the strong affinities between these genera (except for *Karasyazites*), restricted palaeobiogeographic distribution and a problematic phyletic origin, we erect a new family Riasanitidae n. fam. Our re-examination suggests that the occurrence of western Tethyan migrants in the type ‘Ryazanian’ should be ruled out. Pending new

investigation, correlation of the ammonites of the type ‘Ryazanian’ beds with the Berriasian part of the Standard Mediterranean Ammonite Scale (SMAS) should be treated with caution.

Keywords: Ammonites; Berriasian; ‘Ryazanian’; Russian platform; Systematics

1. Introduction

The ammonite faunas at the Jurassic–Cretaceous transition show the highest provincialism in the Mesozoic, reflecting the separation of the Tethyan and the Austral realms and the various boreal basins (Westermann, 2000). Provincialism is also marked within the realms since, for example, Arctic, Boreal-Atlantic and Boreal-Pacific subrealms have been distinguished in the ‘Boreal Realm’ at that time (Lehmann et al., 2015 and references therein). This severe biological restriction has for generations prevented substantial progress in long-distance correlation (Wimbledon, 2008), and strongly influenced the use of regional stage names for these deposits (e.g., “Purbeckian”, “Portlandian”, “Volgian”, and ‘Ryazanian’ for the boreal/sub-boreal regions and beyond) even after the ratification of the Tithonian and Berriasian as the global stages for the uppermost Jurassic and lowermost Cretaceous, respectively (Sarjeant and Wimbledon, 2000; Cope, 2007, 2013; Wimbledon, 2008; Wimbledon et al., 2011). Although the formal selection of a GSSP (Global Boundary Stratotype Section and Point) for the Berriasian is pending, the incoming of small, globular forms of *Calpionella alpina* and the sharp decline in abundance of *Crassicollaria* calpionellid species, which together define the base of the *Calpionella* Zone, have been formally selected as primary boundary markers for the base of the stage (with supporting nannofossils, calcareous dinoflagellates, ammonites, and magnetostratigraphy) (Wimbledon, 2017; Wimbledon et al., 2020). Unfortunately, the extreme isolation of the boreal basins, which lack calpionellids and other secondary markers, prevents the direct recognition of the putative boundary there (Wimbledon, 2014; Schnabl et al., 2015). Furthermore, the correlation of ammonites in Russian Tithonian and Berriasian boreal sections with a standard Mediterranean ammonite scale (SMAS sensu Reboulet et al., 2018) remains an intractable problem (e.g., Sazonova, 1971, 1972, 1977; Casey, 1973; Casey et al., 1988; Mitta, 2005, 2017; Zakharov and Rogov, 2008; Schnabl et al., 2015). This is not only due to condensation and erosional episodes in the Russian platform ‘Ryazanian’ deposits

(see Mesezhnikov et al., 1979; Mitta, 2014), but also the strong endemism of the ammonite faunas (e.g., Casey et al., 1977; Baraboshkin, 1999, 2002; Mitta, 2004, 2005; Zakharov and Rogov, 2008; Lehmann et al., 2015).

Mitta (2017) has recently suggested that the type ‘Ryazanian’ beds of central European Russia can be separated into four zones. These are, from oldest to youngest, the *Hectoroceras kochi*, *Riasanites rjasanensis*, *Surites spasskensis*, and *Surites tzikwinianus* zones. According to Mitta (2017), the *Riasanites rjasanensis* and *Surites spasskensis* zones “approximately correspond to the Occitanica–lower Boissieri Zone of the Berriasian” in the Mediterranean region, because this interval was reputedly the time of an influx of Tethyan neocomitid ammonites of mid- to late Berriasian age (Mitta, 2002, 2004, 2005, 2007a, 2007b, 2008, 2009, 2011a, 2011b, 2017, 2018; Mitta and Bogomolov, 2008; Mitta and Sha, 2011). Those authors recognized the following taxa from the *R. rjasanensis* and *S. spasskensis* zones:

– 6 species of eastern Mediterranean-Caucasian origin, namely *Dalmasiceras crassicostatum* (Djanélidzé, 1922), *Dalmasiceras* ex gr. *djanélidzei* (Mazenot, 1939), *Euthymiceras euthymi* (Pictet, 1867), *Malbosiceras nikolovi* Le Hégarat, 1973, *Malbosiceras* cf. *macphersoni* (Kilian, 1889), *Malbosiceras* aff. *boisseti* Nikolov, 1982; and 4 forms left in open nomenclature (*Dalmasiceras?* sp., *Malbosiceras* sp., *Mazenoticerias* sp., and *Pomeliceras* sp.).

– 3 species of western Mediterranean-Caucasian origin, namely *Karasyazites bajurunasi* (Luppov in Luppov et al., 1988), *Riasanites* aff. *maikopensis* (Grigorieva, 1938), and *Mazenoticerias* cf. *urukhense* Kalacheva and Sey, 2000.

– 16 new and poorly-known Tethyan-derived species; namely *Riasanites rjasanensis* (Nikitin, 1888) [morphs α and β], *Riasanites swistowianus* (Nikitin, 1888), *Riasanites rulevae* (Mitta, 2007a), *Riasanella olorizi* Mitta, 2011b, *Riasanella riasanitoides* Mitta, 2011b, *Riasanella rausingi* Mitta, 2011b, *Riasanella plana* Mitta, 2011b, *Subalpinites krischtafowitschi* Mitta, 2002 (and *S.* aff. *krischtafowitschi* in Mitta, 2009), *Subalpinites faurieformis* Mitta, 2009, *Subalpinites remaneiformis* Mitta, 2009, *Subalpinites gruendeli* Mitta, 2009, *Mazenoticerias ceccai* Mitta, 2011a, *Mazenoticerias robustum* Mitta, 2011a, *Transcapiites transfigurabilis* (Bogoslowsky, 1897) (and *T.* cf./aff. *transfigurabilis* in Mitta, 2018), *Transcapiites tscheffkini* Mitta, 2018, and *Transcapiites transitionis* Mitta, 2018.

It is worth noting that some of the identified species lack systematic description, as previously noticed by Sey and Kalacheva (2005, 2008) and Arkadiev et al. (2007).

In cases where descriptions are given for the newly introduced taxa, comparisons with the type species of the genera are insufficient and some of the generic identifications have been repeatedly revised (compare systematic treatment between Mitta, 2002 and Mitta, 2018 for example).

Research conducted in the past several years within the Berriasian Working Group of the International Subcommission on Cretaceous Stratigraphy questions such systematics and correlation. It has been demonstrated that the provincialism of the neocomitid and himalayitid ammonites is higher than previously assumed in the literature, and that homeomorphy has led to erroneous taxonomic interpretations (see Bulot et al., 2014; Frau et al., 2015, 2016a, 2016b, 2016c; Lehmann et al., 2015). In particular, a re-examination of the Russian literature leads us to challenge the occurrence of western Tethyan-derived ammonites in the ‘Ryazanian’ deposits, as testified by the systematic re-assessment provided in the present contribution.

2. Material and methods

This work is based on a re-examination of the figured Russian later Berriasian (‘Ryazanian’) ammonite taxa of supposed Tethyan origin from the Moscow and Ryazan regions (Fig. 1), as documented by Vasily V. Mitta and collaborators (Mitta, 2002, 2004, 2005, 2007a, 2007b, 2008, 2009, 2011a, 2011b, 2017, 2018; Mitta and Bogomolov, 2008; Mitta and Sha, 2011). Apart from endemic Russian forms, most of the species identified by those authors were assigned to the Neocomitidae Salfeld, 1921, viz. *Berriasella* Uhlig, 1905 (type species: *Ammonites privasensis* Pictet, 1867), *Euthymiceras* Grigorieva, 1938 (type species: *Ammonites euthymi* Pictet, 1867), *Subalpinites* Mazonot, 1939 (type species: *Subalpinites fauriensis* Mazonot, 1939), *Malbosiceras* Grigorieva, 1938 (type species: *Ammonites malbosi* Pictet, 1867), *Mazonoticerases* Nikolov, 1966 (type species: *Berriasella broussei* Mazonot, 1939), *Pomeliceras* Grigorieva, 1938 (type species: *Ammonites breveti* Pomel, 1889), and the Himalayitidae Spath, 1925, viz. *Dalmasiceras* Djanélidzé, 1922 (type species: *Ammonites dalmasi* Pictet, 1867). The type species of all these genera originate from southeast France (Vocontian domain) and the historical type sections for the Berriasian Stage, except those of *Pomeliceras* from Ouled Mimoun, Algeria (Fig. 1). The type material of the French species is still housed in the Grenoble, Lyon, and Genève universities, allowing their re-examination and comparison with the ‘Ryazanian’ ammonites. Repository abbreviations mentioned in the text indicate the

Faculté des Sciences de Lyon of the Claude Bernard-Lyon I University (FSL), the Dolomieu Institute of the Grenoble-Alpes University (UJF-ID), the Muséum National d'Histoire Naturelle of Paris (MNHN), and the Muséum d'Histoire Naturelle de Genève (MHNG).

The ammonites from the type 'Ryazanian' have been re-examined based on illustrations and shared photographs. Unless otherwise mentioned, the revised specimens are deposited in the Palaeontological Institute of the Russian Academy of Sciences (PIN), the Central Scientific Geological Museum (CNIGR Museum, Saint Petersburg), and the All-Russia Geological Oil Research Institute (VNIGNI). Some specimens labelled AVS are housed in the private collection of Andrey Stupachenko (Mitta, 2011a, 2011b). The reader can refer to the papers listed above for further details on the sampling localities and stratigraphic occurrences of the specimens. Other repository abbreviations mentioned in the text indicate the A.P. Karpinsky Russian Geological Research Institute of Saint Petersburg (VSEGEI) and the Museum of the Department of Geology and Paleontology (MDGP) from the I. Javakhishvili Tbilisi State University.

The following abbreviations indicate standard measurements used in the text: D = diameter, Ww = whorl breadth, Wh = whorl height, U = umbilical diameter. The ratios U/D, Wh/D and Ww/D (umbilical dimension, whorl height and whorl breadth as a percentage of the adult diameter), and Ww/Wh (whorl breadth as a percentage of the whorl height), are discussed in systematic descriptions. According to Mitta (2008), the branching coefficient indicates the ratio of the number of the secondary and primary ribs per half-whorl at the end of the *Riasanites* phragmocones.

3. Systematic palaeontology

Order Ammonoidea Zittel, 1884

Suborder Ammonitina Hyatt, 1889

Family Riasanitidae n. fam.

Etymology: Refers to the ammonite genus *Riasanites* Spath, 1923.

Type genus: As here designed, *Riasanites* Spath, 1923. The type species is *Riasanites rjasanensis* (Nikitin, 1888); by original designation. According to Article 12.1 of the ICZN, Nikitin (1888) is the author of the species *rjasanensis* since the previous

introduction of the nominative name by Lahusen (1883) lacks description, definition, or indication for the taxon.

Content: The Riasanitidae n. fam., as herein understood, includes the genera:

- *Gechiceras* Sakharov, 1982, type species: *G. kistense* Sakharov, 1982
- *Tauricoceras* Kvantaliani and Lysenko, 1979, type species: *T. crassicostatus* Kvantaliani and Lysenko, 1979 (= *Subriasanites* Sazonova in Sazonova and Sazonov, 1991, type species: *R. rjasanensis maikopensis* Grigorieva, 1938)
- *Riasanites* Spath, 1923, type species: *Riasanites rjasanensis* (Nikitin, 1888)
- *Riasanella* Mitta, 2011a, type species: *R. rausingi* Mitta, 2011b
- *Prorjasanites* Sazonova, 1977, type species: *P. plumatus* Sazonova, 1977
- *Mittaites* n. gen., type species: *Mazenoticerias ceccai* Mitta, 2011a (see discussion below).

Diagnosis: The new family is defined as grouping earliest Cretaceous small- to large-sized, dimorphic, moderately evolute, planulate ammonites with a compressed, subrectangular, suboval or suboctagonal whorl section marked by a flattened to slightly rounded venter. A narrow ventral furrow occurs in the juvenile whorls, but it weakens and/or disappears in the adult. Microconchs bear lappeted peristomes, whereas it is simple on macroconchs. Ornamentation generally consists of simple, bi- or trifurcate, rarely fasciculate sharp ribs and a variable number of intercalatories. Enlarged, crest- or node-like bulges can develop on the peri-umbilical, lateral and peri-ventral margins. When known, suture lines develop long and more or less symmetrical ventral and first lateral lobes while other ones are small.

Remarks: The lower Berriasian ammonite assemblages of the Mediterranean-Caucasian Subrealm are rather uniform and dominated by the Neocomitidae *Berriasella*, *Pseudosubplanites*, *Malbosiceras*, *Delphinella*, *Strambergella*, *Pseudoneocomites*, and the Himalayitidae *Chapericeras*, *Kilianites*, and *Praedalmsiceras* (Lehmann et al., 2015; Frau et al., 2016a, 2016b, 2016c). This assemblage has no equivalent in the Boreal subprovinces at that time due to paleogeographic restriction (Lehmann et al., 2015). During the middle Berriasian, the paleobiogeographic affinities between the western and eastern Mediterranean-Caucasian ammonite assemblages break out and new endemic ammonite genera develop throughout the Caucasian and Transcaspian areas (Crimea, Caucasus, and Mangyshlak), including *Gechiceras*, *Tauricoceras*, and *Riasanites* (e.g., Luppov et al., 1988; Kvantaliani, 1999; Kalacheva and Sey, 2000; Arkadiev et al., 2012). In the

current state of knowledge, the affinities of this fauna are even stronger with those from the eastern European part of the Boreal Atlantic Subrealm (Polish Lowland and Russian Platform) as exemplified by the dispersion of *Riasanites* (Mitta, 2008; Mitta and Ploch, 2012).

