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Khetoceras (Craspeditidae, Ammonoidea)—A New Genus from the Volgian Stage of Northern Middle Siberia, and Parallel Evolution of Late Volgian Boreal Ammonites

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Abstract—A new ammonite genus, *Khetoceras* (Craspeditinae), is proposed, showing an atypical combination of features for the subfamily (arrowlike cross-section and prominent constrictions). A new subfamily Subcraspeditinae is proposed within the family Craspeditidae. An increase in whorl overlap was the major trend in the evolution of the Late Volgian subfamilies belonging to Craspeditidae (Craspeditinae, Garniericeratinae, and Subcraspeditinae) leading to the appearance of discoid morphotypes with a narrow (or acute) cross-section in all these subfamilies. However, while this evolutionary trend dominated the evolution of Garniericeratinae and less so Subcraspeditinae, it was not so prominent in the Volgian Craspeditinae, in which this morphotype only developed in northern Siberia (genus *Khetoceras*), where at that time the other two subfamilies were absent.

Keywords: ammonites, Volgian, evolution, Siberia

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INTRODUCTION

Most Upper Volgian ammonites from northern Middle Siberia belong to widespread genera known from other regions within the Panboreal biogeographic Superrealm. Among these ammonites the taxonomy of one of the species, distinct from all other craspeditids in an unusual combination of characters not found in other Late Volgian taxa (arrowlike cross-section and prominent constrictions) remained unresolved until very recently. Originally, this species was described by Schulgina (1969) as *Garniericeras margaritae*. This rare species (only four specimens in Schulgina's collection) was found on the Kheta River and has not been discovered anywhere else. Later Schulgina (1985) noted the similarity of this species to species of *Volgidiscus* and *Shulginites* and suggested that it could belong to a new genus. Baraboshkin (1999; 2004) assigned this species to *Volgidiscus* and then to *Shulginites*, whereas Rogov and Zakharov (2009) assigned it to *Shulginites* with a question mark. New material collected by A.V. Dronov, Yu.A. Selivanov, M.O. Savitskaya, and A.S. Savitsky in 2000 on the Kheta River (Fig. 1) suggests that this species should certainly be assigned to a new genus, which is described below.

MATERIAL

The material studied is housed in the Paleontological-Stratigraphic Museum at the Department of Dynamic and Historical Geology of St. Petersburg State University (SPbGU), in the TsNIGR Museum (St. Petersburg), Paleontological Institute, Russian Academy of Sciences (Moscow), and the Natural History Museum (London).

SYSTEMATIC PALEONTOLOGY

Family Craspeditidae Spath, 1924

Subfamily Craspeditinae Spath, 1924

Genus *Khetoceras* Rogov, gen. nov.

E t y m o l o g y. From the Kheta River.

T y p e s p e c i e s. *Garniericeras margaritae* Schulgina, 1969, Upper Volgian of the Khatanga Basin.

D i a g n o s i s. Shells medium-sized (microconchs up to ~10, macroconchs up to ~25 cm in diameter), flattened, discoidal, with acute venter. Cross-section highly oval, tapering ventrally, becoming more strongly rounded on terminal body chamber in microconchs. Umbilicus shallow, ranging from semi-involute to semi-evolute, with gently sloping wall. Ornamentation on the inner whorls, up to diameter about 5 cm represented by prominent riblets appearing approximately on mid-whorl and constrictions associating with prominent non-bifurcating ribs. Later on ontogeny, ribs smoothening, but also appearing near umbilicus, while constriction persists to terminal body chamber in microconchs. Suture in microconchs poorly preserved (Schulgina, 1969). In the macroconch

Fig. 1. Map showing the sections: (1) Spilsby (53°10′29″ N, 0°5′18″ E); (2) Cheremukha River, near village of Mikhalevo (57°58′24″ N, 38°52′52″ E), village of Sel'tso-Voskresenskoe (57°53′15″ N, 38°51′56″ E); (3) quarry near the village of Eganovo (55°32′15″ N, 38°3′35″ E), village of Mil'kovo (55°36′34″ N, 37°47′59″ E); (4) Volga River bank near the village of Kashpir, (53°2′45″ N, 48°26′38″ E); (5) Kheta River (70°33′27″ N, 95°27′00″ E)).

studied, suture with relatively narrow and deep L and U lobes, and wide bipartite saddle between lobes U and ?I, typical of *Craspedites* (Fig. 2.1; lobes indexed as in *Craspedites (Craspedites)*, see Fig. 2.2). Micro- and macroconchs differing in shell size and smoother ornamentation in macroconchs, which is typical for craspeditids and polyptychids (Wright et al., 1996). Aperture simple (Pl. 2, fig. 5).

