

New Species of Spiriferids (Brachiopoda) from the Devonian and Carboniferous of Eastern Europe

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Abstract—In a revision of previously published materials, two new spiriferid species from the Late Tournaisian, *Unispirifer subtornacensis* sp. nov. and *Mesochorispira ussuilensis* sp. nov., and *Atylephorus nalivkini* sp. nov. from the Lytva Horizon of the Upper Devonian of Bashkiria are described. Based on the original collection, a new Serpukhovian subspecies, *Podtsheremia duplicicosta triplicicosta*, from the southern Ural Mountains and a new Late Carboniferous species, *Purdonella kalashnikovi*, from the polar Ural Mountains and adjacent islands are established.

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INTRODUCTION

During the preparation of the Atlas of Carboniferous spiriferids of Eastern Europe, I critically revised almost all published data on this group and, thus, inevitably revised the nomenclature of the order Spiriferida. In the light of the new data, the generic position of some previously established species and even the species diagnoses sometimes required improvement. For example, after the revision of the type material of the widespread Tournaisian species *Spirifer tornacensis* Koninck, (Sartenaer and Plodowski, 1996), it transpired that all fossils described under this name from Eastern Europe should be referred to other genera and even to a new species. *Unispirifer tornacensis* (Koninck) described by Nalivkin (1979) from the Lytva Horizon of the Ural Mountains is here considered as a new species of *Atylephorus* Sartenaer et Plodowski, while the Late Tournaisian *Spirifer* (or *Fusella*) *tornacensis* sensu *auctorum posterium* from the Moscow Region, Ural Mountains, Donets Basin, and part of Belgium is considered as *Unispirifer subtornacensis* sp. nov. *Spirifer striatus* sensu Nalivkin et Fotieva (non Martin, 1793) (Nalivkin and Fotieva, 1973) from the Kizel Horizon of the western slope of the southern Ural Mountains is also here considered as a new species of the genus *Mesochorispira* Carter.

Additionally, in the collections studied, I found new species and subspecies of Carboniferous spiriferids from the Ural Mountains. They are also described in the present paper. Three spiriferid taxa from the Ural Mountains are described based on the material received from V.N. Pazukhin and N.V. Kalashnikov. Two of five new species were established as a result of specification of the former diagnoses based on previously published descriptions and figures of the shells exterior and inte-

rior. The holotypes of four new taxa are currently stored in the monographic hall of the Geological Department of the Central Museum of Natural History (CMNS) of the National Academy of Sciences of Ukraine (collection nos. 2050 and 2446). The holotype of a new mesochorispir species is stored in the Central Research Geological Prospecting Museum (TsNIGR Museum) (collection no. 10124). In the present paper, I follow the spiriferid classification proposed by J.L. Carter et al. in 1994.

SYSTEMATIC PALEONTOLOGY

Order Spiriferida

Family Spiriferidae King, 1846

Subfamily Prospirinae Carter, 1994

Genus *Unispirifer* Campbell, 1957

Unispirifer subtornacensis Rotai et Poletaev, sp. nov.

Plate 7, figs. 1–4 and 10

Spirifer tornacensis: Koninck, 1887 (pars), pp. 110–111, pl. 25, fig. 11 (non cet.); Lebedev, 1913, p. 15, pl. 3, figs. 2–5; Sokol'skaya, 1941, p. 12, pl. 1, figs. 1–14, pl. 9, figs. 1–4; *Atlas of Index Fossils ...*, 1941, p. 110, pl. 24, figs. 4–6 (non cet.); Sarycheva and Sokol'skaya, 1952, p. 182, pl. 50, fig. 280.

Spirifer aff. *tornacensis*: Rotai, 1931, p. 75, pl. 7, figs. 4–11; Aizenverg and Poletaev, 1971, pl. 65, fig. 11.

Spirifer subtornacensis (nom. nud.): Aizenverg et al., 1963, p. 17.

Fusella tornacensis: Ivanova, 1960, pl. 59, fig. 4.

Fusella cf. *tornacensis*: Kalashnikov, 1974, p. 121, pl. 37, fig. 5.

Unispirifer sp.: Sartenaer and Plodowski, 1996, pl. 2, figs. 20–26.

E t y m o l o g y. From the similarity in shell exterior to *Atylephorus tornacensis* (Koninck).