According to Kvantaliani (1999), the genera *Gechiceras*, *Tauricoceras*, and *Riasanites* form a direct lineage rooted in the Neocomitidae *sensu lato* through the *Neocosmoceras* and *Euthymiceras* relatives from the Trans-Caucasian areas (see Kvantaliani, 1999, fig. 22). Unfortunately, the affinities between those forms and the typical *Neocosmoceras* and *Euthymiceras* relatives from the western Mediterranean-Caucasian Subrealm have never been substantiated in the literature. As such, the link between the Neocomitidae and the *Gechiceras*–*Tauricoceras*–*Riasanites* lineage is still to be resolved.

Mitta (2008) documented the variability of the *Riasanites* relatives thanks to abundant collection from the ‘Ryazanian’ deposits of the Russian Platform. Mitta (2011b, p. 17) assigned *Riasanites* — a senior synonym of *Tauricoceras* according to the author — to the Himalayitidae because of a supposed phyletic link with *Transcaspiites* Luppov in Bogdanova et al., 1985 (type species: *Protacanthodiscus transcaspicus* Luppov, Bodylevsky and Glazunova, 1949). *Transcaspiites* share great affinities with the Himalayitidae *Protacanthodiscus* Spath, 1923 in the juvenile whorls, namely an inflated planulate shell and a weak ventral band (Frau et al., 2015). But *Transcaspiites* develops prominent tubercles on the upper flank that enlarge as growth increases and give a sub-coronate section to the whorl (see Bogdanova et al., 1985). Such himalayitid features are not observed in the *Gechiceras*, *Tauricoceras* and *Riasanites* relatives. As such, the link between those forms and the Himalayitidae is doubtful.

Bulot et al. (2014) also suggested that *Riasanites* may have derived from the Himalayitidae through *Pratumidiscus* Bulot et al., 2014 (type species: *Pratumidiscus elsae* Bulot et al., 2014). However, *P. elsae* is a latest Tithonian endemic ammonite from southern France known from a very restricted number of specimens (Bulot et al., 2014, text-fig. 6; Frau et al., 2016b, text-fig. 6H). *Riasanites* differs from *P. elsae* in having a subtrapezoidal whorl section converging towards the venter, a narrow ventral groove, umbilical nodes and a ventral chevron in the adult (Bulot et al., 2014). As a result, the affinities between *Riasanites* and *Pratumidiscus* are unlikely.

Considering their morphological and ornamental affinities, we here follow the views of Kvantaliani (1999) that the genera *Gechiceras*, *Tauricoceras*, and *Riasanites* form a direct lineage. Pending the study of the Trans-Caucasian neocomitid-like forms here referred to as “*Neocosmoceras*” and “*Euthymiceras*”, we propose to separate this lineage by the introduction of the new family Riasanitidae n. fam. Its origin among the neocomitid rootstock cannot be upheld and needs further investigation.

Genus *Riasanites* Spath, 1923

Type species: *Riasanites rjasanensis* (Nikitin, 1888).

Emended diagnosis: *Riasanites* innermost whorls have moderately evolute, planulate shell with a deep umbilicus, depressed, subrectangular to subtrapezoidal whorl section with a flattened venter marked by a slight ventral band (*R. rjasanensis* morphotype) or a deep furrow (*R. swistowianus* morphotype). The species then develops four ornamental stages (Fig. 2A–C): (i) a juvenile stage marked by approximated, straight to slightly convex, robust ribs; (ii) a neocomitid-like sub-adult stage that bears spaced, prorsiradiate to slightly sinuous, broad, mainly bifurcate and simple primary ribs with variable intercalatories. Ribs are enlarged into discrete or distinct bullae on the peri-umbilical margin and they bifurcate above mid-flank. Ribs are interrupted on the venter forming a narrow, shallow groove or they cross it forming a slight chevron at later growth stages; (iii) an adult stage marked by distant, rectiradiate to slightly projected, irregular bifurcate and simple primary ribs and, generally, one sinuous intercalatory. Lateral parts of the ribs or their points of furcation are enlarged as crest-like bulges; (iv) a terminal stage characterized by spaced, simple, annular primary ribs and rare intercalatories. Suture lines bear long and more or less symmetrical ventral and 1st lateral lobes while the other ones are small. *Riasanites* is dimorphic and includes small-sized, microconchs (mean diameter ~38 mm) with scaphitoid outer whorls and potentially with lappets and larger macroconchs (mean diameter ~60 mm) with simple peristome (compare Fig. 2B, C).

Remarks: In the *Fossilium Catalogus*, Klein (2005) listed six species into the genus *Riasanites* including the type species *R. rjasanensis* (Nikitin, 1888) and the subspecies *R. rjasanensis caucasicus* Khimchiashvili, 1976, as well as *R. bogoslowskii* Luppov in Luppov et al., 1988, *R. decorus* Sazonova, 1977, *R. densicostatus* Khimchiashvili, 1976, *R. subrjasanensis* (Nikitin, 1888), and *R.*

swistowianus (Nikitin, 1888). The subspecies *R. rjasanensis maikopensis* Grigorieva, 1938 was considered valid by Klein (2005) and the author kept separate the genus *Subriasanites*. In his study on the *Riasanites*-type population from the Russian Platform, Mitta (2008) subsequently retained only four species into *Riasanites* including *R. rjasanensis* (and its junior synonyms *R. subrjasanensis*, *Prorjasanites plumatus* Sazonova, 1977, *P. vnigni* Sazonova, 1977), *R. swistowianus* (and its junior synonym *R. decorus*), *R. Maikopensis*, and *R. crassicostatus* (Kvantaliani and Lysenko, 1979). The authors thus retained the genera *Subriasanites*, *Prorjasanites*, and *Tauricoceras* as junior synonyms of *Riasanites*.

According to Mitta (2011a), the separation of *R. rjasanensis* to *R. swistowianus* is based on their general morphology. *R. rjasanensis* develops involute shell (U/D ~0.39 and Ww/Wh ~0.76) with distinct subrectangular whorl section and slight ventral band while *R. swistowianus* develops more evolute shells (U/D ~0.46 and Ww/Wh ~0.86) with a subtrapezoidal whorl section and deep furrow (at least during the juvenile stage). Regarding the ornamentation, both species expose the four stages of the genus *Riasanites* defined above. *R. swistowianus* can be distinguished from *R. rjasanensis* by the reduced length of the sub-adult stage and extension of both the adult and terminal ones (compare Fig. 2A, B). Based on the available values, the branching coefficient found in the sub-adult and/or adult stages overlap and range from 1.1 to 2.4 (Mitta, 2011a). The branching coefficient cannot be, therefore, used as a reliable specific character. The morphometrics provided by Mitta (2011b) for 7 specimens assigned to *R. rjasanensis* (including the lectotype) and for 7 specimens assigned to *R. swistowianus* show close covariation of involution and whorl proportions (Fig. 3). They range from virgacone to extreme ophiocone morphotypes ($0.33 \leq U/D \leq 0.50$; $0.20 \leq Ww/D \leq 0.32$). Such variabilities conform to robust *versus* slender poles of the Westermann's laws of shell covariation of a single species (compare Fig. 2D, E and Fig. 2F, G). Considering that the two taxa are concomitant in the 'Ryazanian' deposits, we here consider that *R. rjasanensis* and *R. swistowianus* form a single palaeospecies. *R. rjasanensis* is thereafter retained as the senior name by pagination priority in the work of Nikitin (1888) and its wide use in the literature. Note finally, that the available morphometrics of the Russian species *R. subrjasanensis* and *R. decorus* also fit well with the variability of *R. rjasanensis* (Table 1). Following Sey and Kalacheva (1999) and Mitta (2008), these taxa are synonymised with the type species.

By contrast, the morphometrics of the northern Caucasus species *R. maikopensis*, *R. rjasanensis caucasicus*, and *R. densicostatus* differ from the *Riasanites*-type population by their larger size ($78 \text{ mm} \leq D \leq 145 \text{ mm}$), ophiocone to dactilicone morphotypes ($0.41 \leq U/D \leq 0.52$; $0.23 \leq Ww/D \leq 0.25$) (see Table 1), and the presence of a stronger and simpler bifurcate ribbing through most of the ontogeny (see for example Grigorieva, 1938, pl. 1, fig. 1; Khimchiashvili, 1976, pl. 15, figs. 1, 2; pl. 17, fig. 1). Those taxa co-occur in the northern Caucasus with smaller forms referred to diverse *Riasanites* species (e.g., Khimchiashvili, 1976; Kalacheva and Sey, 2000) and considered as the microconch counterpart of *R. maikopensis* (Mitta, 2008). These microconchs similarly expose a strong and simple ribbing through the ontogeny while they develop a rounded whorl section, steep umbilical wall and flattened venter, at least on part of the phragmocone, lacking a clear ventral band or furrow. As such, the morphological and ornamental features of *R. maikopensis* and its supposed microconchs better conform to those found in the *Tauricoceras* relatives (compare with Kvantaliani and Lysenko, 1979 and Kvantaliani, 1999). Considering the differences in the juvenile morphology (i.e., rounded whorl section, lack of distinct ventral interruption) and restricted palaeogeographic distribution, we thus retain *Tauricoceras* as a valid and distinct genus to which we transfer the species *R. maikopensis*, *R. rjasanensis caucasicus*, and *R. densicostatus*. As such, the genus *Subriasanites* is here synonymized with *Tauricoceras*. Note that *R. rjasanensis caucasicus*, and *R. densicostatus* merely correspond to potential synonyms of *T. maikopensis* but the lack of inner whorls in their type material prevents further confirmation.

Mitta (2008) suggested that the two *Prorjasanites* species *P. plumatus* Sazonova, 1977 and *P. vnigni* Sazonova, 1977, whose type material corresponds to incomplete phragmocones, illustrate the densely ribbed juvenile stage found in *R. rjasanensis*. This view is unlikely since none *Riasanites* specimens develop such dense ribbing in the inner whorls. At same size, the branching coefficient is markedly lower in *Prorjasanites* (estimation at ~ 0.45). As such, we keep separate the genera *Riasanites* and *Prorjasanites* (see further details below).

Finally, the species *R. bogoslovskii* Luppov in Luppov et al., 1988 was based on the hand drawn of a whorl fragment (holotype) from Russia illustrated by Bogoslovsky (1897, pl. 6, fig. 6a, b) and a poorly preserved fragment (paratype) from the Mangyshlak illustrated by Luppov (Luppov et al., 1988, pl. 13, fig. 7). The

Bogoslovsky's hand-drawn specimen is characterized by a compressed, subrectangular whorl section which bears dense primary ribs thickened on the periumbilical margin as nodes and bifurcated on the flank. These features better conform to those found in the juveniles of *Karasyazites* Mitta, 2018 (see below). The Luppov's specimen is a whorl fragment of a Riasanitidae that lack diagnostic features. As such, we therein consider *R. bogoslovskii* as invalid with respect to the ICZN Code.

Content: As herein understood, *Riasanites* should be restricted to the two following species:

- *R. rjasanensis* (Nikitin, 1888), including its junior synonyms *R. subrjasanensis* (Nikitin, 1888), *R. swistowianus* (Nikitin, 1888), and *R. decorus* Sazonova, 1977.
- *R. transitionis* (Mitta, 2018) (see discussion below).

Riasanites rjasanensis (Nikitin, 1888)

(Fig. 2A–G)

1883 *Ammonites rjasanensis* – Wenzky in Lahusen, p. 69.

1888 *Hoplites rjasanensis* (Lahusen) – Nikitin, p. 91, pl. 1, figs. 1–3.

1888 *Hoplites subrjasanensis* – Nikitin, p. 93, pl. 1, fig. 4.

1888 *Hoplites swistowianus* – Nikitin, p. 93, pl. 1, figs. 5–8.

1897 *Hoplites rjasanensis* (Lahusen) – Bogoslovsky, p. 83, pl. 5, figs. 3a, b, 4, 5a, b.

1897 *Hoplites subrjasanensis* Nikitin – Bogoslovsky, p. 87, pl. 5, fig. 6a–c.

non 1906 *Hoplites* cfr. *rjasanensis* (Lahusen) – Burckhardt, p. 135, pl. 34, figs. 15–18 (= *Perisphinctoidea* gen. et sp. indet.).

1949 *Hoplites swistowianus* (Nikitin) – Luppov et al., p. 221, text-fig. 46, pl. 63, fig. 3 (= Nikitin, 1888, pl. 1, fig. 8).

1949 *Riasanites rjasanensis* Wenzky (Nikitin) – Luppov et al., p. 220, pl. 63, fig. 2a, b (= Bogoslovsky, 1897, pl. 5, fig. 5a, b).

1951 *Riasanites rjasanensis* (Lahusen) – Bodylevsky, p. 101, pl. 50, fig. 187a, b (= Bogoslovsky, 1897, pl. 5, fig. 5a, b).

1956 *Riasanites rjasanensis* (Lahusen) – Arkell, p. 46, fig. 1a, b (= Nikitin, 1888, pl. 1, fig. 1).

1957 *Riasanites rjasanensis* (Lahusen) – Arkell et al., p. 352, fig. 462.5a, b (= Nikitin, 1888, pl. 1, fig. 1).