Composition. *K. margaritae* (Schulgina, 1969) [m] (Pl. 2, figs. 4, 5), *K. craspeditiformis* sp. nov. [M] (Fig. 3), Upper Volgian (*Okensis* Zone) and, possibly, a new species from the *Chetae* Zone, without constrictions (Schulgina, 1969, pl. 38, fig. 3), basin of the Kheta River (Khatanga Depression, northern Middle Siberia). The specimen of *K. margaritae* figured from "the *Taimyrensis* Zone" (Schulgina, 1969, pl. 38, fig. 2) was found in Member 4 of the reference section on the Kheta River, which does not contain ammonites that allow recognition of the *Taimyrensis* Zone, so this specimen is tentatively referred to the *Okensis* Zone.

Comparison. Early appearance of ribs near the venter and disappearance of ornamentation on the terminal body chamber (TBC) as well as the general shell shape and the suture in *Khetoceras* are similar to those in *Craspedites* (Fig. 2.2), from which the new genus differs in the shape of the shell cross-section and presence of prominent constrictions. In craspeditids constrictions can be present in early whorls (Shevyrev, 1960), but at a diameter over 20 mm they usually disappear, remaining only rarely on larger shells of *C. (Trautscholdiceras)* from the *Nodiger* Zone (Gerasi-

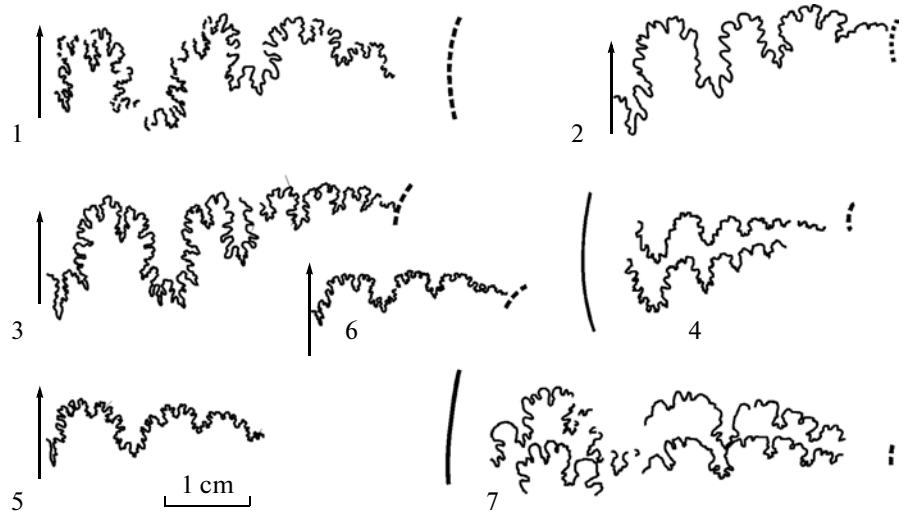


Fig. 2. Comparison of sutures of some Upper Volgian craspeditids: (1, 2) Craspeditinae, (3, 4) Subcraspeditinae, (5–7) Garniericeratinae. All sutures are drawn by the author. (1) *Khetoceras craspeditiformis* sp. nov., holotype SPbGU, no. 302500-1; Kheta River, loose; (2) *Craspedites* (*Craspedites*) *okensis* (d'Orb.), specimen PIN, no. 5515/4; village of Mikhalevo, Upper Volgian, *Fulgens* (?) Zone; (3) *Volgidiscus* cf. *lamplughi* (Spath) (= *Garniericeras* aff. *tolijense*, Schulgina, 1969, pl. 38, fig. 1), specimen TsNIGR Museum, no. 86/9565; Kheta River, outcrop 20, *Chetae* Zone; (4) *Volgidiscus* (*Volgidiscus*) *singularis* Kiselev, 2003, specimen PIN, no. 5515/5; quarry near the village of Sel'tso-Voskresenskoe, biohorizon *Volgidiscus* (*Volgidiscus*) *singularis*; (5) *Kachpurites* cf. *cheremkhensis* Mitta, I. Michailova et Sumin, specimen PIN, no. 5515/6; village of Mikhalevo, Upper Volgian, *Fulgens* Zone; (6) *Garniericeras catenulatum* (Fischer), specimen PIN, no. 5515/7; quarry near the village of Eganovo, *Catenulatum* Zone, *catenulatum* biohorizon; (7) *Garniericeras subclypeiforme* (Milash.), specimen PIN, no. 5515/7; village of Mil'kovo, *Nodiger* Zone.