H o l o t y p e. CMNS, no. 2050/64, complete shell; Donets Coal Field, Mokraya Volnovakha River, village of Razdol'noe, Dal'nii Mine; Lower Carboniferous, Tournaisian Stage, Volnovakha Horizon (C_1^c) (Aizenverg and Poletaev, 1971, pl. 65, figs. 11a–11d).

D e s c r i p t i o n. An exhaustive description of this species was introduced by Sokol'skaya (1941). Here outer and inner structures are described briefly.

The shell is medium-sized and moderately convex, semicircular or subtriangular in outline. The width always exceeds the length. The cardinal angles are always pointed or attenuate to form small ears. The fold and sulcus are well pronounced but not clearly defined.

The ventral valve is slightly more convex than the dorsal valve, with the greatest convexity near the midlength. The ventral margin is rounded and slightly curved near the sulcus. The apical angle is about 115° . The umbo is small and slightly curved over a low (up to 3–4 mm), slightly triangular or almost parallel to the marginal area. The ends of the area are cut off. Its surface, except for the triangular delthyrium, is longitudinally and transversely hatched. The sulcus is always clearly defined, starts from the umbo in the shape of a deep groove, gradually broadens and becomes shallow. Anteriorly, it is shallow, with badly defined margins but still angular in cross section.

The dorsal area is narrow and almost straight. The planes of the ventral and dorsal areas form almost a right angle. The umbo is poorly pronounced. The fold is relatively low but well developed and bordered sharply laterally by two grooves that are deeper than the grooves between other ribs.

The ribs in both valves are numerous, relatively narrow, with the width at the anterior margin not exceeding 1 mm, and mainly simple and rounded in cross section. The intercostal grooves are shallow and half as narrow as the ribs. The number of ribs is about 40 on the shell surface, usually 6 in the sulcus, and 4 on the fold. The rib surface bears regular, well pronounced, wavy trans-

verse growth lines and hardly visible thin longitudinal striae. Their intersections form imbricate rather than netlike microornamentation. In addition, the shell surface has coarser concentric lamellae of arrested growth, which are better pronounced near the anterior margin of adult shells.

Inside the ventral valve, the dental plates are relatively short, wedge-shaped, and abruptly diverging. The anterior ends of the dental plates are narrow and border a deep posterior region of the rounded muscle field, which is divided in half by a low longitudinal myophragm. The short delthyrial plate at the top of the delthyrium is clearly seen only in young specimens. In adult shells, it is merged with the well-developed secondary thickening of the ventral umbo.

Inside the dorsal valve, the cardinal process is developed at the top of the notothyrium. The notothyrial keels are short, hanging, and bear dental sockets at the anterior tips.

M e a s u r e m e n t s, mm. The shell is medium-sized and moderately convex. The greatest width is on the hinge line and is usually at most 35 mm. The length is no more than 22–23 mm and thickness is no more than 16–17 mm.

C o m p a r i s o n. *U. subtornacensis* sp. nov. is probably one of the oldest known European unispirifers; the Early Tournaisian unispirifers mentioned by Legrand-Blain and Martinez Chacon (1988) have not been described nor determined to species.

The new species differs from the similarly shaped Early Visean *U. posttornacensis* Garan' from the Radaevskoe and Bobriki Horizons of the Ural Mountains (Garan', 1970) in the shell being less transversely expanded and smaller, and having shorter ears. The younger Late Visean and Serpukhovian species more clearly differ in shape and size (Poletaev, 2000); their ribs increase considerably in absolute width with the growth of shell.