- 1958 *Riasanites rjasanensis* (Wenetzky in Lahusen) – Luppov and Drushchits, p. 97, pl. 43, fig. 3a, b (= Nikitin, 1888, pl. 1, fig. 1).
- 1958 *Riasanites swistowianus* (Nikitin) – Luppov and Drushchits, text-fig. 79c (= Nikitin, 1888, pl. 1, fig. 8).
- non 1960 *Riasanites rjasanensis* (Nikitin) – Drushchits, p. 278, pl. 22, figs. 3, 4a, b (= *Tauricoceras crassicostatus*).
- 1962 *Riasanites rjasanensis* (Lahusen) – Bodylevsky, p. 122, pl. 59, fig. 1a, b (= Nikitin, 1888, pl. 1, fig. 1).
- 1967 *Riasanites rjasanensis* (Wenetzky in Lahusen) – Marek, p. 187, pl. 1, figs. 8a, b, 9a–c, 10; pl. 2, figs. 1–4.
- 1969 *Riasanites rjasanensis* (Lahusen) – Witkowski, p. 92, pl. 19, fig. 3.
- non 1976 *Riasanites rjasanensis* (Nikitin) – Khimchiashvili, p. 103, pl. 5, fig. 5; pl. 16, fig. 5 (= ?*Tauricoceras maikopensis*).
- non 1976 *Riasanites rjasanensis caucasicus* – Khimchiashvili, p. 104, pl. 15, figs. 1, 2 (= ?*Tauricoceras maikopensis*).
- non 1976 *Riasanites swistowianus* (Nikitin) – Khimchiashvili, p. 105, pl. 18, fig. 1 (= *Tauricoceras maikopensis*).
- 1977 *Riasanites decorus* – Sazonova, p. 87, pl. 19, figs. 4a, b, 7a, b.
- 1977 *Riasanites rjasanensis* (Wenetzky) – Sazonova, p. 85, pl. 18, figs. 1a, b, 2a, b, 3a, b; pl. 19, figs. 1a, b, 2a, b; pl. 20, fig. 2a, b; pl. 21, fig. 13 (= Bogoslovsky, 1897, pl. 5, fig. 4).
- 1977 *Riasanites subrjasanensis* (Nikitin) – Sazonova, p. 86, pl. 18, fig. 4a, b; pl. 19, figs. 5a, b, 6a, b, 8a, b, 9a, b.
- 1977 *Riasanites swistowianus* (Nikitin) – Sazonova, p. 86, pl. 18, fig. 5a, b; pl. 20, fig. 1a, b
- 1979 *Riasanites rjasanensis* (Nikitin) – Luppov et al., p. 161, pl. 1, fig. 7.
- 1984 *Riasanites rjasanensis* (Nikitin) – Marek and Rajska, p. 110, pl. 40, fig. 4 (= Marek, 1967, pl. 2, fig. 1).
- 1984 *Riasanites rjasanensis* (Nikitin) – Sakharov, p. 184, pl. 6, fig. 2a, b; pl. 7, fig. 2.
- 1984 *Riasanites subrjasanensis* (Nikitin) – Sakharov, p. 40, pl. 7, fig. 3.
- 1988 *Riasanites rjasanensis* (Nikitin) – Luppov in Luppov et al., p. 130, pl. 17, figs. 4, 6 (= Luppov et al., 1979, pl. 1, fig. 7).

- 1988 *Riasanites* cf. *swistowianus* (Nikitin) – Luppov in Luppov et al., p. 133, pl. 13, fig. 5a, b.
- ? 1988 *Riasanites subrjasanensis* (Nikitin) – Luppov in Luppov et al., p. 132, pl. 13, figs. 6, 8.
- non 1988 *Riasanites* aff. *rjasanensis* (Nikitin) – Luppov in Luppov et al., p. 131, pl. 17, fig. 5 (= ?*Tauricoceras* sp.).
- non 1988 *Riasanites* ex gr. *rjasanensis* (Nikitin) – Luppov in Luppov, p. 131, pl. 17, fig. 7a, b (= ?*Tauricoceras maikopensis*).
- 1989 *Riasanites rjasanensis* (Nikitin) – Marek et al., p. 85, pl. 41, fig. 2 (= Marek, 1967, pl. 2, fig. 1).
- 1996 *Riasanites rjasanensis* (Lahusen) – Wright et al., p. 50, fig. 37.3a, b (= Nikitin, 1888, pl. 1, fig. 1).
- non 1998 *Riasanites rjasanensis* (Lahusen) – Howarth, p. 93, pl. 21, fig. 6a, b (= *Perisphinctoidea* gen. et sp. indet.).
- 1999 *Riasanites rjasanensis* (Nikitin) – Kvantaliani, p. 148, pl. 40, figs. 1a, b, 2a, b; pl. 41, figs. 1a, b, 2a, b, 3a, b.
- 1999 *Riasanites subrjasanensis* (Nikitin) – Kvantaliani, p. 150, pl. 41, figs. 4a, b, 5a, b; pl. 42, figs. 1a, b, 2a, b; pl. 43, figs. 1a, b, 2a, b.
- 1999 *Riasanites swistowianus* (Nikitin) – Kvantaliani, p. 151, pl. 43, figs. 3a–e (= Nikitin, 1888, pl. 1, fig. 5), 4a, b.
- non 1999 *Riasanites rjasanensis* (Nikitin) – Sey and Kalacheva, pl. 1, figs. 1, 2a, b; pl. 3, fig. 1 (= *Tauricoceras maikopensis*).
- non 1999 *Riasanites subrjasanensis* (Nikitin) – Sey and Kalacheva, pl. 1, fig. 3; pl. 3, figs. 2a, b, 3a, b (= *Tauricoceras maikopensis*).
- non 1999 *Riasanites swistowianus* (Nikitin) – Sey and Kalacheva, pl. 3, fig. 4 (= *Tauricoceras* sp. juv.).
- non 2000 *Riasanites rjasanensis* (Nikitin) – Kalacheva and Sey, p. 96, pl. 12, figs. 2a, b, 3, 4a, b (= Sey and Kalacheva, 1999, pl. 3, fig. 1); pl. 13, fig. 1a, b; pl. 22, fig. 2 (= *Tauricoceras maikopensis*).
- non 2000 *Riasanites subrjasanensis* (Nikitin) – Kalacheva and Sey, p. 97, pl. 12, fig. 5a, b (= Sey and Kalacheva, 1999, pl. 3, fig. 3a, b); pl. 13, figs. 2a, b, 3a, b (= Sey and Kalacheva, 1999, pl. 3, fig. 2a, b); pl. 14, fig. 1 (= Sey and Kalacheva, 1999, pl. 1, fig. 3), 3a, b (= *T. maikopensis*).

non 2000 *Riasanites swistowianus* (Nikitin) – Kalacheva and Sey, p. 98, pl. 14, fig. 4
(= Sey and Kalacheva, 1999, pl. 3, fig. 4).

2007a *Riasanites rjasanensis* (Nikitin) – Mitta, pl. 2, fig. 1; pl. 3, figs. 3, 4.

2008 *Riasanites rjasanensis* (Nikitin) – Mitta, p. 256, text-fig. 1, pl. 5, figs. 1a, b, 2a, b (= Mitta, 2007a, pl. 2, fig. 1), 3, 4a, b, 6a, b, 7, 8, 9a, b.

2011 *Riasanites rjasanensis* (Nikitin) – Mitta and Sha, pl. 3, fig. 4.

? 2015 *Riasanites* sp. – Rogov et al., pl. 7, fig. 5.

? 2015 *Riasanites* cf. *rjasanensis* (Nikitin) – Rogov et al., pl. 7, fig. 4.

? 2015 *Riasanites* cf. *swistowianus* (Nikitin) – Rogov et al., pl. 7, fig. 9.

non 2016 *Riasanites* cf. *swistowianus* (Nikitin) – Vašíček and Skupien, fig. 7B, C.

2018 *Riasanites rjasanensis* (Nikitin) morph β – Mitta, pl. 5, fig. 5.

Type and studied material: The lectotype designated by Kalacheva and Sey (2000) is specimen VSEGEI 1/81 (Nikitin's collection) from the Oka River, Ryazan region; hand-drawn by Nikitin (1888, pl. 1, fig. 1). The biometric study in Fig. 3 is based on the measured specimens from Mitta (2008) and those from Kvantaliani (1999) for *R. subrjasanensis* and Sazonova (1977) for *R. decorus* (see also Table 1)

Diagnosis: See above.

Remarks: *Riasanites transitionis* (Mitta, 2018) was originally assigned to the genus *Transcaspiites*. The species is close to *R. rjasanensis* from which it only differs by more inflated juvenile whorls with denser ribbing, thickened nodes on the adult whorl, and compressed whorl section in the adult microconchs (Mitta, 2018, p. 251).

Occurrence: In the Russian Platform, *R. rjasanensis* flourishes during the *Riasanites rjasanensis* and *Surites spasskensis* zones as defined by Mitta (2017). Beside Russia, the species also occurs in the Caucasus (e.g., Kvantaliani, 1999), Mangyshlak (Luppov in Luppov et al., 1988), Polish Lowland (e.g., Marek, 1967; Mitta and Ploch, 2012), and doubtfully in the Middle Volga (Rogov et al., 2015). The record of *R. cf. swistowianus* from Štramberg (Vašíček and Skupien, 2016, fig. 7B, C) should be ruled out since the corresponding specimen conforms well to small-sized (?microconch) individuals of *T. crassicostatum* (compare with Kvantaliani, 1999, pl. 35, fig. 2a, b for example). Finally, the reports of *Riasanites* from Mexico (*Hoplites* cfr. *rjasanensis*? in Burckhardt, 1906) and Yemen (*R. rjasanensis* in Howarth, 1998) are based on misinterpretation of doubtful perisphinctoid specimens, while those from

Argentina (*Riasanites rjasanenoides* Krantz in Krantz, 1928) have been re-assigned to *Corongoceras* (see Parent et al., 2011).

Genus *Riasanella* Mitta, 2011b

Type species: *R. rausingi* Mitta, 2011b; by original designation.

Diagnosis: See diagnosis of the type species, below.

Remarks: Mitta (2011b) introduced the genus *Riasanella* — based on *R. riasanitoides*, *R. plana*, *R. rausingi*, and *R. olorizi* the type species — for small-sized, neocomitid-like ammonites from the Russian platform. Their material originates from a thin, phosphatized sandstone horizon cropping out in quarry no. 12-2 of the Lopatinskii Phosphorite Mine, Moscow region. According to Mitta (2011b), *R. olorizi* differs from *R. rausingi* and *R. plana* by a larger size (average value of 60 mm for *R. olorizi* compared to 40 mm for the two other species), a lesser number of simple and intercalated ribs at a same diameter, and distinctly developed umbilical and lateral nodes in the adult. The predominance of intercalated and simple ribs on the phragmocone and the weakness or lack of crest-like bulges would also distinguish *R. plana* from *R. rausingi* and *R. riasanitoides* (Mitta, 2011b).

Mitta (2011b) recognized the lineage *R. olorizi* → *R. rausingi* → *R. plana* but the condensation of their type horizon strongly suggests that this distinction is unlikely. Differences in ribbing are not conclusive for specific identification, because *Riasanella* relatives display complex ribbing composed of slightly convex, simple, bi-, trifurcate and fasciculate ribs and irregular intercalatories (Fig. 2H–K). The thickening of the lateral crest-like bulges in the adult shows little variability among the population and cannot be used as a reliable diagnostic character. Finally, the morphometrics provided by Mitta (2011b) for the 29 known *Riasanella* type specimens most probably reflect intraspecific variability within a single palaeobiological taxon, rather than four distinct species. This is reflected by the covariation of involution and whorl proportions of the four *Riasanella* relatives (Fig. 4). The four species are here tentatively synonymised with the type species *R. rausingi*.

Furthermore, Mitta (2009, 2011b) recognized the lineage *Riasanella riasanitoides* → *Riasanites swistowianus* → *Riasanites rjasanensis* morph α → *Riasanites rjasanensis* morph β . However, except for reports of doubtful relatives (i.e., *Riasanites* sp., ?*Riasanites* sp.) in underlying and overlying beds, all the *Riasanites*

species co-occur in a restricted condensed horizon of 20 to 120 cm in thickness (Mitta, 2017, fig. 2). Contrary to Mitta (2008, pp. 252–253), the phyletic relationships between and among the *Riasanella*–*Riasanites* plexus remain uncertain, since *Riasanites* can only be distinguished by the reduced length of its adult stage, and a more depressed whorl section in the juvenile and involute coiling (Fig. 2H–K). Pending more material, we suggest keeping separate the two genera.

Content: *Riasanella rausingi* Mitta, 2011b.

Riasanella rausingi Mitta, 2011b emend. herein

(Fig. 2H–K)

2007a Himalayitidae gen. et sp. nov. – Mitta, pl. 2, fig. 3.

2011b *Riasanella olorizi* – Mitta, p. 20, text-fig. 1a–d.

2011b *Riasanella plana* – Mitta, p. 17, pl. 2, figs. 1a, b, 2, 3a, b, 4a–c, 5, 6, 7a, b, 8a–c, 9, 10, 11a, b.

2011b *Riasanella rausingi* – Mitta, p. 17, pl. 2, figs. 1a, b, 2a–c, 3a, b, 4a, b (= Mitta, 2007a, pl. 2, fig. 3), 5, 6a, b, 7a, b, 8a, b, 9, 10a–c, 11a, b.

2011b *Riasanella riasanitoides* – Mitta, p. 20, text-fig. 2a, b, c–e.

non 2016 *Riasanella* cf. *rausingi* Mitta – Vašíček and Skupien, p. 22, fig. 7A (= *Perisphinctoidea* gen. et sp. indet.).

Type and studied material: The holotype designated by Mitta (2011b, pl. 2, fig. 4a, b) is specimen PIN 3990/264; here re-illustrated on Fig. 2H, I). It originates from the lower part of the *Riasanites rjasanensis* Zone as defined by Mitta (2017) from the quarry no. 12-2, Lopatinskii Phosphorite Mine, Moscow region. The biometric study conducted in Fig. 4 is based on the 29 type specimens measured by Mitta (2011b) (see also Table 1).

Emended diagnosis: Small-sized, dimorphic, planulate ammonite with evolute to moderately involute coiling, subrectangular whorl section in the juvenile becoming subtrapezoidal to suboval in the adult. Umbilical wall is low, with rounded or gently sloping margin. Ornamentation encompasses, fully or partly, the four stages typical of *Riasanites* defined above. Suture line remains unknown.

Remarks: Specimens PIN 3990/369 and PIN 3990/371 were tentatively assigned to *Malbosiceras* sp. by Mitta (2011a, text-fig. 1a–c, d, e). Both specimens lack inner

whorls but their last preserved whorls show close affinities with *Riasanella* relatives. These specimens are tentatively referred to as *Riasanella* sp.