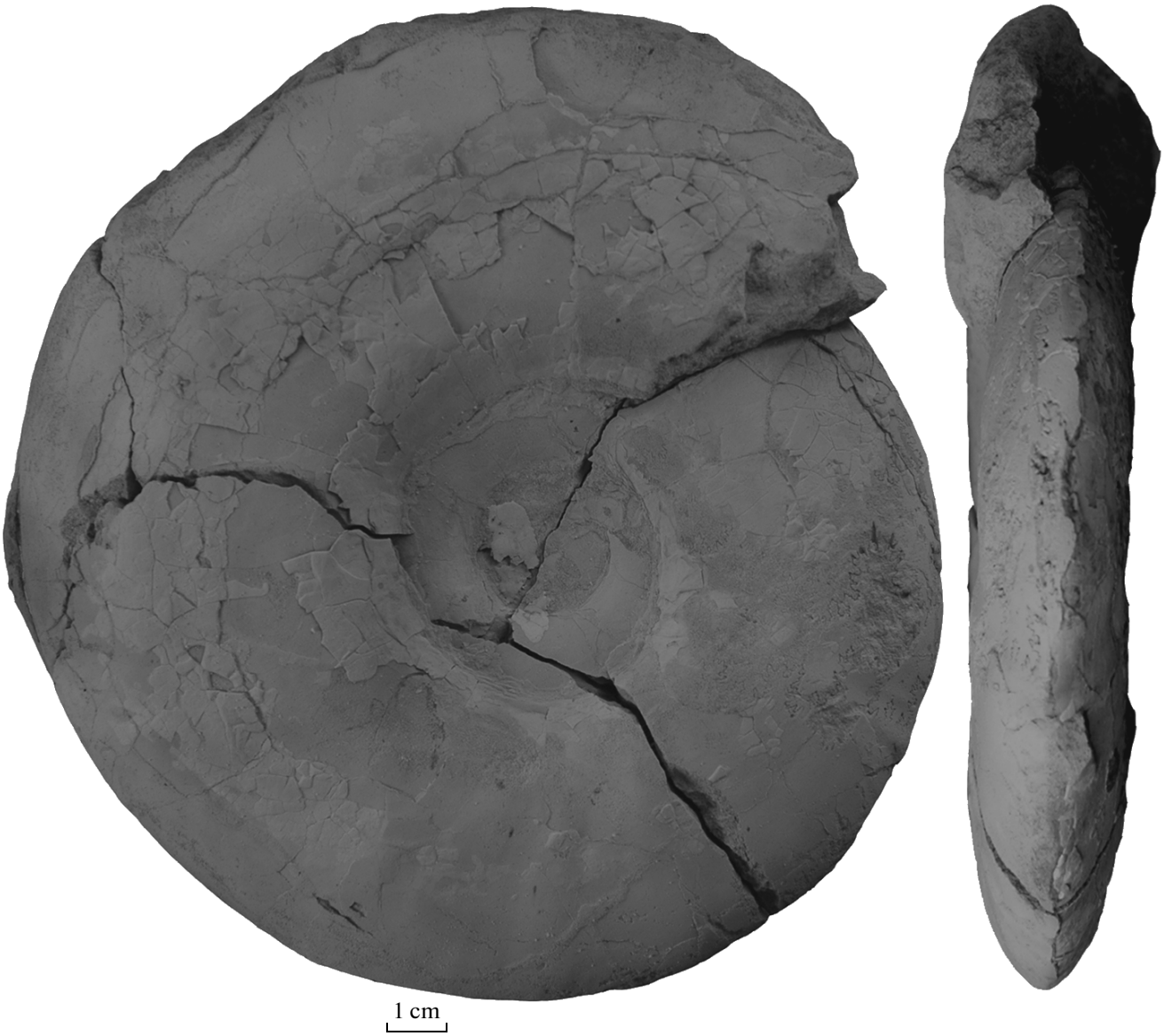


Fig. 3. *Khetoceras craspeditiformis*, sp. nov., holotype SPbGU, no. 302500-1.

mov, 1969, pl. 25, fig. 2), the shell shape of which is distinctly different from that of *Khetoceras*.