Explanation of Plate 7

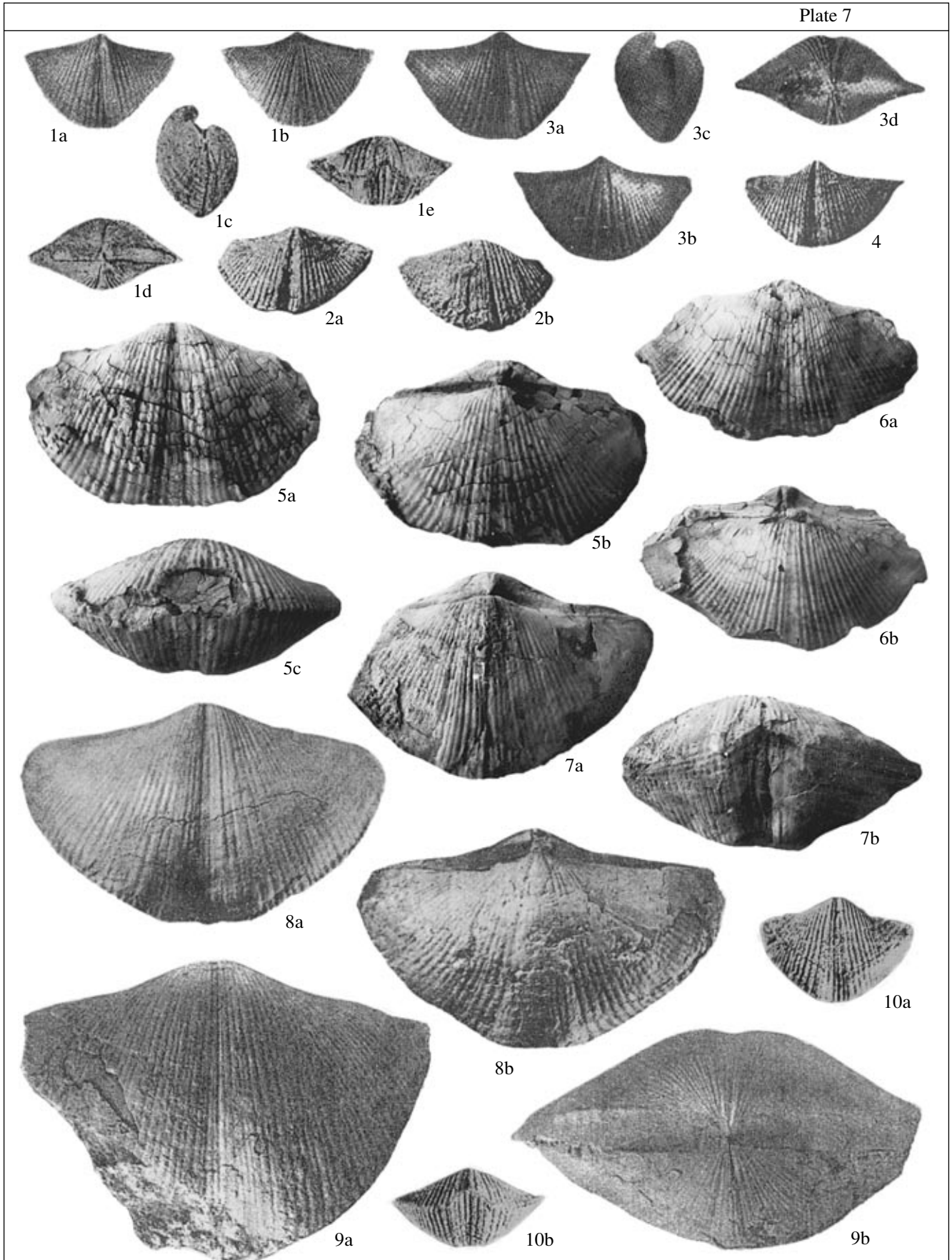
All sizes are natural.

Figs. 1–4 and 10. *Unispirifer subtornacensis* sp. nov.: (1a–1e) specimen CMNS, no. 406, complete shell in five positions; Moscow Basin, village of Chernyshino; Upper Tournaisian Substage, Cherepet' Horizon (Sokol'skaya, 1941, pl. 1, fig. 1); (2a, 2b) specimen TsNIGR Museum, no. 2992, shell in two positions; Donets Basin, Kal'mius River, village of Razdol'noe, Vodyanaya gully; Upper Tournaisian Substage, Volnovakha Formation (C_1^c Zone) (Rotai, 1931, pl. 7, fig. 7); (3a–3d) holotype CMNS, no. 2050/64, complete shell in four positions; Donets Basin, Mokraya Volnovakha River, village of Razdol'noe, Dal'nii Mine; Upper Tournaisian Substage, Volnovakha Formation (C_1^c Zone) (Aizenverg and Poletaev, 1971, pl. 65, fig. 11); (4) ventral valve of a young shell; Belgium, Tournais outskirts; uppermost Tournaisian (Rotai, 1931, pl. 7, fig. 5); (10a, 10b) specimen no. a5580a, complete shell in two positions; age and locality the same as above (Sartenaer and Plodowski, 1996, pl. 2, figs. 20, 22; pl. 5, figs. 74, 75).