Occurrence: The species *R. rausingi* is restricted to the *Rjasanites rjasanensis* Zone of the Russian Platform — Moscow and (?) Ryazan region — according to Mitta (2008). The report of a single specimen assigned to *R. cf. rausingi* from the early Berriasian of Štramberk (Czech Republic) is doubtful since based on a poorly preserved perisphinctoid fragment that lacks any valuable diagnostic features (see Vašíček and Skupien, 2016, fig. 7A).

Genus *Prorjasanites* Sazonova, 1977

Type species: *Prorjasanites plumatus* Sazonova, 1977; by original designation.

Diagnosis: see Sazonova (1977, p. 88).

Remarks: Mitta (2008) synonymised *Prorjasanites* with *Riasanites* considering that the *Prorjasanites* taxa *P. plumatus* and *P. vnigni* illustrate densely ribbed juveniles of *Riasanites rjasanensis*. As discussed above, the juveniles of *R. rjasanensis* never develop such dense ribbing (> 30 ventral ribs on the last preserved whorls at D ~30 mm) as those observed on *Prorjasanites* (compare with Mitta, 2008, pl. 5, figs. 5, 7 and pl. 6, figs. 1, 2 for example). As such, we prefer keeping separate the two genera.

The type material of *P. plumatus* and *P. vnigni* correspond to small-sized phragmocones (Fig. 5A–E). Their adult whorls thus remain unknown. Nevertheless, Mitta (2007a, pl. 3, figs. 6a, b, 7a, b) figured two Russian platform individuals (PIN 3990/260 and PIN 3990/261) whose inner whorls match well those of *Prorjasanites* (see Fig. 5F–H). The Mitta's specimen figured on Fig. 5F–G was selected as holotype of the species *Berriasella rulevae* Mitta, 2007a. This species has been subsequently transferred into *Riasanites* by Mitta (2011b) without explanation. The holotypes of *B. rulevae* and *P. plumatus* both originate from the *Surites spasskensis* Zone of the Spassk district (Sazonova, 1977; Mitta, 2007a). Their strong affinities and identical stratigraphical origin support a co-specificity between the two species. Pending more material, *B. rulevae* is thereafter transferred into *Prorjasanites*.

Content: The genus *Prorjasanites*, as herein understood, includes *P. plumatus*, *P. vnigni*, and *P. rulevae*.

Prorjasanites rulevae (Mitta, 2007a)

(Fig. 5)

2007a *Berriasella rulevae* – Mitta, p. 201, pl. 3, figs. 6a, b, 7a, b.

2011b *Riasanites* aff. *maikopensis* Grigorieva – Mitta, fig. 3a, b.

2018 *Riasanites* aff. *maikopensis* Grigorieva – Mitta, pl. 5, fig. 6 (= ventral view of Mitta, 2011b, fig. 3a, b).

Type and studied material: The holotype designated by Mitta (2007a, pl. 3, fig. 6a, b) is specimen PIN 3990/260 from the *Surites spasskensis* Zone of the Oka River, downstream of the Nikitino village, Spassk district, Ryazan region; here re-illustrated in Fig. 5F, G. Other studied specimen includes PIN 3990/402 of same origin (Mitta, 2011b, 2018). It is re-illustrated on Fig. 5H.

Diagnosis: Medium-sized, planulate ammonite with a subrectangular whorl section in the juvenile, which changes into a suboval whorl section, with flattened venter, slightly convex flanks and moderately low umbilical wall in the adult. Juvenile ornamentation composed of sharp, slightly flexuous to falcid primary ribs and irregular intercalatories. Ribs are simple, bi- or trifurcate at mid-flank and they thicken towards the umbilicus. On the peri-ventral margin, branches of the ribs are slightly elevated, and there is a weak ventral furrow. In later growth stages, ribbing becomes more spaced and composed of irregular simple, bifurcate, rarely trifurcate, primary ribs with one or two intercalatories on the upper flank. Ribs tend to cross a rounded venter without weakening.

Remarks: Specimen PIN 3990/402 was tentatively assigned to *Riasanites* aff. *maikopensis* by Mitta (2011b, fig. 3a, b). This specimen can be distinguished from this species by its medium-sized, planulate shell with a suboval whorl section, slightly convex flanks, rounded venter and moderately low umbilical wall in the adult. The ornamentation comprises two stages marked by (i) dense, slightly flexuous to falcid, mostly simple and bifurcate ribs and simple intercalatories; (ii) spaced and irregular simple and bifurcate ribs with generally one intercalatory in the upper flank. Ribs cross the venter without weakening on the last preserved whorl. By its morphological and ornamental features, specimen PIN 3990/402 is identical to *P. rulevae*.

Occurrence: *Prorjasanites* relatives are endemic to the Russian Platform and restricted to the lower part of the *Surites spasskensis* Zone as defined by Mitta (2017).

Genus *Mittaites* n. gen.

Etymology: Named in honour of the Russian ammonitologist Vasily V. Mitter for his contribution to the systematics of the ‘Ryazanian’-type ammonites.

Type species: As designed herein, *Mazenoticerias ceccai* Mitter, 2011a.

Type locality: Lopatinskii Phosphorite Mine, Moscow region.

Diagnosis: *Mittaites* n. gen. groups dimorphic, medium- to large-sized, riasanitid planulate ammonites.

In the microconchs, the ornamentation shows three ornamental stages: (i) rigid, simple ribs in the juvenile which are more or less thickened on the upper flank; (ii) ribs spaced, prorsiradiate, simple and bifurcate, rarely trifurcate with, commonly, one single intercalatory in the subadult. Point of furcation of bifurcate ribs occur in the upper flank and thickens as growth increases; (iii) ribbing is markedly thickened and irregular in the adult. Ribbing is mainly composed of bifurcate or trifurcate ribs that form two sur-elevated, rounded node- or spine-like tubercles on the flanks and thickenings on the peri-ventral margin. The number of intercalatories is variable. The whorl section is compressed, sub-hexagonal during this stage, with a flattened to rounded venter with a narrow furrow. The last tends to disappear near the aperture. Rare bifurcations of the primary ribs are observed from the umbilical nodes in *M. ceccai*, but they bifurcate also at mid flank.

The macroconchs show the three ornamental stages described above, and they develop a terminal stage characterised by markedly spaced, elevated, mostly simple rib folds with smooth interspaces. The maximum rib thickness is reached on the venter.

Remarks: Mitter (2011a) introduced two new species assigned to the western Mediterranean-Caucasian neocomitid genus *Mazenoticerias*, namely *M. robustum* (holotype re-illustrated in Fig. 6A, B) and *M. ceccai* (Fig. 6C–E). Both species are characteristically medium- to large-sized, planulate, dimorphic shell with moderately evolute coiling. The whorl section is suboval, compressed (*M. robustum*) to depressed (*M. ceccai*) throughout ontogeny. The rounded umbilical wall becomes slightly steeper as at later growth stages. In juveniles, flanks and venter are flattened. By comparison, the type species *Mazenoticerias broussei* (Mazenot, 1939) differs distinctly from the Russian relatives by its less evolute coiling and its rectangular, higher-than-wide whorl section throughout ontogeny. *M. broussei* is also characterized by a flattened venter with a smooth band, except approaching the aperture. Its ornamentation changes little during ontogeny since it is characterised by

gracile, bituberculate primary ribs that bi- or trifurcate on the mid-flank with a variable number of intercalatories. Pending comprehensive revision, the Russian forms cannot be included into *Mazenoticerias* given their low degree of similarity with the latter. The introduction of *Mittaites* n. gen., based on *Mazenoticerias ceccai* Mitta, 2011a, is here proposed to separate the Russian platform taxa.

Content: *Mittaites* n. gen. includes *M. ceccai*, *M. robustum*, and *Hoplites micheicus* Bogoslovsky, 1897 (see discussion below).

Mittaites ceccai (Mitta, 2011a)

(Fig. 6C–E)

2002 *Euthymicerias euthymi* (Pictet) – Mitta, pl. 3, fig. 4.

2005 *Malbosicerias* aff. *boisseti* Nikolov – Mitta, pl. 2, fig. 1a–c.

2006 *Mazenoticerias* cf. *urukhense* Kalacheva and Sey – Mitta, text-fig. 2.

2007a *Mazenoticerias* cf. *urukhense* Kalacheva and Sey – Mitta, pl. 2, fig. 4.

2011a *Mazenoticerias ceccai* – Mitta, p. 152, text-fig. 2, pl. 5, figs. 5a, b, 6a, b, 7; pl. 6, figs. 1a–c, 2a, b, 3a, b.

Type and studied material: The holotype designated by Mitta (2011a, pl. 6, fig. 1a–c) is specimen PIN 3990/386 from the Lopatinskii Phosphorite Mine, Moscow region; here re-illustrated in Fig. 6C–E. Other specimens include those figured by Mitta (2002, 2005, 2006, 2007a, 2011a) (see synonymy list above).

Diagnosis: See Mitta (2011a, p. 152) and genus diagnosis above.

Remarks: The large-sized body chamber PIN 3990/265, lacking inner whorls, was assigned to the species *Mazenoticerias* cf. *urukhense* by Mitta (2007a, pl. 2, fig. 4). Superficially, its morphological and ornamental features match those of the type series of *M. urukhense*, such as the largest examples from northern Caucasus illustrated by Kalacheva and Sey (2000, pl. 9, fig. 4 and pl. 10, fig. 2). Unfortunately, the lack of inner whorls prevents further comparison, as well as any discussion about the supposed coevality of *M. urukhense* and the genus *Mazenoticerias*. As herein understood, the specimen better compares with the body chamber of *M. ceccai* (compare with its holotype PIN 3990/386).

Two specimens (VNIGNI CR-2564 and CR-2565) were first assigned to *Euthymicerias euthymi* by Mitta (2002, pl. 3, fig. 4a, b) and Mitta (2002, pl. 3, fig. 5a,

b). Both specimens were subsequently re-assigned to *Mazenoticerias ceccai* by Mitta (2011a, p. 147), a view followed here (see synonymy list above).

One specimen (PIN 3900/246) was assigned to *Malbosiceras* aff. *boisseti* by Mitta (2005, pl. 2, fig. 1a–c). In agreement with the subsequent revision by Mitta (2011a, p. 147), it is here re-assigned to *M. ceccai*.

Two further specimens (PIN 3990/387 and PIN 3990/392) were tentatively assigned to *Mazenoticerias* sp. by Mitta (2011a, text-figs. 3g, h, 4a–d). Both seemingly belong to *M. robustum*, since they closely match the specimen PIN 3990/383 (Mitta, 2011b, pl. 5, fig. 3a, b).

A specimen (AVS 1236) was identified as *Pomeliceras* sp. by Mitta (2011a, fig. 3a, b). However, it shows robust diagnostic juvenile features of *M. robustum* such as those observed in specimen PIN 3990/375 (Mitta, 2011b, text-fig. 3c, d); viz. a depressed, inflated shell with deep umbilicus, rounded venter with ventral weakening, and inflated upper lateral spines with a bundle of branches. Both specimens can be interpreted as to robust form of *M. robustum* with respect to its holotype.

Note finally that the specimen PIN 3900/248 identified as *Malbosiceras nikolovi* by Mitta (2005, pl. 2, fig. 4a–c) is here re-assigned to *R. transitionis*.

Occurrence: Representatives of *Mittaites* n. gen. are endemic to the Russian Platform and restricted to the lower part of the *Riasanites rjasanensis* Zone as defined by Mitta (2017). According to Mitta (2011a), *M. robustum* is stratigraphically older than *M. ceccai*. The latter was to be distinguished by its more inflated juvenile morphology and less coarse ribbing.

Mittaites micheicus (Bogoslovsky, 1897)

(Fig. 7A–C)

1897 *Hoplites micheicus* – Bogoslovsky, p. 94, pl. 6, fig. 1a–c.

non 1964 *Berriasella (Protacanthodiscus)* aff. *micheicus* (Bogoslovsky) – Jeletzky, pl. 2, fig. 11a–c (= *Perisphinctoidea* gen. et sp. indet.).

non 1965 *Berriasella (Protacanthodiscus)* aff. *micheicus* (Bogoslovsky) – Jeletzky, pl. 11, fig. 4A, C, D (= Jeletzky, 1964, pl. 2, fig. 11a–c).

2007a *Transcaspiites transfigurabilis* (Bogoslovsky) – Mitta, pl. 3, figs. 1a–d, 2.

2008 *Transcaspiites transfigurabilis* (Bogoslovsky) – Mitta and Bogomolov, text-fig. 1.2.

2018 *Transcaspiites tscheffkini* – Mitta, p. 249, pl. 4, figs. 1 (= Mitta and Bogomolov, 2008, text-fig. 1.2), 2 (= Mitta, 2007a, pl. 3, fig. 1c, d).

Type and studied material: The holotype by monotypy is specimen VSEGEI 63-62/623 from the Pozhva River, downstream of the village of Mikhei, Sapozhok district. Photographs of the holotype are illustrated for the first time in Fig. 7A–C. Other specimens include specimens figured by Mitta (2007a) and Mitta and Bogomolov (2018) which were assigned to *Transcaspiites tscheffkini*.

Emended diagnosis: Small to medium size, planulate ammonite with an evolute coiling with a deep umbilicus. Whorl section is inflated and subhexagonal in the juvenile and becomes suboval, but markedly depressed, in the adult with a distinctly rounded umbilical wall. Venter is slightly flattened in the adult. Ornamentation encompasses the three ontogenetic stages of the microconch relatives. Stage (ii) is shorter than in the type species and marked by inflated ribs with massive tubercles at the point of furcation. Rib branches define a distinct ventral furrow. Stage (iii) comprises most of the last whorl, which is dominated by straight to prorsiradiate bifurcate ribs with elevated, extended tubercles on the flank. The number of intercalatories is variable. The rib section is sub-hexagonal with flattened to rounded venter without ventral weakening of the ribs.