Remarks. The new genus is similar to *Garniericeras* (Garniericeratinae) in the shape of the whorl cross-section, but it is distinguished from Garniericeratinae by a different suture composed of considerably narrow elements (Figs. 2.5–2.7) and constrictions. The ammonite from the *Taimyrensis* Zone of the Kheta River identified as *"G." margaritae* by M.S. Mesezhnikov et al. (1983) should be assigned to *Volgidiscus* judging from the ornamentation (prominent ribs in the umbilical zone) and the suture (higher number of elements). The interpretation of recognized micro- and macroconchs remain uncertain (sexual dimorphism, polymorphism, discrete adaptive forms, etc.), and they are considered as separate species.

***Khetoceras craspeditiformis* Rogov, sp. nov. [M]**

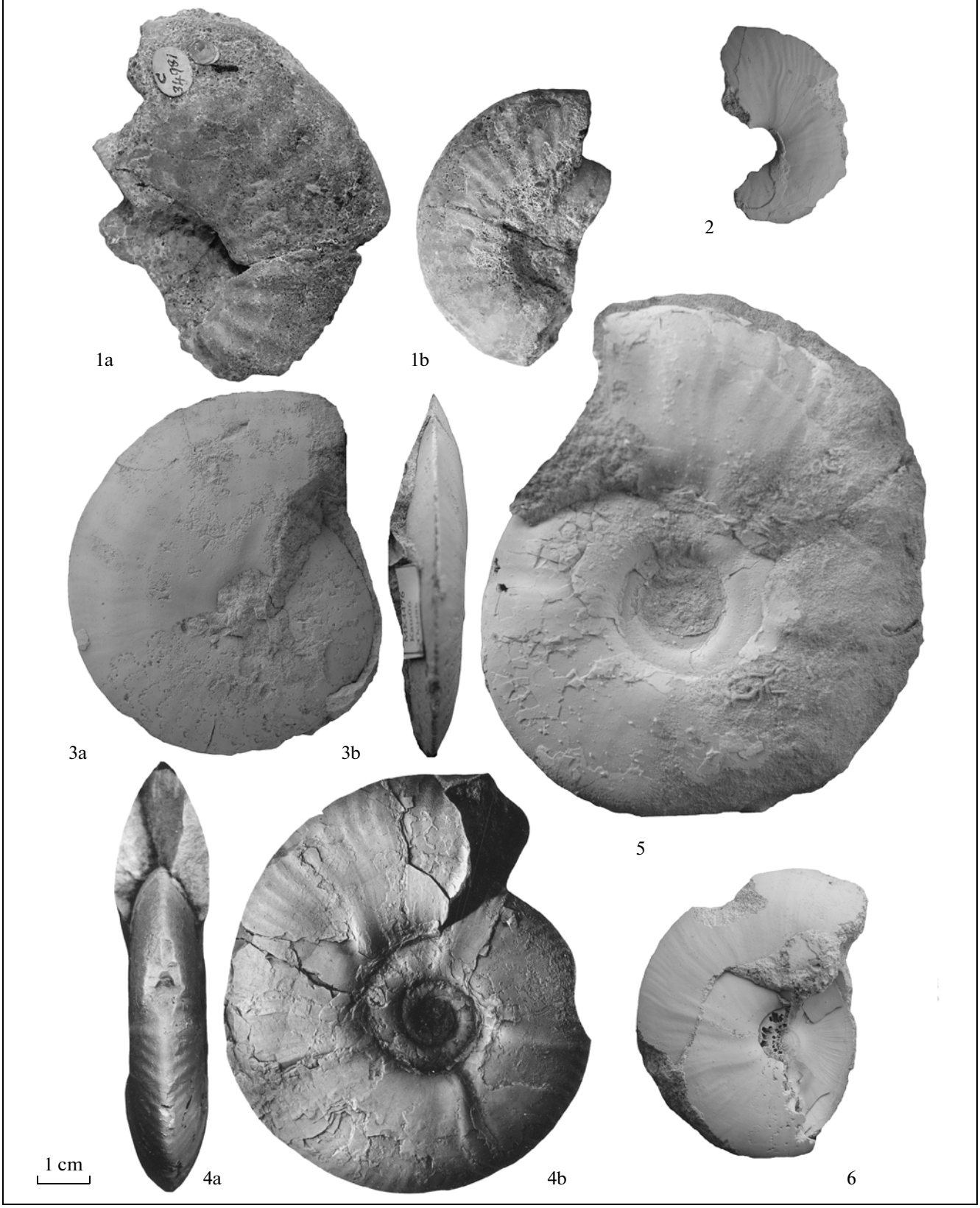
Etymology. From the genus *Craspedites*, macroconchs of which are similar to this species.