Figs. 5–7. *Atylephorus nalivkini* sp. nov.: (5a–5c) holotype CMNS, no. 2446/51, shell with two closed valves, ears are broken off, three positions; (6a, 6b) specimen CMNS, no. 2446/50, slightly damaged shell in two positions; (7a, 7b) specimen CMNS, no. 2446/53, adult shell in two positions; southern Ural Mountains, Bashkiria, Zigan River; Upper Devonian, Upper Famennian, Lytva Horizon.

Figs. 8 and 9. *Mesochorispira ussuilensis* sp. nov.: (8a, 8b) specimen published by Lapina (1975, pl. 83, fig. 5) as *Spirifer striatus* and by Nalivkin (1979, pl. 51, fig. 1) as *S. theodorovichi*, young shell in two positions; (9a–9c) holotype TsNIGR Museum, no. 193/10124, adult shell in two positions (= *Spirifer striatus* (Nalivkin and Fotieva, 1973, pl. 20, fig. 1)); southern Ural Mountains, Usuli Stream; Upper Tournaisian, Kizel Horizon.

Plate 7



Remarks. For a long time, the majority of Russian researchers confused *U. subtornacensis* sp. nov. with the Western European *Atylephorus tornacensis*. However, Rotai (1931) noted that Eastern European specimens of *Spirifer tornacensis* differ somewhat from the topotypical form. Rotai gave a new species name, *S. subtornacensis*, to the Donets form (Aizenverg et al., 1963) but, up to this point, the name has been a *nomen nudum*.

U. subtornacensis differs from *A. tornacensis* in the size of the adult shell, which in the new species is half the size of *A. tornacensis*, and in the clearly outlined fold projecting over the dorsal valve surface. Sartenaer and Plodowski (1996) considered the smooth (almost absent) fold to be the main generic character of *Atylephorus*. The Central Asian *Spirifer* (*S.*) *tornacensis* sensu Gladchenko (1955) with the same character probably also belongs to *Atylephorus*.

Unlike most Russian researchers, Nalivkin (1979) believed that, in the Ural Mountains, the true "Spirifer tornacensis" was *Unispirifer tornacensis* sensu Nalivkin (non Koninck) from the Late Devonian (Lytva Formation) rather than the form from the Late Tournaisian. A comparison of the Ural Mountains topotypes of *U. tornacensis* sensu Nalivkin from the Zigan River with the Belgian type specimens of *A. tornacensis* has proven that Nalivkin was right to a considerable extent. The forms from the Ural Mountains almost lack a fold and, consequently, along with the Belgian *A. tornacensis*, belong to *Atylephorus*. However, representatives of *Atylephorus* from the Ural Mountains and Belgium differ at the species level, and these differences will be considered below in the description of the new species.

Before *Atylephorus* was established, Simakov et al. (Resolution of a symposium, Moscow, 1988) and Nalivkin proposed that the spiriferids from the Lytva Formation of the Ural Mountains should be assigned to *Unispirifer*, although they were more closely related to *Imbrixia ulbanensis* Bublichenko from the Reteporine Beds of the Tarkhan Formation of the Rudnyi Altai (Bublichenko, 1971) than to *Spirifer tornacensis*. In addition, the participants of the symposium supposed that the Altai species possibly represented the oldest members of *Unispirifer*. *U. subtornacensis* sp. nov. differs from *Unispirifer? ulbanensis* (Bublichenko) in the smaller and more convex shell and in the wider ribs at the same distance from the umbo. Additional material from collections of Early Tournaisian from the Altai must be studied before they can with certainty be assigned to *Unispirifer*.

The generic assignment of a group of spiriferid species from the Lower Carboniferous of the Kuznetsk Basin should also be revised. Originally, this group was erroneously assigned to *Fusella* McCoy (Beznosova, 1959), and then, without reexamination, it was transferred to *Unispirifer* (Afanasjeva, 1975). Judging from the published data, this group includes representatives

of two or three genera and, probably, of the genus *Unispirifer* as well.

U. subtornacensis differs from *Unispirifer?* (or *Parallelora?*) *ussiensis* (Tolmatchow) from the Lower Tournaisian of the Kuznetsk Basin (Tolmatchow, 1924) in the smaller relative width of the shell and in the much wider and less numerous ribs.