Remarks: Mitta (2007a, pl. 3, figs. 1a–d, 2) and Mitta and Bogomolov (2008, text-fig. 1.2) reported three closely allied specimens from the Oka River (PIN 3990/255, 3990/416, and 3990/256) identified as *Transcaspiites transfigurabilis*. The first two specimens have been subsequently re-interpreted as *Transcaspiites tscheffkini* Mitta, 2018. In our opinion, none of these specimens share the morphology and ornament that characterise the genus *Transcaspiites*. Indeed, the holotype of the type species *T. transfigurabilis* (re-illustrated by Luppov et al., 1949, pl. 64, fig. 3a, b) is a body chamber fragment that differs from Mitta's specimens in having a compressed, subhexagonal whorl section with a flattened venter bordered by enlarged bulges on the peri-ventral margin. The inner whorls of the holotype of *T. transfigurabilis* are lacking and prevent further comparison.

The early whorls of *T. tscheffkini* (Fig. 7D, E) share superficial affinities with those of the holotype of *T. transcaspicus* (here re-illustrated on Fig. 7H–J), such as the depressed, inflated shell with deep umbilicus, ventral band, rounded venter with ventral weakening of the ribs, inflated upper lateral spines with bundle of branches.

However, *T. tscheffkini* differs in having a depressed, subrounded whorl section in the adult that only bears uni-tuberculate bifurcate ribs and irregular intercalatories (Fig. 7F, G). Thus, *T. tscheffkini* does not truly compare to *Transcaspiites*.

Re-examination of the Bogoslovsky (1897)'s material from the Oka River suggests that *T. tscheffkini* is closely allied to the holotype of *Hoplites micheicus* Bogoslovsky, 1897 (see Fig. 7A–C), as illustrated in the emended diagnosis given above. To the difference of Luppov in Luppov et al. (1988, p. 128), we are reluctant to consider *H. micheicus* as a *Transcaspiites* representative. The general features of *H. micheicus* share more similarities with those of *Mittaites* n. gen. *ceccai* and *Mittaites* n. gen. *robustum*. It is tempting to consider *H. micheicus* as a derivative of *M. robustum* by modification of the juvenile whorl shape which affected the robustness of the tuberculation mostly during the sub-adult stage. Pending further investigation, *H. micheicus* is retained as a senior subjective synonym of *T. tscheffkini* and referred to *Mittaites* n. gen.

Finally, Mitta (2018, figs. 3a–d, 4) assigned three incomplete specimens (PIN 3990/423, PIN 3990/424, and PIN 3990/442) from the Russian platform to *Transcaspiites transfigurabilis*. We are also reluctant to refer these specimens to *Transcaspiites* to which they only share a sub-hexagonal whorl section with a flattened venter in the adult. The Russian forms are far closer to 'Euthymiceras' from North Caucasus and Crimea, such as 'E.' *euthymi* as understood by Kvantaliani (1999), Kalacheva and Sey (2000) and Arkadiev and Bogdanova (2009). Pending the systematic revision of the genus *Euthymiceras*, the occurrence of *Transcaspiites* in the Russian Platform should be ruled out.

Occurrence: The precise stratigraphical origin of *M. micheicus* remains unknown. However, its potential subjective synonym *T. tscheffkini* occurs in the lower part of the *Surites spasskensis* Zone as defined by Mitta (2017) in the Oka River section, downstream of the village of Nikitino, Ryazan district.

Family ?Neocomitidae Salfeld, 1921

Genus *Karasyazites* Mitta, 2018

Type species: *Subalpinites bajarunasi* (Luppov in Luppov et al., 1988); by original designation.

Emended diagnosis: Small to medium-sized, neocomitid-like, dimorphic ammonite.

Microconchs characterized by moderately involute shell with a compressed, subrectangular to suboval whorl section marked by convex flanks, flattened venter and a moderately deep umbilicus, at least on the juvenile and sub-adult whorls. Rounded in the juvenile, the umbilical wall becomes markedly steeper on the adult whorl. Ornamentation composed of dense, prorsiradiate to slightly flexuous, simple and bifurcate, rarely fasciculate ribs and rare intercalatories. Primary ribs thicken on the peri-umbilical margin as nodes, from which two ribs can branch. Ribs weaken on the venter and generally form a narrow ventral band that disappears at later growth stages.

Macroconchs are larger ($D \leq 140$ mm) Inner whorls of which match those of the microconchs. They develop an adult stage marked by more evolute coiling with a compressed, subrectangular whorl section. Flanks are still convex, but the venter is subrounded. Umbilical wall is high, slightly oblique to rounded. Ornamentation changes to distant, prorsiradiate, uni- or bituberculate primary ribs that bi- or trifurcate on the upper flank, with a variable number of intercalatories. On body chamber, point of furcation can thicken and form slight tubercles. In the largest specimens, macroconchs develop a terminal stage marked by irregular, sparsely spaced attenuated ribs with enlarged peri-ventral clavi near the aperture.

Remarks: The genus *Karasyazites* was recently introduced by Mitta (2018) based on *Subalpinites bajarunasi* from the Mangyshlak Peninsula. The holotype VSEGEI 11104/9a and paratype VSEGEI 11104/9b of *S. bajarunasi* selected in Luppov et al. (1998) are herein re-illustrated in Fig. 8A–C and Fig. 8D, E, respectively. Mitta (2018) referred two specimens (PIN 3990/418 and AC 1112) from the Russia platform to the Luppov's taxon.

Specimen PIN 3990/418 (re-illustrated in Fig. 8F, G) is a large-sized incomplete individual while specimen AC 1112 is considered as its microconch counterpart. Specimen PIN 3990/418 conforms well to the holotype of *K. bajarunasi* but its affinities with AC 1112 are questionable. From our point of view, specimen AC 1112 better compares to *Riasanites transitionis* (compare with specimens figured by Mitta, 2018, pl. 5).

There is close affinity between specimen PIN 3990/418 and the Russian taxa referred to the genus *Subalpinites*; namely *S. krischtafowitschi*, *S. Faurieformis*, and *S. gruendeli* (see Mitta, 2002, 2009). These species form a homogenous dimorphic group whose macroconchs are closely allied to *K. bajarunasi* (compare holotype

VNIGNI CR-2562 of *S. krischtafowitschi* or paratype PIN 3990/329 of *S. faurieformis* for example — Fig. 8H-I). Unfortunately, Mitta (2018) only briefly discussed the relationships between *K. bajarunasi* and the genus *Subalpinites*, based on *S. fauriensis*. In our opinion, the Russian forms only exhibit superficial similarities with that genus. The type species *S. fauriensis* can be distinguished by its compressed, subrectangular whorl section with flattened venter, and its markedly steep umbilical wall that is found in all ontogenetic stages. This species also differs in showing an early appearance of a complex, uni- or bituberculate ornamental stage and in never developing the adult stage of the Russian forms. The largest specimens of *S. fauriensis* show dense or spaced, simple ribs that can branch from discrete or robust peri-umbilical bullae (see Le Hégarat, 1973, pl. 53, fig. 9; Nikolov, 1982, pl. 70, fig. 6a, b). As a result, the supposed affinities between the Trans-Caucasian and Mediterranean forms likely result from a basic case of homeomorphy. We, therefore, propose to gather the ‘*Subalpinites*’ relatives from the Russian Platform in the genus *Karasyazites*.

Content: *Subalpinites krischtafowitschi*, *S. faurieformis*, and *S. gruendeli* are close to *K. bajarunasi* and they are herein transferred to *Karasyazites*. The Russian species *Subalpinites remaneiformis* Mitta, 2009 is provisionally kept in *Karasyazites* since its adult stage develop a peculiar ribbing that never occurs in *Karasyazites* (see Fig. 9A). Note that Mitta (2005, 2007a) assigned three specimens to the Mediterranean Himalayitidae *Dalmasiceras*, namely *Dalmasiceras* ex gr. *djanelidzei* (PIN 3900/249 — Fig. 9D, E), *D. crassicostatum* (PIN 3900/247 — Fig. 9F, G) and *D.?* sp. (PIN 3990/266). None of them can be accommodated into the *Dalmasiceratinae* as understood by Frau et al. (2016a). The Russian forms merely belong to ?*Karasyazites remaneiformis* (compare with its paratype AVS 1002 re-illustrated in Fig. 9B, C).

Karasyazites bajarunasi (Luppov in Luppov et al., 1988)
(Fig. 8A–E)

1988 *Subalpinites bajarunasi* – Luppov in Luppov et al., text-fig. 43, p. 118, pl. 14, fig. 7; pl. 15, fig. 1.

? 2007a *Malbosiceras* cf. *macphersoni* (Kilian) – Mitta, pl. 2, fig. 6.

? 2018 *Karasyazites bajarunasi* (Luppov in Luppov et al.) – Mitta, p. 251, pl. 4, fig. 3a, b.

non 2018 *Karasyazites bajarunasi* (Luppov in Luppov et al.) – Mitta, p. 251, pl. 4, fig. 4a–c (= *R. transitionis*).

Type and studied material: As designated by Luppov in Luppov et al. (1988), the holotype is specimen VSEGEI 11104/9 from the vicinity of Karasyaz Well, Mangyshlak. It was illustrated by Luppov in Luppov et al. (1988, pl. 15, fig. 1a, b) and re-illustrated herein in Fig. 8A, B. Other material includes the specimens figured by Mitta (2007a, 2018) (see synonymy list above).

Diagnosis: See Mitta (2018, p. 251).

Remarks: The early whorls/juveniles of *Karasyazites* relatives display a neocomitid pattern exemplified by a compressed, subrectangular planulate shell, ventral furrow, regular bifurcate or fasciculate ribbing with umbilical bullae (see for example specimen PIN 3990/332 or PIN 3990/329 of *K. faurieformis*). The closest affinities of *Karasyazites* relatives are found with the Trans-Caucasian ‘*Dalmsiceras*’ of the group of ‘*D.*’ *abkhasica* Khimchiashvili, 1976 (including *D. belbekense* Bogdanova and Arkadiev, 1999, *D. miriani* Kvantaliani, 1999, *D. subtoucasii* Bogdanova and Arkadiev, 1999, and *D. tauricum* Bogdanova and Arkadiev, 1999). Both forms co-occur in Crimea (Arkadiev et al., 2012), northern Caucasus (Kalacheva and Sey, 2000) and Mangyshlak (Luppov et al., 1988). In our view, this species group deserves a full generic status since they only superficially match the type species *D. dalmasi*. Pending such systematic revision, we provisionally refer *Karasyazites* to the Neocomitidae.

One specimen (PIN 3990/26) was assigned by Mitta (2007a, pl. 2, fig. 6a, b) to *Malbosiceras* cf. *macphersoni*. It corresponds to a medium-sized, chambered fragment with morphological (depressed suboval whorl section) and ornamental (peri-umbilical bullae, ventral weakening) features better match those observed in *K. faurieformis*. It should be noted that the species *macphersoni* was considered as a subjective synonym of *Ammonites chaperi* Pictet, 1867; the type species of the genus *Lopeziceras* Frau et al., 2016a, but the genus should be considered as a junior subjective synonym of *Chapericeras* Hoedemaeker in Hoedemaeker et al., 2016, due to its later date of acceptance for publication.

Occurrence: The taxon was originally reported from the *Neocosmoceras* and *Septaliphoria semenovi* Zone of the Mangyshlak (Luppov et al., 1988) and from the lower part of the *Surites spasskensis* Zone in the Russian Platform (Mitta, 2017).

4. Significance of the fauna

Most ammonite determinations introduced by Mitta and collaborators do not stand up well when comparisons and verification are attempted with the Mediterranean Neocomitidae and Himalayitidae. Our re-examination casts doubt on the occurrence of ammonites of western Tethyan-origin/affinity on the Russian Platform. A comparative account revising Mitta's taxonomy is given in Table 2. Our re-interpretation suggests that endemism in that basin was higher than previously suggested, and this reinforces the view of that strong provincialism characterised it during the earliest Cretaceous (Lehmann et al., 2015).

Considering that no ammonite species enables correlation between the Tethyan and Boreal basins, magnetostratigraphy appears to be the most reliable tool to establish long-distance correlation (Schnabl et al., 2015). It is now admitted that the putative base of the Berriasian approximately falls in the *Craspedites taimyrensis* Zone that marks the middle part of the upper 'Volgian' in the Arctic (Schnabl et al., 2015; Rogov et al., 2016) (see also Fig. 10). According to these authors, the *C. taimyrensis* Zone and the overlying *Chetaites chetae* Zone, which terminates the 'Volgian', encompass the mid-M19r to upper-M18n magnetic zones. The overlying *Chetaites sibiricus* Zone — which starts the 'Ryazanian' — mostly correlates to the M17 to mid-M16r magnetic zones. The base of the overlying *Hectoroceras kochi* Zone is placed in M16r. Comparing the ammonite scale of the Arctic, the *Craspedites taimyrensis* Zone to lower *Chetaites sibiricus* Zone span the highest upper Tithonian and lower Berriasian in the Mediterranean region while the upper *Chetaites sibiricus* Zone to lower *Hectoroceras kochi* Zone span the middle Berriasian to lowest upper Berriasian (see Fig. 10).

On the Russian platform, the upper 'Volgian' includes the *Kachpurites fulgens*, *Garniericeras catenulatum*, and *Craspedites nodiger* zones, which have been tentatively correlated to the M20n.1n to the mid-M18r (Rogov, 2014) (Fig. 10). Above, the palaeomagnetic calibration of the 'Ryazanian' ammonite zones — *Hectoroceras kochi*, *Riasanites rjasanensis*, *Surites spasskensis*, and *Surites tzikwinianus* zones (Mitta, 2017) — remains unknown. As the 'Ryazanian' sedimentation is considered continuous although strongly condensed, a highest lower Berriasian to upper Berriasian can be provisionally assigned to the *Hectoroceras kochi* and *Riasanites rjasanensis* zones (Fig. 10). The lack of constraining microfossil

and palaeomagnetic evidence in Russia prevents any precise correlation between such boreal basins and oceanic Tethys. As a result, and pending new investigation, current correlations of the 'Ryazanian' type deposits with the Mediterranean sections should be cited with caution.