Holotype. Paleontological-Stratigraphic Museum at the Department of Dynamic and Historical Geology of St. Petersburg State University (SPbGU), no. 302500-1; Kheta River; loosely collected from the Upper Volgian.

Shell shape. (Fig. 3). The shell is large, flattened, with an acute venter. The whorl cross-section is highly oval, narrowing ventrally. The umbilicus is shallow semi-involute, with a gently sloping umbilical wall. The suture is described above (in the genus description).

Ornamentation of the inner whorls is not observed. The last visible whorl shows hardly notice-

Plate 2



able ribs-folds and weak constrictions, which are absent on the body chamber.

Dimensions in mm and ratios in %:

Specimen no.	WW	WH	Dm	UW	WW/WH	WW/Dm	WH/Dm	UW/Dm
Holotype	36.2	60.3	167.6	53.3	60	21.6	35.9	31.8

Comparison. *K. craspeditiformis* is similar to *K. margaritae* (Pl. 2, figs. 4, 5) in shell shape and whorl cross-section but differs from the latter in the weaker ornamentation and significantly larger size (approximately three times as large).

Remarks. *K. craspeditiformis* sp. nov. is very similar to early members of *Craspedites* (*C.*) ex gr. *okensis* (d'Orb.) in the shell shape, poorly developed ornamentation, and the suture, but it is distinguished from the latter by the subacute shape of the venter and in the presence of the poorly developed constrictions.

Material. Holotype.

Up to now most authors considered the family Craspeditidae Spath, 1924 as an entire taxon, and those who recognized a subfamily Garniericeratinae Spath, 1924 within that family, usually assigned to it ammonites similar morphologically rather than genetically related. New data (Rogov, 2013) suggest that craspeditids originally evolved in three separate phylogenetic lineages in the Late Volgian in a semi-isolated region. It is reasonable to consider these lineages as subfamilies of this family (Craspeditinae, Garniericeratinae, and Subcraspeditinae, subfam. nov.).

Subfamily Subcraspeditinae Rogov, subfam. nov.

Type genus. *Subcraspedites* Spath, 1924.

Diagnosis. Shells mainly small (most Volgian representatives less than 10 cm in diameter and only Ryazanian specimens are up to 20–25 cm), from semievolute to semi-involute. Whorl cross-section from widely oval to highly oval (in discoidal shells of *Volgidiscus* (Pl. 2, figs. 1a, 1b), *Shulginites, Hectoroceras*). The venter is rounded, from relatively wide to narrow; keel absent. Early members (*Swinnertonia*) occasionally with well-developed umbilical nodes, in later genera replaced by ribs. Rib ratio usually high, more than 3–4. Ribs crossing venter straight or forming weak curvature toward aperture. In some genera (*Volgidiscus, Hectoroceras*) ribs disappearing ventrally. In *Volgidiscus* and *Shulginites* ornamentation weak or nearly absent. Suture (Figs. 2.3, 2.4) with many (up to 6–8 in adult whorls) weakly dissected lobes and saddles, the width of which approximately equals the saddle height or slightly exceeds it. In Volgian genera, suture in umbilical zone of whorls usually noticeably slants toward aperture. Sutural ontogeny studied by Alekseev (1982) (genera *Praetollia*, *Hectoroceras, Shulginites*) and Schulgina (1985) (genera *Pseudocraspedites, Hectoroceras, Shulginites*), defined by the formula: $(V_1V_1)LUI_{vv}I^1_vI^2_vI^3_vI^4_v{:}I^5{:}I^4_dI^3_dI^2_dI^1_dD$ (Alekseev, 1982). Dimorphism poorly studied; aperture modifications absent in all craspeditids. Micro- and macroconchs can be suggested for the Volgian *Shulginites* (Mesezhnikov et al., 1983), *Swinnertonia, Subcraspedites, Volgidiscus* (Wright et al., 1996; Abbink et al., 2001; Kiselev, 2003), and also in Ryazanian *Borealites* (Igolnikov, 2014), *Praetollia* and *Hectoroceras* (Abbink et al., 2001). Microconchs, with a shell diameter usually around 5–7 cm, retain ornamentation up to the end of the terminal body chamber (and sometimes its increase, see Kiselev, 2003). Body chambers of macroconchs, with a diameter of 10–25 cm are usually smooth or possess weakened ornamentation. Sizes of presumable micro- and macroconchs in the genus *Shulginites* are somewhat different, with microconchs being about 4.5 cm in diameter, and macroconchs slightly over 6 cm (Mesezhnikov et al., 1983). Taxonomically micro- and macroconchs are assigned to the same species (indexed as "m" and "M", see Abbink et al., 2001), or assigned to different subgenera (Kiselev, 2003). However, some Volgian subcraspeditins in northwestern Europe and occasionally insufficiently detailed stratigraphic assignments make recognition of micro- and macroconchs difficult. The major trends in the evolution of subcraspeditins included a gradual decrease in ornamentation (Fig. 4b), increase in size in phylogeny (especially clearly observed in the Ryazanian taxa), and in the lineage leading to *Hectoroceras*, also considerable narrowing of the umbilicus and the whorls resulting in the development of compressed, discoidal shells (Fig. 4a).

