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On the First Record of *Infragarantiana* (Ammonoidea: Perisphinctidae) from the Upper Bajocian *Niortense* Zone (Middle Jurassic) of the Northern Caucasus, Russia

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Abstract—*Infragarantiana primitiva* (Wetzel) is recorded for the first time from the Upper Bajocian of Karachay-Cherkessia. The species "*Garantiana*" *primitiva* was previously known only from the holotype, originating from the lower part of the *Niortense* Zone of Germany, and is the type species of the monotypic genus *Infragarantiana* Westermann. New material from the Northern Caucasus makes it possible to clarify the diagnosis and systematic position of the genus *Infragarantiana* [M] (Perisphinctidae: Leptosphinctinae).

Keywords: Ammonoidea, Middle Jurassic, Upper Bajocian, Niortense Zone, *Infragarantiana*, Perisphinctidae, Leptosphinctinae, Northern Caucasus

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INTRODUCTION

Almost a hundred years ago, a new species of ammonite, *Garantiana primitiva* Wetzel, 1936, was described based on the holotype from the Upper Bajocian of Germany. Later, this species was proposed as the type species for the monotypic genus *Infragarantiana* Westermann, 1956. *I. primitiva* is significant because the authors of the species and genus considered it the most ancient representative of the subfamily Garantianinae (Wetzel, 1954, p. 557), and its ancestor (Westermann, 1956, p. 268, appendix 2). In the absence of new finds of *Infragarantiana*, the position of this taxon in the Middle Jurassic ammonoid system remained unclear; various authors assigned it to different families, including Perisphinctidae, Parkinsoniidae, Stephanoceratidae, and Spiroceratidae; the name *Infragarantiana* was considered to be a junior synonym. New collections from the Bajocian of the Northern Caucasus make it possible to substantiate the status of the genus *Infragarantiana* Westermann, as well as to clarify the systematic position and diagnosis of this genus and its type species *I. primitiva* (Wetzel).

LOCALITY AND MATERIAL

The ammonites discussed in the paper were collected by the author during fieldwork in 2020 in an outcrop along the left bank of the Kyafar River (left tributary of the Bolshoi Zelenchuk River) downstream of the village of Storozhevaya (Zelenchuk District of Karachay-Cherkessia) (Fig. 1, locality 31a). This locality represents a succession of clay beds (Fig. 2) with interbeds of predominantly carbonate nodules of the upper subformation of the Djangura Formation (Besnosov, 1967). The outcrop is part of a section exposed at about 150 m upstream along the Kyafar River and further in a large ravine (locality 31), the mouth of which is located directly downstream of the mouth of the Bizhgon River (left tributary of the Kyafar River). *Keppleritiana*[1] *rostovtsevi* Mitta was recently described from locality 31, and beds with *rostovtsevi* attributed to the middle part of the *Niortense* Zone of the standard Western European scale were established (Mitta, 2017b). New finds of ammonites come from an irregularly shaped siderite nodule extracted from clays of the Djangura Formation containing abundant remains of ammonites and their jaws, bivalves, and brachiopods.

In addition to the *Infragatantiana primitiva* (Wetzel) discussed below, shells of *Oppelia subradiata* (Sowerby) were found, a species characteristic of the interval from the Lower Bajocian *Stephanoceras hum-*

[1] Here I must admit and correct my mistake in establishing the genus *Keppleritiana*. In recent collections, together with macroconch species originally assigned to this genus (including in their body chambers), microconchs *Strenoceras* Hyatt (*S.* ex gr. *niortense* (d'Orbigny) / *bajocense* (de Blainville), which are associated with the macroconchs *Orthogarantiana* Bentz. Therefore, the species *"Keppleritiana" rostovtsevi* Mitta and *"K." graebenschteini* Mitta must belong to the genus *Orthogarantiana*, a senior subjective synonym of *Keppleritiana* Mitta.