5. Conclusions

Our systematic re-assessment suggests an overlooked diversity in ammonite assemblages from the Russian Platform during the Berriasian, here reflected by the introduction of the Riasanitidae n. fam. Although its origin remains unclear, the *Gechiceras–Tauricoceras* lineage may have given way to the *Riasanella–Riasanites* plexus which spreads throughout the European part of the Boreal Atlantic Subrealm (Polish Lowland and Russian Platform) during the *Rjasanites rjasanensis* Zone. The *Riasanella–Riasanites* plexus represents the basal rootstock from which other riasanitid genera derived, i.e., *Prorjasanites*, *Mittaites* n. gen. Only the origin of *Karasyazites* remains in doubt. We hope that the present contribution will stimulate renewed discussion and investigation of the systematics and phyletic relationships of ammonites from the boreal regions.

Acknowledgements

We wish to express our warmest thanks to Emmanuel Robert (Claude Bernard-Lyon I University), Fabienne Giraud (Grenoble-Alpes Université), Isabelle Rouget and Philippe Loubry (UPMC/MNHN, Paris), and Christian Meister (MHN, Genève) who allowed us access to the collections in their care and Aleksey Sokolov (A.P. Karpinsky Russian Geological Research Institute) for sharing photographs of the Bogoslovsky's material. Yi-Chun Zhang, associate editor of Palaeoworld, Rafel Matamales-Andreu (Universitat Autònoma de Barcelona), and an anonymous reviewer greatly improved the original version of the manuscript by their insightful comments on the ammonite systematic. One of us (A.P.) has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No. 838373.

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Figure captions

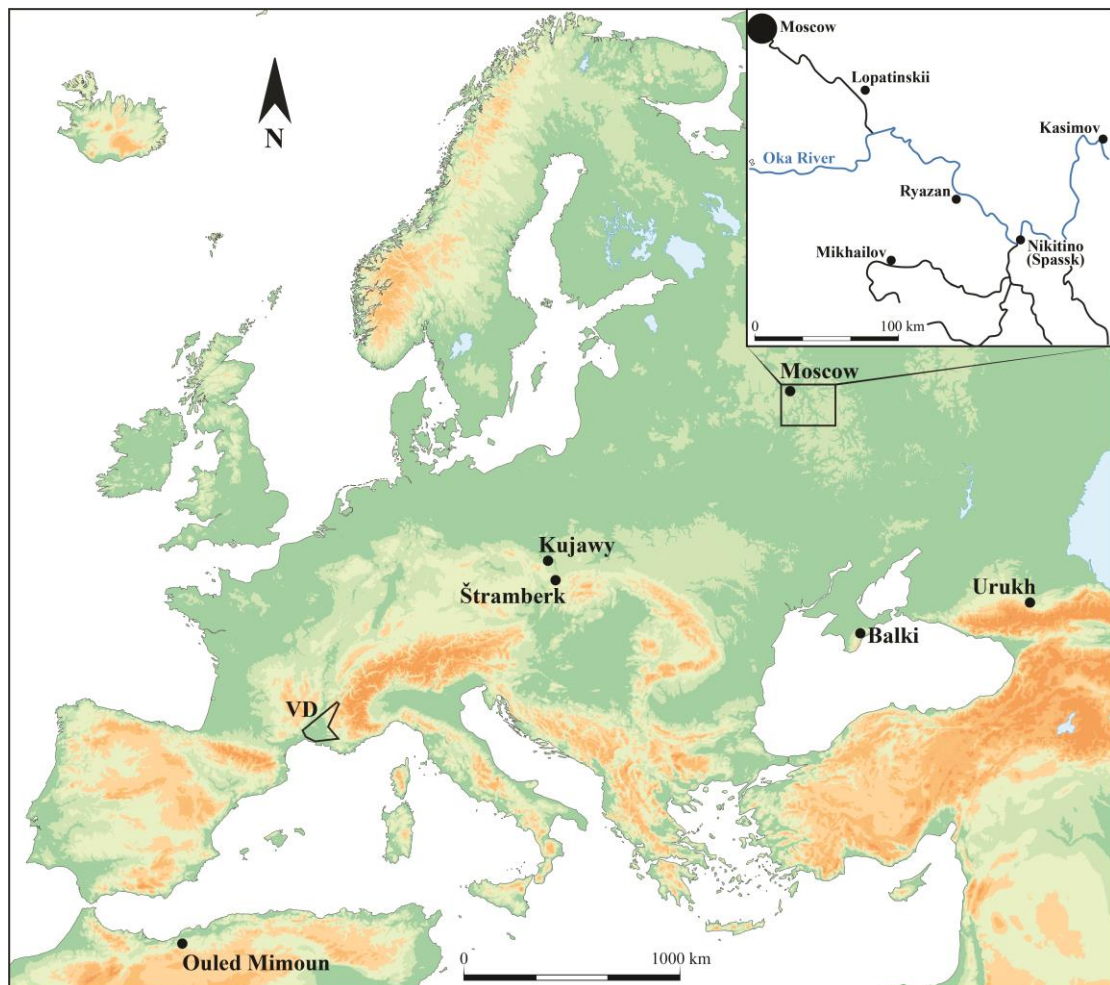


Fig. 1. Map of Europe and focus on the Russian platform study area including the main ‘Ryazanian’ ammonite localities cited in the text. VD indicates Vocontian Domain (southeastern France).

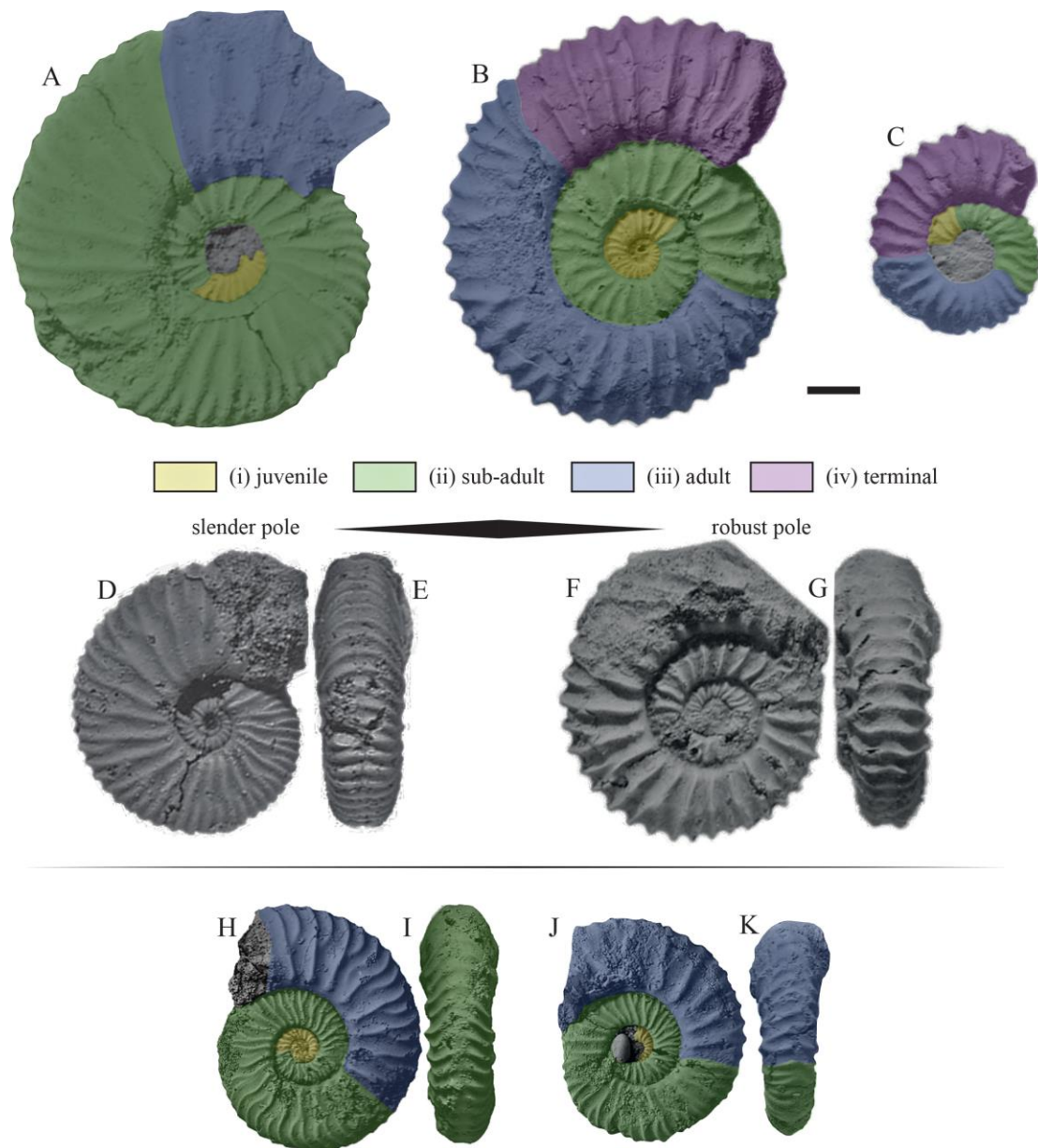


Fig. 2. Re-illustration of *Riasanites* (A–G) and *Riasanella* relatives (H–K) from the the type ‘Ryazanian’ and illustration of the four ornamental stages; (D–G) illustrate intraspecific covariation in the species *Riasanites rjasanensis*. (A) Specimen PIN 3990/294 of *Riasanites rjasanensis* (Nikitin, 1888) (Mitta, 2011b, fig. 1). (B) Specimen PIN 3390/290 of *Riasanites swistowianus* (Nikitin, 1888) (Mitta, 2011b, pl. 6, fig. 8a, b). (C) Specimen PIN 3390/286 of *Riasanites swistowianus* (Nikitin, 1888) (Mitta, 2011b, pl. 6, fig. 5). (D, E) Specimen PIN 3990/275 of *Riasanites rjasanensis* (Nikitin, 1888) (Mitta, 2011b, pl. 5, fig. 4a, b). (F, G) Specimen PIN 3390/291 of *Riasanites swistowianus* (Nikitin, 1888) (Mitta, 2011b, pl. 6, fig. 10a, b). (H, I) Specimen PIN 3990/264 of *Riasanella rausingi* Mitta, 2011b (Mitta, 2011b, pl. 2, fig.

4a, b), holotype. (J, K) Specimen PIN 3990/352 of *Riasanella rausingi* Mitta, 2011b (Mitta, 2011b, pl. 2, fig. 6a, b), paratype. Scale bar is 10 mm.

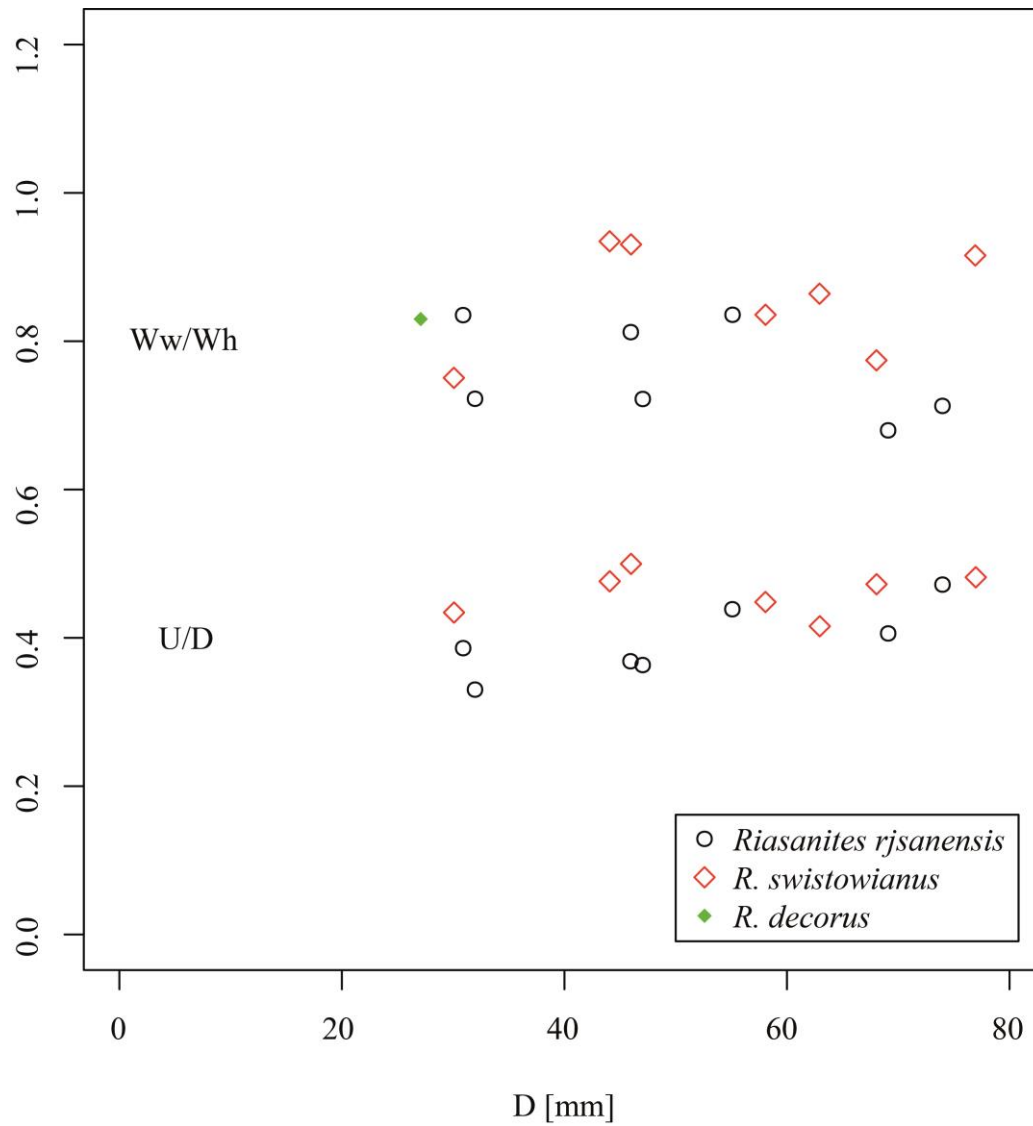


Fig. 3. Morphological relationships between the U/D and Ww/Wh ratios (common y-axis) during ontogenesis of the *Riasanites* species (data from Mitta, 2011b and Sazonova, 1977).