Composition. Genera *Swinnertonia* Schulgina, 1972, *Subcraspedites* Spath, 1924, *Volgidiscus* Casey, 1973 (including the macroconch subgenus *Anivanovia* Kiselev, 2003), *Shulginites* Casey, 1973, *Hectoroceras* Spath, 1947, *Praetollia* Spath, 1952, *Borealites* Klimova, 1969; upper Middle Volgian

Explanation of Plate 2

Upper Volgian Craspeditidae.

Fig. 1. *Volgidiscus* (*Volgidiscus*) *lamplughi* Spath, holotype NHM, no. C34981; Spilsby Sandstone, Spilsby, Lincolnshire; *Lamplughi* Zone, Lamplugh collection (Pavlow, 1892, pl. 13, fig. 5): (1a) external whorl, (1b) ornamentation of the internal whorls.

Figs. 2 and 6. *Garniericeras* sp. [m], *Catenulatum* Zone, Cheremukha River, village of Mikhalevo (2) specimen PIN, no. 5515/1; (6) specimen PIN, no. 5515/2.

Fig. 3. *Garniericeras subclypeiforme* (Milash.) [M], specimen PIN, no. 5515/3; Kashpir, *Nodiger* Zone, loose.

Figs. 4 and 5. *Khetoceras margaritae* (Schulg.), Kheta River: (4) holotype TsNIGR Museum, no. 85/9565, outcrop 122, Bed 4, *Okensis* Zone and Subzone; (5) specimen SPbGU., no. 401401-41, l.