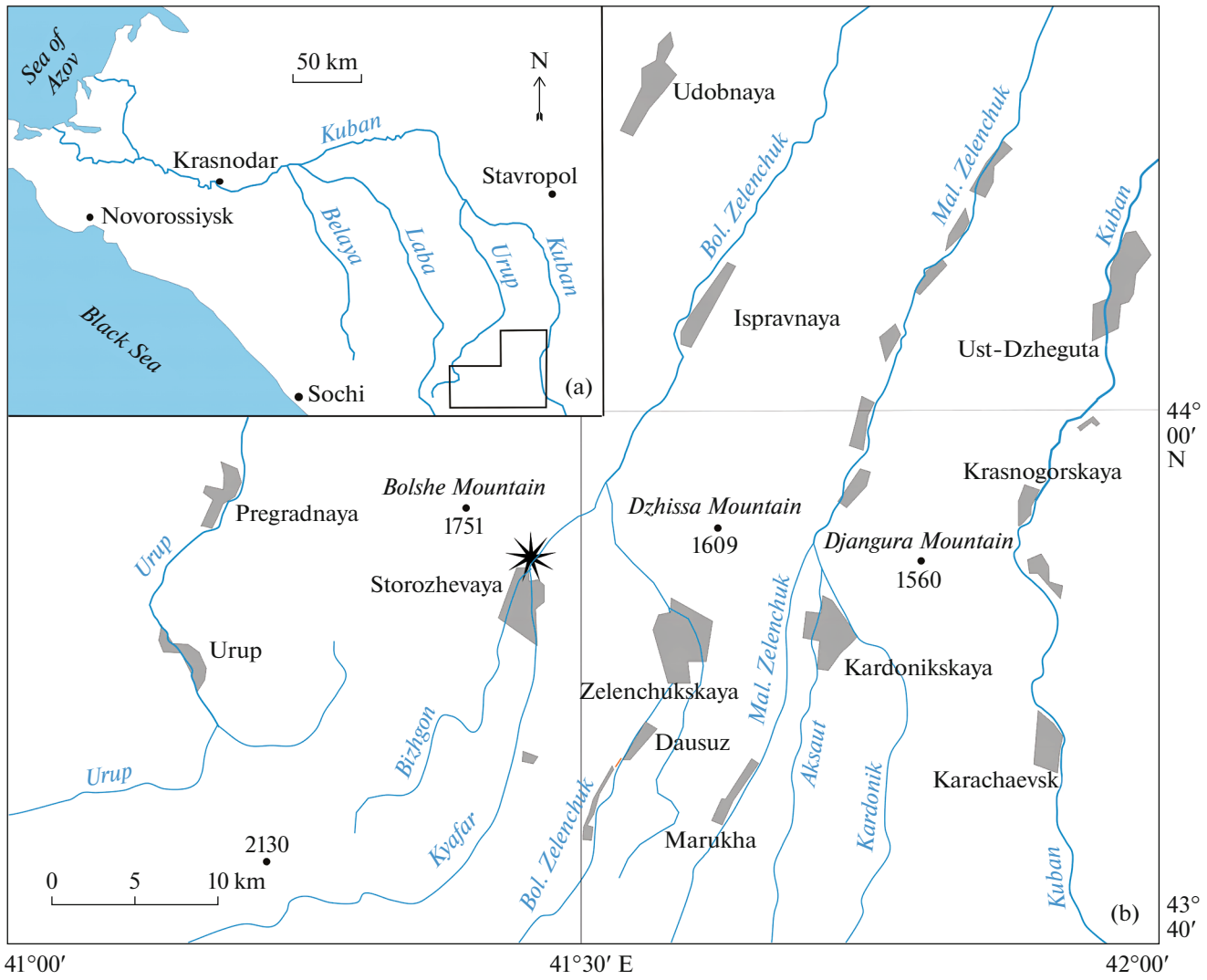

Fig. 1. Location of the site: (a) general scheme, the frame shows the outline of the detailed map; (b) map of localities nos. 31, 31a (left bank of the Kyafar River downstream the mouth of the Bizhgon River).

phriesianum Zone (Gauthier et al., 2002), along the lower *Teloceras banksii* subzone of the *Strenoceras niortense* Zone inclusive (Rioult et al., 1997). In addition, phylloceratids *Adabofoloceras, Holcophylloceras, Pseudophylloceras,* and the lithoceratid *Nannolytoceras*, mostly represented by shell fragments or juvenile specimens, were found in the same nodule.

The material is housed at the Borissiak Paleontological Institute (PIN RAS), col. no. 5546.