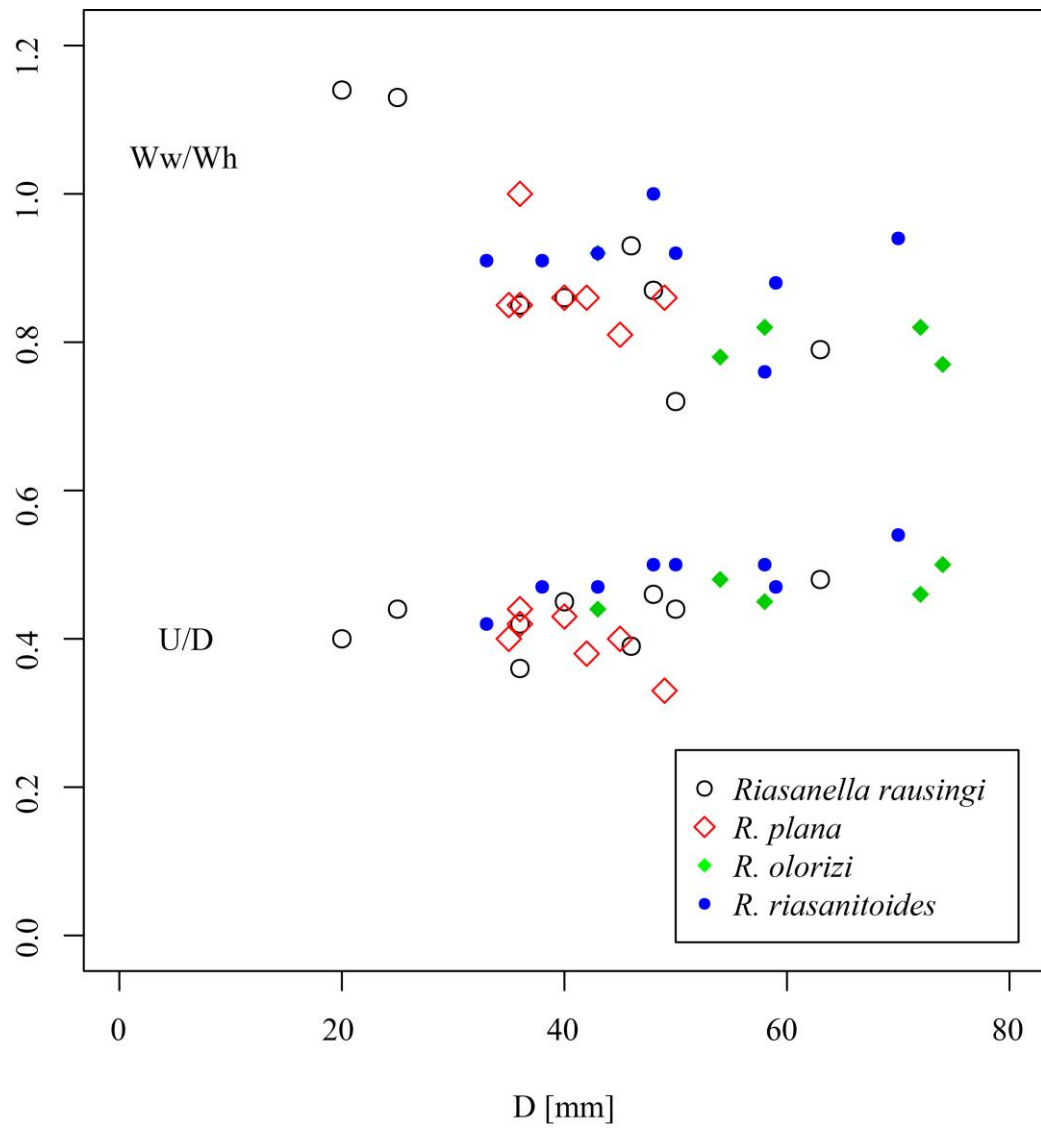


Fig. 4. Morphological relationships between the U/D and Ww/Wh ratios (common y-axis) during ontogenesis of the *Riasanella* species (data from Mitta, 2011b).

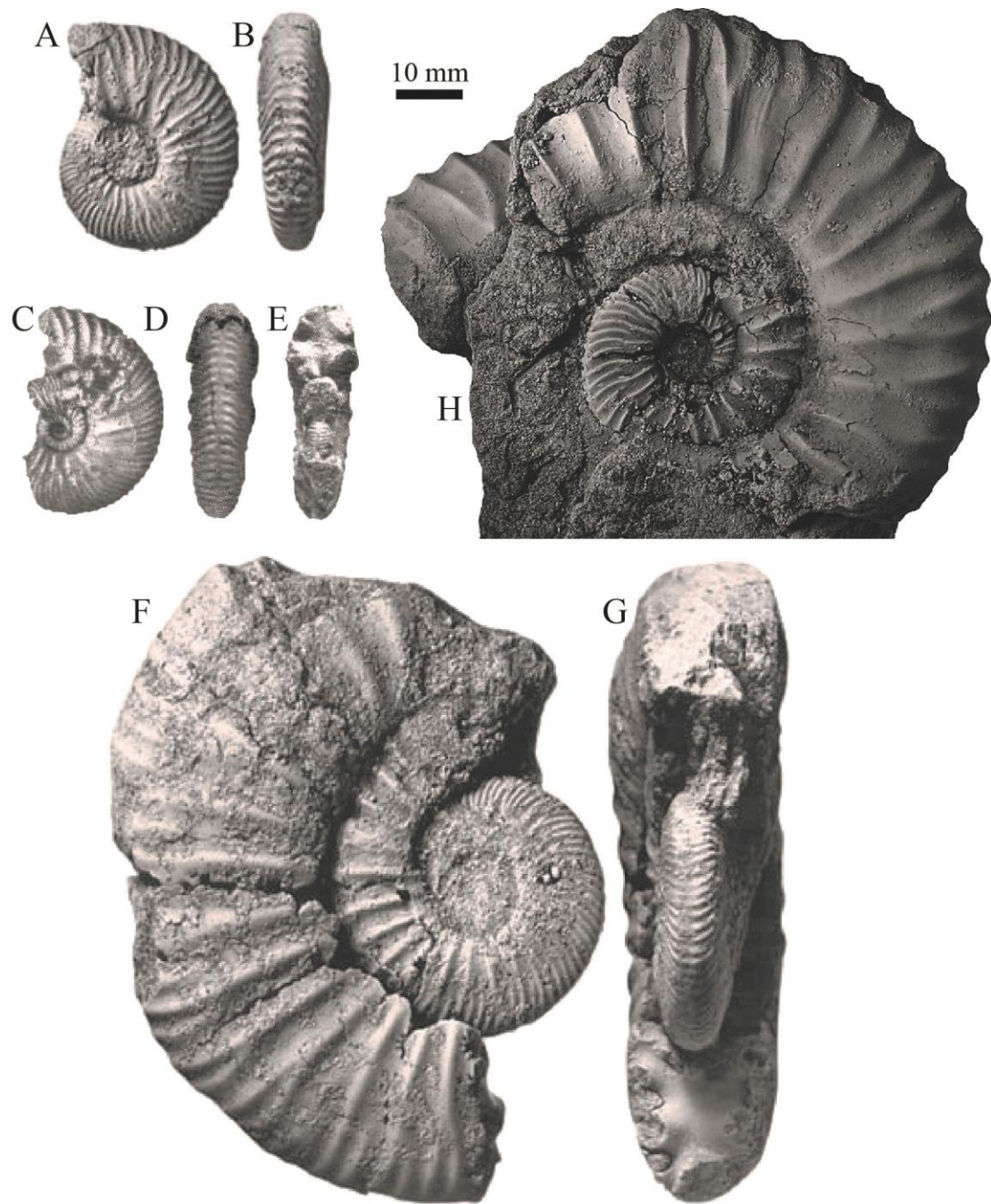


Fig. 5. Re-illustration of *Prorjasanites* relatives. (A, B) Specimen VSEGEI 113/10223 of *P. plumatus* Sazonova, 1977 (Sazonova, 1977, pl. 19, fig. 3), holotype. (C–E) Specimen VSEGEI 124/10223 of *P. vnigni* Sazonova, 1977 (Sazonova, 1977, pl. 20, fig. 4a, b), holotype. (F, G) Specimen PIN 3990/260 of *P. rulevae* (Mitta, 2007a) (Mitta, 2007a, pl. 3, fig. 6a, b), holotype. (H) Specimen PIN 3990/402 of *P. rulevae* (Mitta, 2007a) (previously assigned to *Riasanites* aff. *maikopensis* Grigorjeva, 1938 in Mitta, 2011b, text-fig. 3a, b).

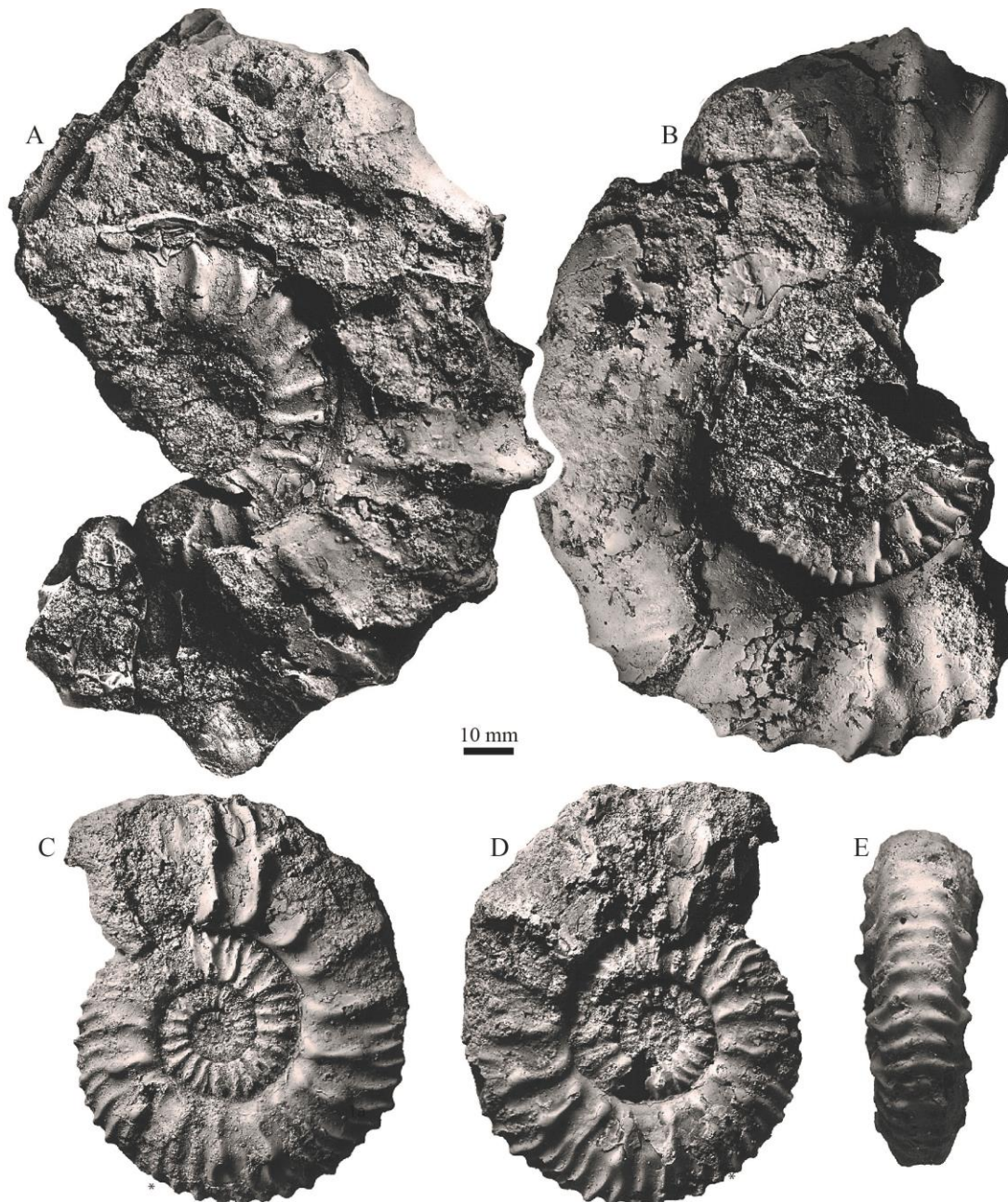


Fig. 6. Re-illustration of *Malbosiceras* relatives from the type 'Ryazanian' here re-assigned to *Mittaites* n. gen. (A, B) The holotype of *M. robustum* Mitta, 2011a (PIN 3990/373, Mitta, 2011a, pl. 5, fig. 4). (C–E) The holotype of *M. ceccai* (Mitta, 2011a) (PIN 3990/386, Mitta, 2011a, pl. 6, fig. 1a–c).