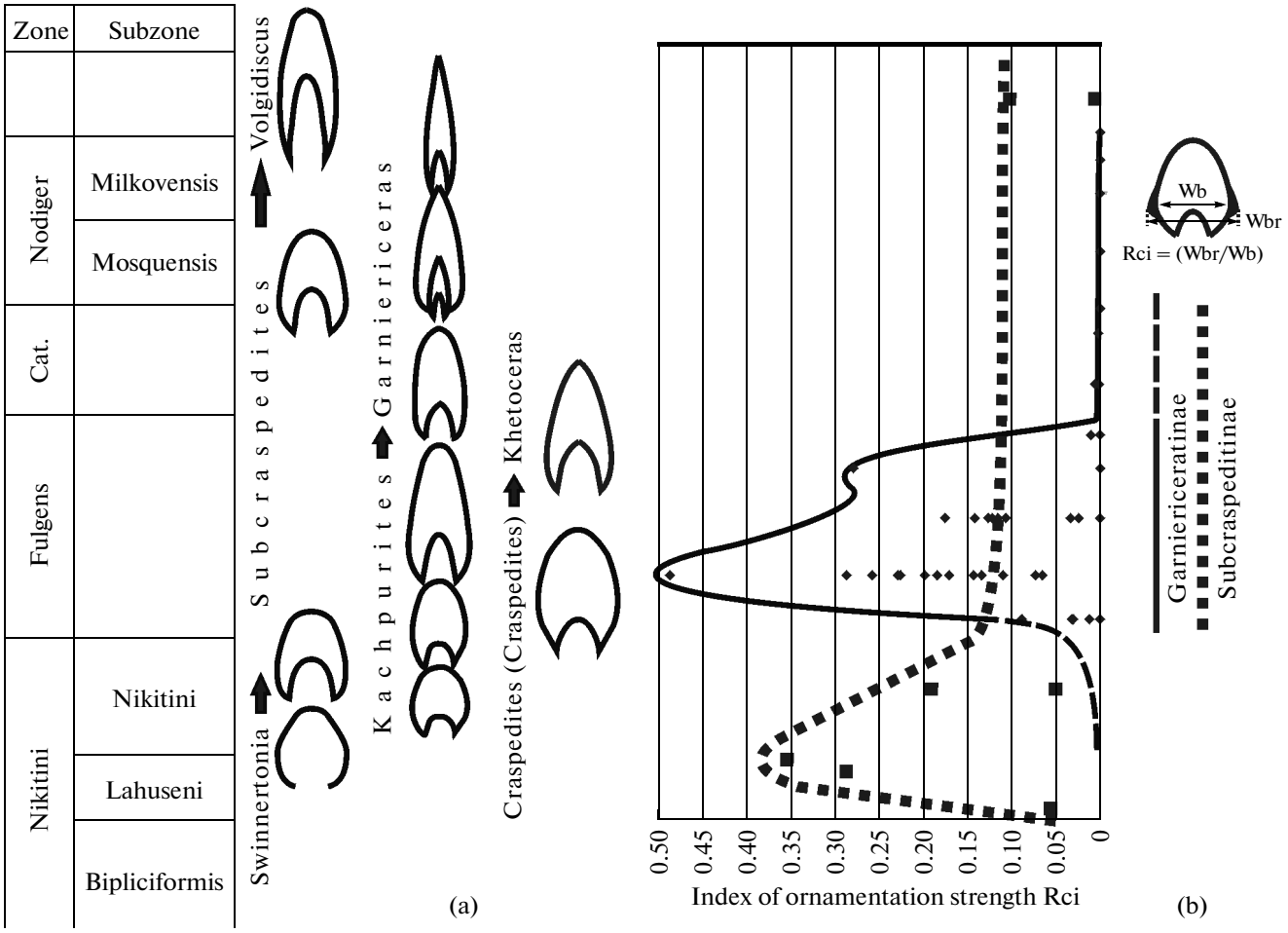


Fig. 4. Change in the shape of the (a) whorl cross-section and (b) index of ornamentation strength in some Middle–Late Volgian craspeditids, of the subfamilies Subcraspeditinae, Craspeditinae, and Garniericeratinae. The stratigraphic distribution of the taxa is shown in accordance with the Russian Platform scale (for correspondence to the scale of northeastern Europe and northern Siberia see Rogov and Zakharov, 2009). *Cat.*—*Catenulatum*.

(*Nikitini* Zone and Subzone of the European Russia scale, *Preplicomphalus* Zone of northeastern Europe)–middle part of the Ryazanian Stage (*Analogus* Zone of the northern Siberia scale). It occurs mainly in northeastern Europe in the Volgian, and across the entire Pan-Boreal biogeographic realm beginning from the terminal Volgian zone.

C o m p a r i s o n. Subcraspeditins are most similar to the Middle-Upper Volgian subfamily Garniericeratinae, including the genera *Kachpurites* and *Garniericeras* (Pl. 2, figs. 2, 3, 6) in the presence of nodes in early representatives and dominating trend towards an increase in the whorl overlap and narrowing during the Late Volgian. The subfamilies are mainly different in their sutural outlines. The Garniericeratinae have a suture with very low elements, with the saddles usually considerably wider than the lobes (Figs. 2.5–2.7). In addition, later Garniericeratinae (genus *Garniericeras*) possessed a keel, not found in subcraspeditins. Dimorphism is also different in these subfamilies: in Garniericeratinae microconchs are usually very small (3–4 cm in diameter, Pl. 2, figs. 2, 6), whereas two size groups are recognized in macroconchs (approximately 5–7 (Pl. 2, fig. 3) and 10–15 cm in diameter), which are difficult to assess. Only in *Shulginites* the size of the presumed micro- and macroconchs are similar to those in garniericeratins. However, differences in the sutural outline, ornamentation and shell shape in *Garniericeras* and *Shulginites* are so high that they cannot be considered as phylogenetically related genera, as is sometimes suggested (Mitta, 2007; Mitta and Sha, 2011). They are particularly different from *Shulginites*. The latest representatives of *Garniericeras* (*G. subclypeiforme*, Pl. 2, fig. 3), with a well-developed keel, no ornamentation, and with a very unusual suture are particularly strongly distinct from *Shulginites* (Casey, 1973, pl. 6, fig. 4; Mesezhnikov et al., 1983, text-fig. 6) in having low, wide saddles and the entire shape of elements of the suture. Some subcraspeditins (primarily *Subcraspedites* and Ryazanian taxa) are similar to members of Craspeditinae in the shell shape and ornamentation

but differ from those in the usually higher number of sutural elements and in the absence of cadicone shells, like *Craspedites (Trautscholdiceras)* from the terminal Volgian of the Russian Platform.