HISTORY OF STUDY

The species *Garantiana primitiva* was described by Wetzel (1936, p. 540) from a single incompletely preserved shell with a final diameter of about 20 mm, found in a nodule from the "*Teloceras* Beds" (the lower part of the Upper Bajocian *Niortense* Zone, *Banksii* Subzone, in modern understanding) in a quarry in the vicinity of Bielefeld. As the photographs of this small-sized specimen (illustrated full-size in the original publication) did not give a complete impression of the species, its author later provided a schematic sketch of the holotype, showing the umbilical width and the location of the ribs, which are only partially preserved (Wetzel, 1954, p. 557, fig. 5; here Fig. 3).

Westermann (1956) established the genus *Infragarantiana* with the type species *Garantiana primitiva* Wetzel without description, indicating that *Ammonites caumontii* d'Orbigny also belonged to the same genus. Westermann pointed out, as a difference from the genus *Infraparkinsonia* established in the same work, which has rib terminations directed forward, straight and opposed terminations of the secondary ribs in *Infragarantiana* (in both cases, the ornamentation is interrupted in the middle of the venter). He also noted

Fig. 2. Section of the Djangura Formation at locality 31a on the left bank of the Kyafar River; the arrow shows the level of occurrence of the nodule with *Infragarantiana primitiva*, etc.

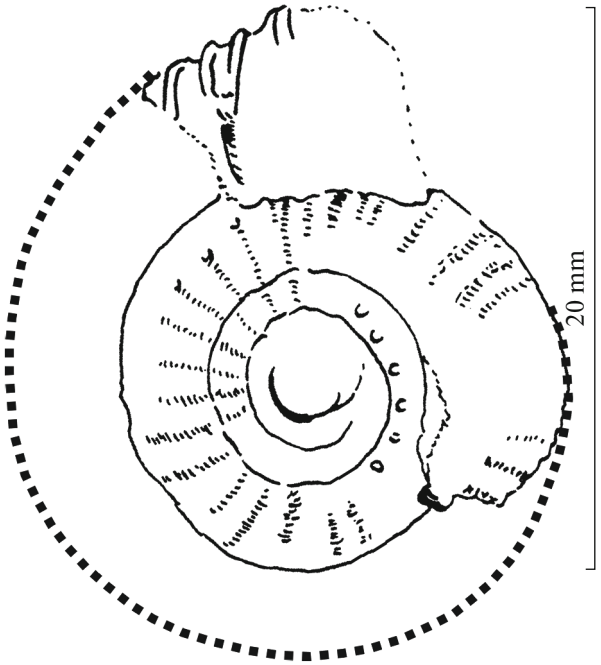

Fig. 3. Reproduction of a schematic drawing of the holotype of *Infragarantiana primitiva* (Wetzel, 1954, text-fig. 5), modified and supplemented.

that, most likely, the shells of both new genera lack constrictions.

Infragarantiana and *Infraparkinsonia* were formally assigned to the subfamily Leptosphinctinae, family Perisphinctidae, although further in the text it is indicated (Westermann, 1956, p. 269) that *Garantiana, Orthogarantiana, Pseudogarantiana, Strenoceras*, etc., descended from *Infragarantiana*, i.e., representatives of the subfamily Garantianinae in the family Stephanoceratidae in the modern sense (but assigned by Westermann to the subfamily Parkinsoniinae of the family Parkinsoniidae). It was also suggested that the genus *Parkinsonia* evolved from the genus *Infraparkinsonia*. In the next work (Westermann, 1958, p. 454), this researcher confirms the already expressed opinion about the origin of *Garantiana* "and probably also *Strenoceras*" from *Infragarantiana*.

Dietl (1980a), followed by other researchers (Schlegelmilch, 1985; Metz, 1992), considered the name *Infragarantiana* as a junior subjective synonym of *Caumontisphinctes*; this genus (with the subgenera *Caumontisphinctes* Buckman [M] and *Infraparkinsonia* Westermann [m]) is recognized as the ancestor of Parkinsoniidae (Dietl, 1980a; Besnosov and Kutuzova, 1982). In a recent summary on perisphinctoids, Énay and Howarth (2019) agreed with this opinion,

although they assigned *Caumontisphinctes* to the subfamily Leptosphinctinae in the family Perisphinctidae. The subfamilies Parkinsoniinae and Pseudocosmoceratinae, in my opinion belonging to the family Parkinsoniidae (Mitta, 2004, 2009, 2017c; Mitta and Bakaryukina, 2020), are also referred to by the above authors to the Perisphinctidae.