It differs from *Unispirifer? taidonensis* (Tolmatchow) from the Lower Tournaisian of the Kuznetsk Basin in the smaller relative width of its semicircular (rather than subrhombic) and somewhat more convex shell.

Occurrence. Upper Tournaisian, Cherepet' Horizon of the Moscow Basin; Upper Tournaisian of the northern Ural Mountains; Volnovakha Horizon (C¹c) of the Upper Tournaisian of the Donets Basin; Upper Tournaisian (Ivorian)—Tn3(a+b) of Belgium.

Material. Fifteen variously preserved shells.

Genus *Atylephorus* Sartenaer et Plodowski, 1996

Atylephorus nalivkini Poletaev, sp. nov.

Plate 7, figs. 5–7

Spirifer (*S.*) aff. *tornacensis*: Krestovnikov and Karpyshev, 1948, p. 55, pl. 1, fig. 10.

Spirifer tornacensis: Lapina, 1975, p. 186, pl. 83, figs. 3 and 4.

Unispirifer tornacensis: Nalivkin, 1979, p. 136, pl. 46, figs. 4–11 and 13–15.

Etymology. In honor of D.V. Nalivkin.

Holotype. CMNS, no. 2446/51, almost complete adult shell; Bashkiria, southern Ural Mountains, Zigan River; Upper Devonian, Lytva Horizon, Zigan Beds (Pl. 7, fig. 5).

Description (Figs. 1e and 1f). The shell is transversely extended, medium-sized or large (up to 60–65 mm wide, 40 mm long, and 27–28 mm thick). At all growth stages, the greatest width is at the hinge line. In young specimens, the cardinal ends are attenuated, forming small acute ears. In adults, the cardinal angles gradually approach a right angle. In young specimens, the lateral and anterior commissures form an almost regular semicircle, which curves slightly near the anterior termination of the sulcus because of the absence of a linguliform extension. The adult shells are subrhombic. In ontogeny, the length to width ratio changes from 1 : 2 to 1 : 1.5.

The ventral valve is transversely rhombic and moderately and evenly convex. The ventral umbo is short, obtuse-angled, and slightly overhangs the generally flattened and widely triangular area. The apical angle is about 150°. The area is up to 7–8 mm high. Its ends are splayed and its upper margin is sharpened closer to the angles (forming a cutting edge). The sulcus is poorly outlined, relatively narrow and shallow. Its greatest depth is near the midlength of the valve. The sulcus slopes gently slope towards the anterior margin.

The ribs bordering the sulcus appear in the umbo and diverge at an angle about 15°. Outside the umbo, an additional rib deviates from these ribs inside the sulcus.

Almost simultaneously with the primary (boundary) ribs, a pair of symmetrical ribs appears on the slopes of the sulcus. Each rib bifurcates in the posterior or middle region of the valve. The primary axial rib also appears in the umbo and forthright bifurcates. The secondary axial rib sometimes appears in the sulcus axis in the middle or anterior region of the valve, i.e., the axial rib appears to trifurcate. Thus, 10 or 11 equally thick ribs are usually present in the sulcus of an adult shell (Fig. 1). The ribs on the lateral slopes are usually simple but some may bifurcate (usually in the umbonal region) or even trifurcate. Each lateral side has at least 24 ribs. In adults, the density of ribs in the anterior margin near the sulcus is usually 8 per 10 mm. The ribs are relatively low, rounded in section, with grooves of approximately the same width as the ribs. The surface microornamentation is unknown.

The dorsal valve is usually semicircular in outline, slightly less convex than the ventral valve, with a poorly pronounced umbo and a low and almost linear area. The notothyrium is obtuse-angled and open. The fold is usually hardly discernible, i.e., projects only slightly above the valve surface and is slightly defined by the sharper grooves along its edges. A characteristic feature of *A. nalivkini* is two or three smooth median ribs which form a bald area in the middle of the fold. The fold bears 8 or 9 ribs; 2 or 3 median ribs are smoothed. The ribs on the lateral slopes bifurcate more often than those on the ventral valve; some of them trifurcate.

Measurements. The largest syntype of *A. nalivkini* sp. nov. is 40 mm long, 65 mm wide, and 27–28 mm thick; with a 7–8-mm-high area.

Inner structure. The shell wall is moderately thick even in the umbonal region. In the ventral valve, the dental plates are relatively short, diverging at an angle of 25°. The muscle field is oviform rhombic and divided by the myophragm. In the dorsal valve, the cardinal process is lamellar.