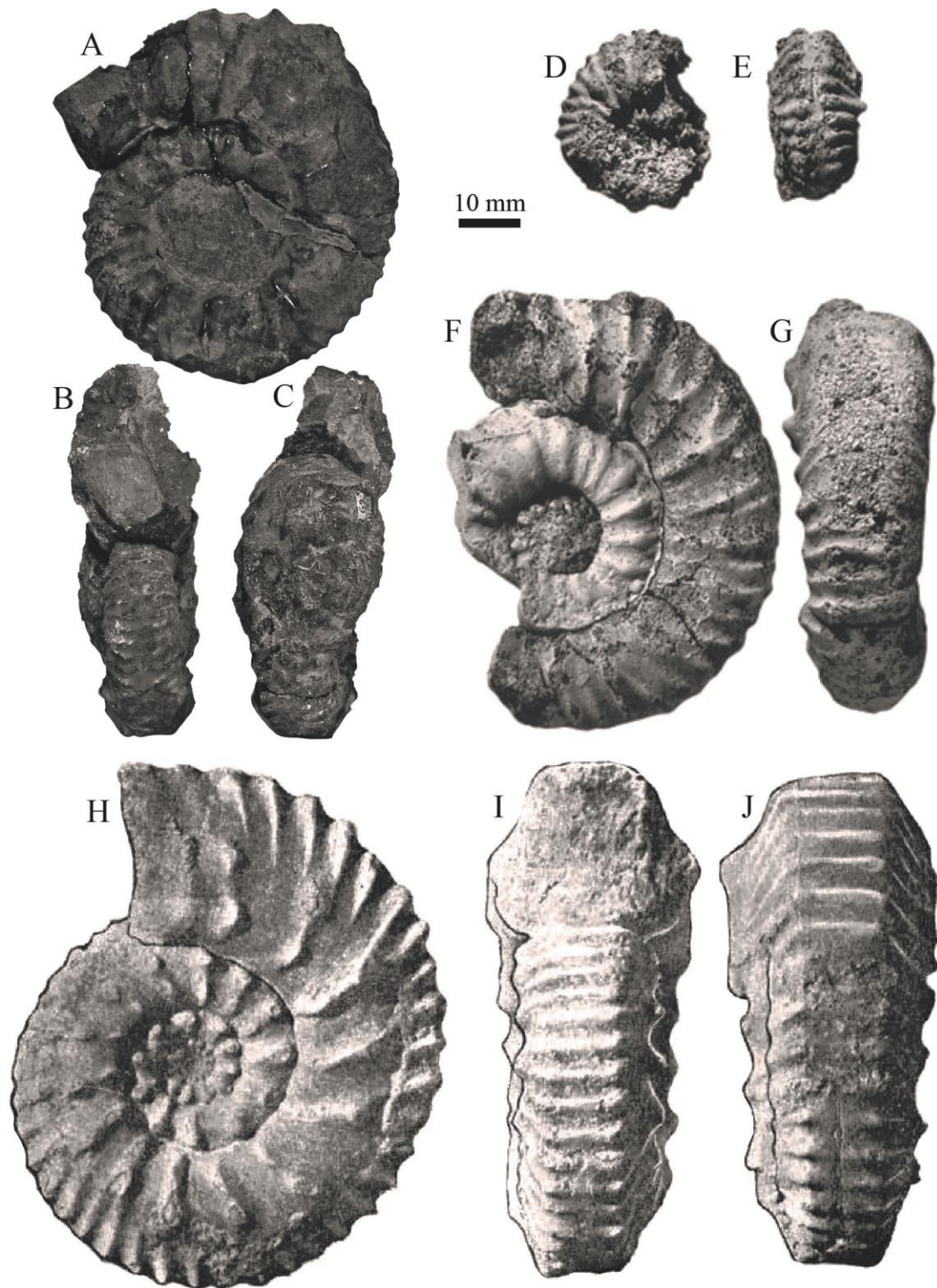


Fig. 7. Comparison between *Mittaites micheicus*, *Transcaspiites tscheffkini*, and *Transcaspiites transcaspicus*. (A–C) The holotype of *M. micheicus* (Bogoslovsky, 1897) (VSEGEI 63-62/623) here re-assigned to *Mittaites* n. gen. (D–G) Specimen PIN 3990/255 (including its isolated inner whorls in (D, E)) of *Transcaspiites tscheffkini* Mitta, 2018 (pl. 4, fig. 2a, b) re-assigned to *M. micheicus* (Bogoslovsky).

(H–J) The holotype of *Transcaspiites transcaspicus* (Luppov, Bodylevsky and Glazunova., 1949) (VSEGEI 10/6801).

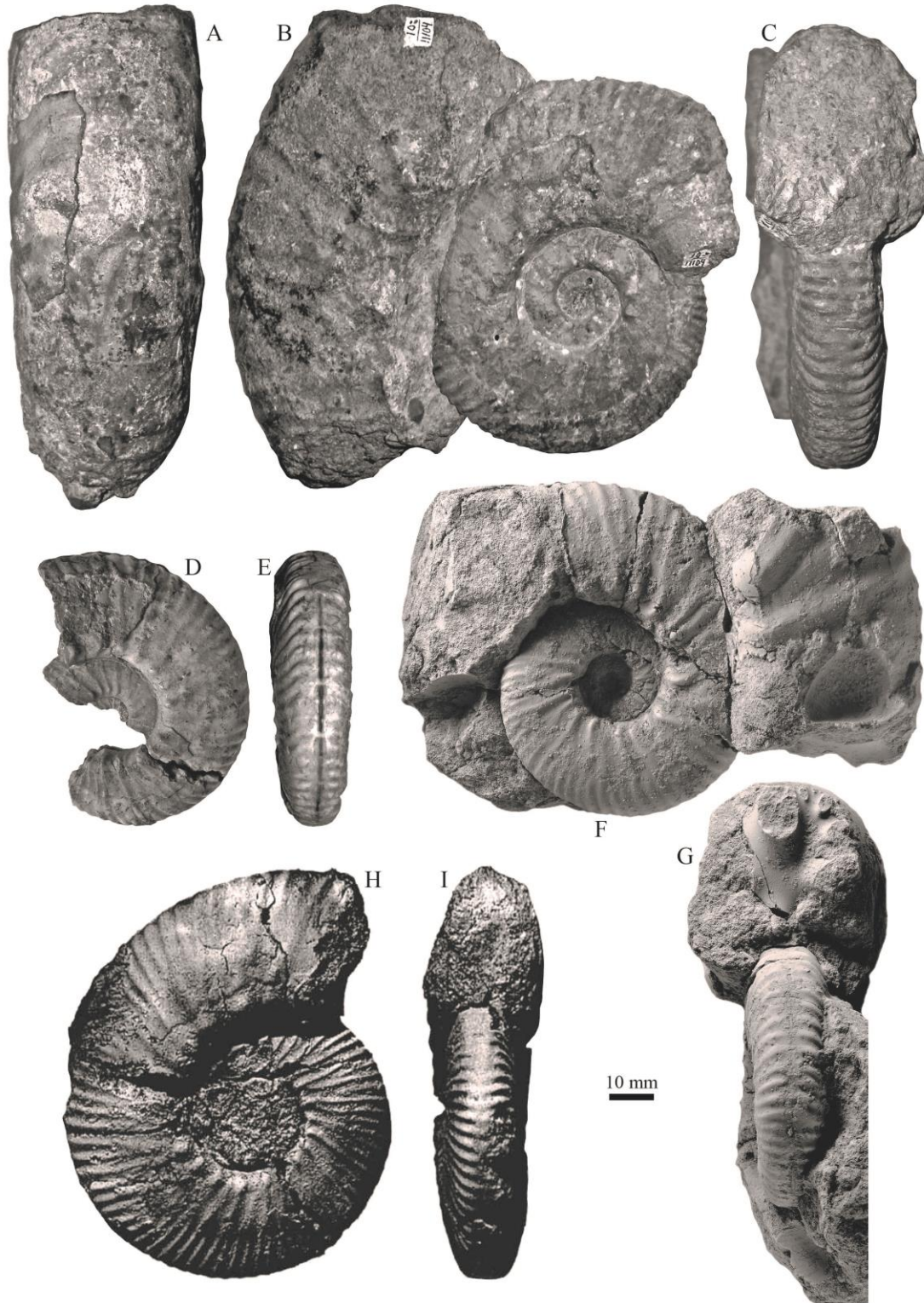


Fig. 8. Comparison between *Subalpinites bajarunasi* and *Subalpinites krischtalofowitschi* from the type 'Ryazanian'. (A–E) *Subalpinites bajarunasi* (Luppov

in Luppov et al., 1988) from the Mangyshlak Peninsula; (A–C) holotype, VSEGEI 11104/9a; (D, E) paratype, VSEGEI 11104/9b. (F, G) Specimen PIN 3990/418 of *Subalpinites bajarunasi* (Mitta, 2018, pl. 6, fig. 3a, b). (H, I) Specimen VNIGNI CR.2562 of *Subalpinites krischtafowitschi* (Mitta, 2002, pl. 3, fig. 2a, b), holotype.

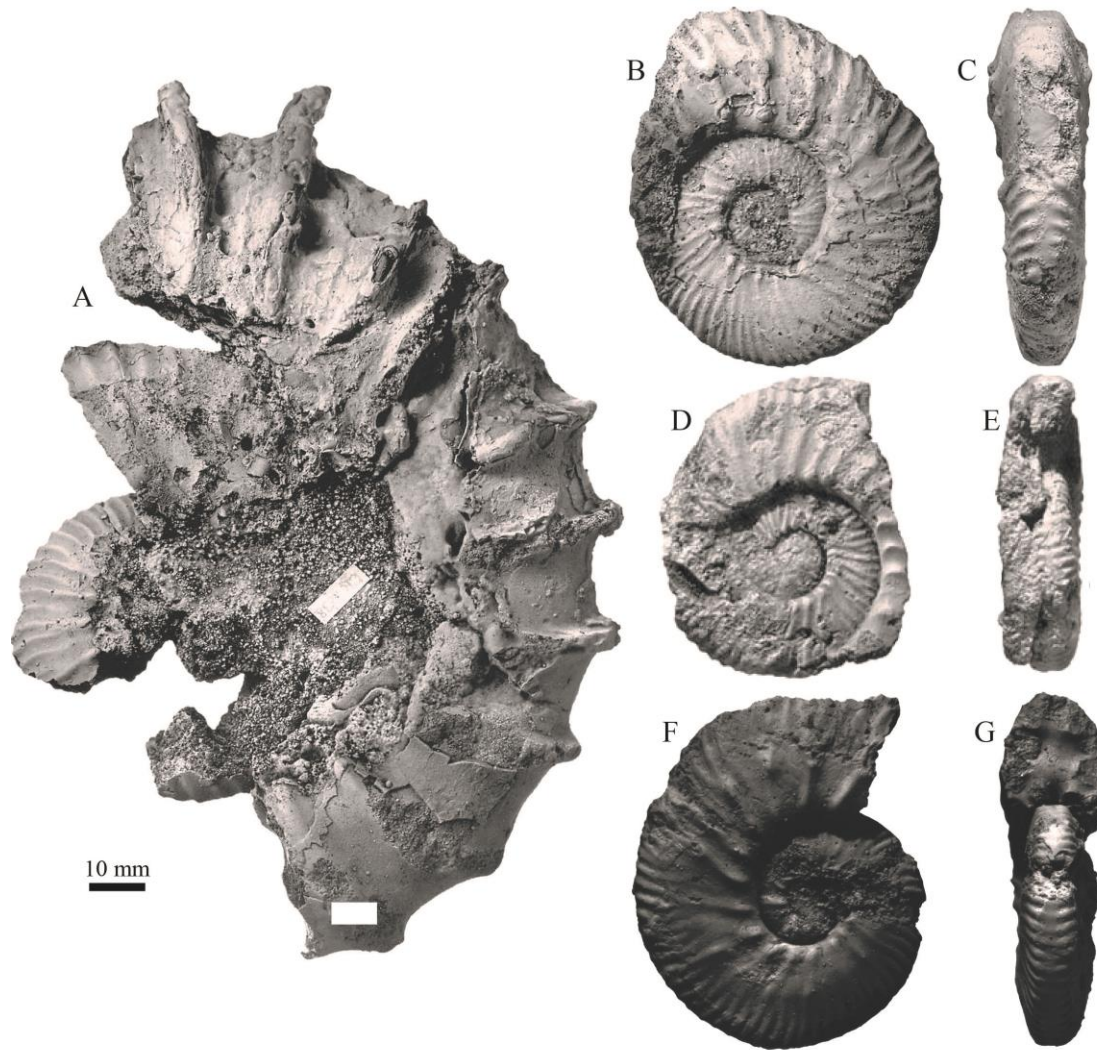


Fig. 9. Comparison between *Subalpinites remaneiformis*, *Dalmasiceras* ex gr. *djanelidzei*, and *Dalmasiceras crassicostatum* from the type ‘Ryazanian’. (A–C) *Subalpinites remaneiformis* (Mitta, 2009, text-fig. 2a–c); (A) holotype, PIN 3990/336; (B, C) paratype, AVS 1002. (D, E) Specimen PIN 3990/249 assigned to *Dalmasiceras* ex gr. *djanelidzei* (Mazenot, 1939) by Mitta (2005, pl. 2, fig. 2a, b). (F, G) Specimen PIN 3990/247 assigned to *Dalmasiceras crassicostatum* (Djanélidzé, 1922) by Mitta (2005, pl. 2, fig. 3a, b).

Table 1. Measurements of *Riasanites* and *Riasanella* relatives used in the text (after Grigorieva, 1938; Khimchiashvili, 1976; Sazonova, 1977; Mitta, 2008, 2011a, 2018). Acronyms indicate D = diameter, Ww = whorl breadth, Wh = whorl height, U = umbilical diameter, U/D = ratio of umbilical dimension as a percentage of the adult diameter, and Ww/Wh = ratio of whorl breadth as a percentage of the whorl height; and Bcoeff = branching coefficient as defined by Mitta (2008).

Table 2. Comparative systematic treatment of the ammonite taxa of supposed Tethyan affinity from the the type 'Ryazanian' between Mitta (2002, 2005, 2007a, 2008, 2009, 2011a, 2011b, 2017, 2018), Mitta and Bogomolov (2008), Mitta and Sha (2011), and this work.