Besnosov in Besnosov and Mitta (1993) considered the name *Infragarantiana* to be a junior subjective synonym of *Pseudogarantiana* Bentz, which he understood as a normomorphic microconch of heteromorphic Spiroceratidae (Besnosov and Kutuzova, 1990).

Summarizing the above, the position of the genus *Infragarantiana* in the ammonoid system remains controversial, since previous researchers understood it differently: as a member of Garantianinae (family Stephanoceratidae), Parkinsoniinae (family Parkinsoniidae), Leptosphinctinae (family Perisphinctidae), or Spiroceratinae (family Spiroceratidae).

DISCUSSION

The most significant species characteristics indicated by Wetzel (1936) in the first description of *"Garantiana" primitiva* can be summarized as follows:

— a poorly preserved specimen of a dwarf (final diameter 20 mm) species, with the surviving initial part of the body chamber and the last two septa located close together (which indicates the adult stage);

— the whorl section is almost rounded; its width is greater than its height;

— primary ribs are raised subradial, bifurcating on the flank with the formation of nodes at the point of branching;

— secondary ribs on the outside are interrupted, their ends are located almost opposite each other.

Later, the author of the species considered it necessary to emphasize that the holotype at Dm = 20 mm, based on the degree of evolution, is a completely adult shell, excluding the possibility of its further growth; and indicated the absence of nodes on the external side (Wetzel, 1954).

Comparison of the Northern Caucasian specimens (Fig. 4) with photographs and a sketch of the holotype of Wetzel's species shows their great similarity. Obviously, when determining the final diameter of the holotype, Wetzel did not take into account the height of the missing middle part of the last whorl (I have drawn its outline in Fig. 3 with a dotted line). In addition, the apertural area of the shell with single ribs is not preserved in the holotype. As a result, its real diameter should have been ~30 mm, which is quite consistent with the final dimensions of my shells. In terms of the shell shape and sculpture, as far as can be judged from the available data, my specimens do not differ from the holotype of *I. primitiva*.

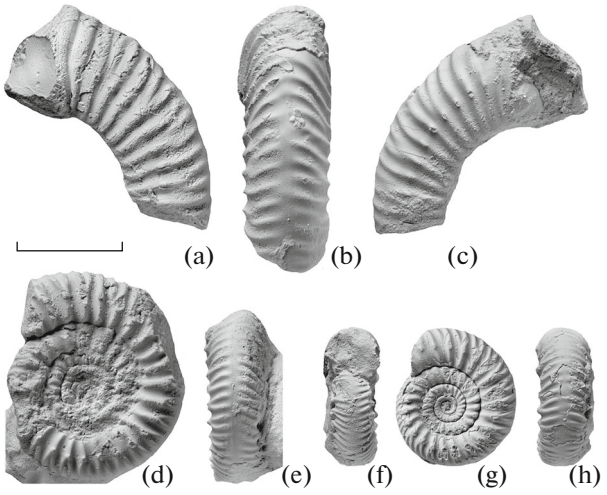

Fig. 4. *Infragarantiana primitiva* (Wetzel) [M]: (a–c) specimen. PIN, no. 5546/313, anterior part of the body chamber with the aperture preserved on one side (a); (d, e) specimen. PIN, no. 5546/314, phragmocone: (d) lateral view, (d) ventral view; (f–h) specimen. PIN, no. 5546/315, phragmocone: (f) apertural view, (g) lateral view, (h) ventral view; Karachay-Cherkessia, Zelenchuk District, left bank of the Kyafar River downstream of the mouth of the Bizhgon River, locality no. 31a; Djangura Formation; lower part of the *Strenoceras niortense* Zone; author's collection, 2020.

Our findings of the anterior part of the body chamber (albeit fragmentary) of *I. primitiva*, clearly demonstrating a simple (without lappets) aperture margin, allow *Infragarantiana* to be classified as an undoubted macroconch. This immediately narrows the circle of possible close relatives of *Infragarantiana*.

Pseudogarantiana are microconchs (forming a dimorphic pair with *Garantiana* macroconchs) and appear for the first time only in the *Garantiana garantiana* Zone (Gauthier et al., 1996; Dietze et al., 2002). In addition, due to the findings of *Spiroceras* microconchs with lappets (Mitta, 2017a) dimorphism within this genus of Spiroceratinae was finally established. In the dimorphic pair *Orthogarantiana* [M] and *Strenoceras* [m] at Dm 15–20 mm, whorls are much more swollen, the umbilicus is noticeably narrower, the ornamentation is rough, the ventral groove is sharply cut, the tips of the secondary branches are crest-like raised (Mitta, 2020, text-fig. 3). Correspondingly, a close relationship between *Infragarantiana* and Garantianinae is unlikely, and with Spiroceratinae, it is excluded.