Remarks. Subfamilies within the family Craspeditidae, in the initial stages of their evolution mainly inhabited different basins: Subcraspeditinae were mainly characteristic of northeastern Europe, Garniericeratinae of the Middle Russian Sea, whereas Craspeditinae occurred almost everywhere in the Arctic. These subfamilies evolved independently from *Laugeites* (subfamily Laugeitiinae, sharing features of both Dorsoplanitidae and Craspeditidae). Recognition and interpretation of dimorphism in craspeditids and in other Volgian Boreal ammonites are difficult because aperture modifications in Volgian ammonites (except Pectinatitinae) are absent, and often the only criterion for recognition of micro- and macroconchs is the relative size of the shells, which leads to mistakes in assessment of supposed micro- and macroconchs. For instance, Callomon (in Abbink et al., 2001) considered *Subcraspedites sowerbyi* to be a microconch of *Craspedites plicomphalus* because these two species supposedly co-occur and because of the similarity between the terminal body chambers of large *S. sowerbyi* and *C. plicomphalus*. However, differences in the structure of the inner whorls and presence among *C. plicomphalus* of small specimens, which could be interpreted as possible microconchs (Casey, 1973, pl. 2, fig. 2), do not support such an interpretation.

Some Features of Evolution and Biogeography of Late Volgian Craspeditids

The three subfamilies of the Craspeditidae, existing in the Late Volgian in spatially isolated basins, show similar trends in the evolution of the suture, shell shape, and ornamentation, especially clearly observed in the comparison of the Western European Subcraspeditinae with Eastern European Garniericeratinae (Fig. 4) and, to a lesser extent, when these subfamilies are compared with Craspeditinae. The earliest Middle Volgian Subcraspeditinae, such as *Subcraspedites intermedius* (Donovan, 1964, pl. 1, figs. 1, 2, 4, 5; pl. 2, figs. 3, 4; pl. 8, fig. 5) and Garniericeratinae (an undescribed species of *Kachpurites*; see Shkolin and Rogov, 2012, pl. 80, figs. 4, 5) had semievolute shells possessing thin ribs similar to those of the ancestral genus *Laugeites*. Later members of Subcraspeditinae (*Swinnertonia* from the upper Middle Volgian and Garniericeratinae (macroconchs of *Kachpurites* from the Upper Volgian *Fulgens* Zone, apart from the two uppermost biohorizons) usually possessed well-developed umbilical nodes and had the coarsest (for craspeditids) ornamentation (Fig. 4b). In the future in both compared subfamilies, the whorl overlap degree increased, while the ornamentation weakened. While in subcraspeditins this was a comparatively gradual and long process leading to the discoidal forms only having appeared at the end of the Volgian (*Volgidiscus*), in the subfamily Garniericeratinae the transition from the coarsely ornamented *Kachpurites* to discoidal smooth *Garniericeras* was much quicker (Fig. 4b). In subcraspeditins, the appearance of discoidal weakly ornamented shells coincided with their wide distribution over the entire Arctic at the end of the Late Volgian, whereas in Garniericeratinae specialized discoidal *Garniericeras* were distributed in a narrower range than *Kachpurites* and were generally less abundant.

Ranges of members of Subcraspeditinae and Garniericeratinae in the Late Volgian virtually did not overlap (subcraspeditins are very rarely found in the Russian Platform, whereas occurrences of Garniericeratinae are unknown west of Spitsbergen). The evolution of craspeditins, which were found alongside members of the above two subfamilies, were mainly characterized by a gradual increase in ornamentation and a widening of the shell (see Rogov, 2013). Only in northern Siberia, where at the beginning of the Late Volgian, garniericeratins and subcraspeditins were completely absent, did craspeditins with a narrow subconical shell appear (the above-described genus *Khetoceras*). However they remained rare (up to now only 10 specimens belonging to this genus have been found) and had an extremely narrow geographical range.

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