The question of whether *Infragarantiana* belongs to Parkinsoniinae or Leptosphinctinae is more complicated. These first true Perisphinctoidea, represented by dimorphic pairs Caumontisphinctes [M]/Infraparkinsonia [m] and Leptosphinctes [M]/Kubanoceras [m], respectively, separated from Stephanoceratoidea almost simultaneously, in the *Teloceras blagdeni* upper subzone of the *Humphriesianum* Zone (uppermost

Lower Bajocian) (Pavia, 1973; Dietl, 1980a; Galácz, 2012; Pavia and Zunino, 2012). These ammonites, at least the most ancient species, had a similar shell shape and ornamentation (it was noted above that some researchers still refer them to the same family Perisphinctidae). The main differences lie in the outlines of the secondary ribs, especially on the venter.

In Parkinsoniinae (*Caumontisphinctes* [M]/*Infraparkinsonia* [m]), secondary ribs, divided on the venter by a median groove, approach it alternately on each side and at an angle (branches are inclined forward). However, these characters are not always maintained in the ontogeny of individual shells and species. In *Leptosphinctes* [M] / *Kubanoceras* [m], the tips of the branches, interrupted on the venter to form a smooth median stripe, approach it directly and are located oppositely.

In the ornamentation of the first Leptosphinctinae there is one feature that is not characteristic of the earliest Parkinsoniinae. The lateral nodes, developed to some extent in both taxa, are usually observed at the point of rib branching, but in some *Leptosphinctes*, the branch point may be located closer to the ventrolateral area, and the nodes are still expressed on the primary rib (Dietl, 1980b, text-fig. 7; Mitta, 2021, pl. 3, fig. 5). In this case, nodes are observed, including on simple (single) ribs. The latter character is also observed in the putative descendant of *Leptosphinctes*, the genus *Vermisphinctes* Buckman (Mitta, 2019, pl. 17, fig. 3).

Smoothing of ribs in the middle of the venter with predominantly opposing ends of branches, and the presence of single ribs with lateral tubercles, testifies in favor of the assignment of *Infragarantiana* to the subfamily Leptosphinctinae in the family Perisphinctidae. Thus, the correctness of the actions of the author of the genus regarding his position in the perisphinctoid system is formally confirmed (Westermann, 1956). At the same time, the genus *Infragarantiana* is unlikely to be related to Garantianinae, as Wetzel and Westermann believed.

The association of ammonites found in the Caucasus in the same nodule with *I. primitiva* indicates the interval of the uppermost Lower to lowermost Upper Bajocian. In the absence of more accurate data, I accept the stratigraphic position of the *primitiva* species proposed by Wetzel (1936) as the lower part of the Upper Bajocian *Niortense* Zone (*Banksii* Subzone). If this is true, then representatives of *Infragarantiana* could not be the ancestors of Leptosphinctinae (or even Parkinsoniinae), which appeared in the upper part of the Lower Bajocian. Most likely, this genus was an evolutionary dead-end, but it nevertheless spread its range to vast areas of the Western Tethys. Below is an updated description of this genus and its type species.

SYSTEMATIC PALEONTOLOGY

Superfamily Perisphinctoidea Steinmann, 1890

Family Perisphinctidae Steinmann, 1890

Subfamily Leptosphinctinae Arkell, 1950

Genus *Infragarantiana* Westermann, 1956 [M]

Infragarantiana: Westermann, 1956, c. 268.

Caumontisphinctes (part.): Dietl, 1980a, p. 7; Schlegelmilch, 1985, p. 84; Metz, 1992, p. 54; Énay and Howarth, 2019, c. 5.

Pseudogarantiana (part.): Besnosov and Mitta, 1993, c. 224.

Type species. *Garantiana primitiva* Wetzel.

Diagnosis. Shells very small, up to 30 mm in diameter, at adult stage with moderately wide whorls, rounded and (at the end of the living chamber) oval in cross section. Umbilicus very wide, shallow; the umbilical wall steep; shoulder rounded. Living chamber length unknown, apertural margin simple. Ornamentation represented mainly by sparse, bifurcating single ribs, with small nodes developed at mid-flank. On venter of phragmocones, ribs interrupted, forming a smooth median band. At end of body chamber, rib branches connect again over venter.

Species composition. Type species from Northern Germany (North Rhine-Westphalia) and Southern Russia (Karachay-Cherkessia, Bolshoi Zelenchuk River basin); upper Bajocian, *Strenoceras niortense* Zone, *Teloceras banksii* Subzone.

Comparison. The genus described is very similar to *Leptosphinctes* in shell shape and ornamentation (especially lateral nodes, developed on single ribs, as well as smoothing of ribs at mid-venter). The differences are expressed in the final size, as the adult shells of even microconchs of *L. (Kubanoceras)* reach a diameter of 40–50 mm (Mitta, 2021).

Remarks. As mentioned above, the author of the genus also included in it the species *"Ammonites" caumontii* d'Orbigny, 1846. At present, this species is included in the genus *Parastrenoceras* (Ochoterena, 1963; Sturani, 1971; Rioult, 1994; Énay and Howarth, 2019).

***Infragarantiana primitiva* (Wetzel, 1936)**

Garantiana primitiva: Wetzel, 1936, p. 540, fig. 9, pl. 21, figs. 6, 7; 1954, p. 557, fig. 5.

Holotype (by monotypy). Specimen figured by Wetzel (1936, text-fig. 9, pl. 21, figs. 6, 7; 1954, text-fig. 5), whereabouts is unknown; Germany, North Rhine-Westphalia, Bielefeld; upper Bajocian, basal part of the *Strenoceras niortense* Zone ("*Teloceras*-*Schichten*").

Description (Figs. 3, 4). *Shell shape.* The shells of adult specimens reach a diameter of 30 mm. Up to Dm = 10 mm, the whorls are inflated, transversely-oval in cross-section. Later whorls are of medium thickness, rounded in cross-section; the whorl width is slightly greater than its height. In the apertural part of the body chamber of adult shells,

the cross section is oval, with the whorl height being greater than the width. The umbilicus is shallow, wide at Dm = 5–7 mm, expands with age to become very wide; the umbilical wall is steep; the shoulder is rounded. The length of the body chamber is unknown; the aperture is simple with a small flare.

Ornamentation. At Dm up to 7 mm, only simple primary ribs are expressed, ending with nodes at the ventrolateral shoulder. Further, on the venter, secondary branches appear, at first only barely noticeable, crossing it without interruption with a slight forward inclination. When Dm is more than 10 mm, the nodes at the branching point of the primary ribs move to the mid-flank; secondary ribs become more noticeable, and when Dm is more than 12 mm, they begin to weaken at mid-flank. Later whorls of the phragmocone possess prominent subradial primary ribs bifurcating at mid-flank, with small tubercles at the branching point. Occasionally there are single ribs, also with a node at mid-flank. Secondary ribs are slightly inclined forward (usually anterior branches); in the middle of the venter they are interrupted, forming a smooth median band. The tips of the branches are usually opposite, but sometimes approaching the middle of the venter alternately. At the end of the body chamber, bipartite and single ribs alternate, in the apertural part the last three or four ribs are single, they are preceded by an intercalating rib and then again single; nodes weaken at the mid-flank, but they are still present on simple ribs. Near the apertural margin, the branches of the ribs again meet on the venter.

Dimensions in mm and ratios:

Specimen no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5546/313	–	9.2	7.6	–	–	–	–
5546/314	20.1	5.6	6.3	11	0.28	0.31	0.55
	16.1	4.1	5.1	9.1	0.25	0.32	0.56
5546/315	12.9	3.6	4.9	6.6	0.28	0.38	0.51
	10.5	2.3	4.2	5	0.22	0.4	0.48
5546/316	7	2	3.2	3	0.29	0.46	0.43

Variability. As far as can be judged from the available material, the species has rather stable morphological features of the shell. For example, a fragment of the anterior part of the body chamber with a preserved apertural margin, which has not been shown, is completely identical in the shape of cross-section and ornamentation to a similar, more fully preserved fragment in Figs. 4a–4c.

Material. Seven specimens in varying state of preservation, from one nodule; Karachay-Cherkessia, locality 31a; Djangura Formation, Upper Bajocian, lower part of the *Strenoceras niortense* Zone.

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