Comparison. The new species is similar to *A. tornacensis* (Koninck) from the Late Tournaisian of Belgium in size and shape and differs in the somewhat smaller and more transversely extended adult shell, thinner ribs (8 ribs per 10 mm of the anterior margin versus 6 or 7 in *A. tornacensis*), and especially in the median ribs of the sulcus and fold. In *A. tornacensis*, the median rib of the sulcus bifurcates closer to the middle of the valve, and the secondary median rib is absent or poorly developed in the anterior region of the sulcus. In *A. nalivkini* sp. nov., the median rib of the sulcus bifurcates in the umbo and shortly thereafter the secondary axial rib appears; this looks like trifurcation. The median ribs in the fold of *A. nalivkini* are smoothed, while in *A. tornacensis*, they are as convex as the lateral ribs.

Remarks. The new species is similar in shape, size, and poorly developed fold to *Unispirifer? ulbanensis* (Bublichenko) of approximately the same geolog-

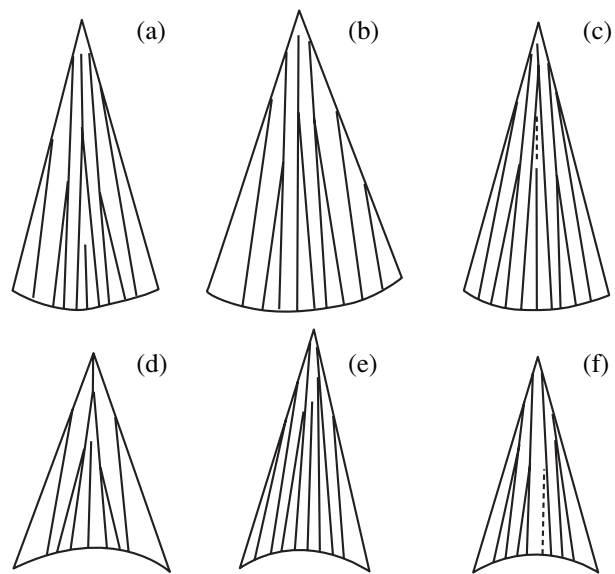


Fig. 1. Arrangement of ribs in the sulcus and fold: (a–d) *Atylephorus tornacensis* (Koninck): (a, b) fold (from Sartenaer and Plodowski, 1996, pl. 5, figs. 63, 65); (c, d) fold (from Sartenaer and Plodowski, 1996, pl. 5, figs. 67, 69); (e, f) *Atylephorus nalivkini* sp. nov.: (e) sulcus, specimen CMNS, no. 2446/51; (f) sulcus, specimen CMNS, no. 2446/50.

ical age, as it comes from the Upper Tarkhan Formation of the Lower Tournaisian of the Altai (Bublichenko, 1971). It is possible that after a revision *U.? ulbanensis* will be transferred to the genus *Atylephorus*. The new species differs from *U.? ulbanensis* in the much smaller number of ribs on the lateral sides (24–27 in *A. nalivkini* and up to 40 in *U.? ulbanensis*) and in the triple median rib in the sulcus of *A. nalivkini* (*U.? ulbanensis* has a single axial rib in the sulcus).

The new species differs from *U.? praeulbanensis* Bublichenko from the Lower Tarkhan Formation of the Lower Devonian of the Altai (Bublichenko, 1971), which is rather similar to *U.? ulbanensis*, in the shallower sulcus with ribs closely resembling other ribs bordering the sulcus (the sulcus of *U.? praeulbanensis* is deep and clearly defined by thickened ribs and its axial rib is also thickened).

Occurrence. Upper Devonian, upper part of the Famennian Stage, Lytva Horizon; Bashkiria, southern Ural Mountains, Zigan River.

Material. Ten almost complete shells and ten satisfactory preserved shell fragments from the type locality.

Subfamily Spiriferinae King, 1846

Genus *Mesochorispira* (Carter, 1992)

Mesochorispira ussuilensis Poletaev, sp. nov.

Plate 7, figs. 8 and 9

Spirifer striatus: Nalivkin and Fotieva, 1973, p. 62, pl. 20, figs. 1 and 2, fig. 7; Lapina, 1975, p. 186, pl. 83, fig. 5.

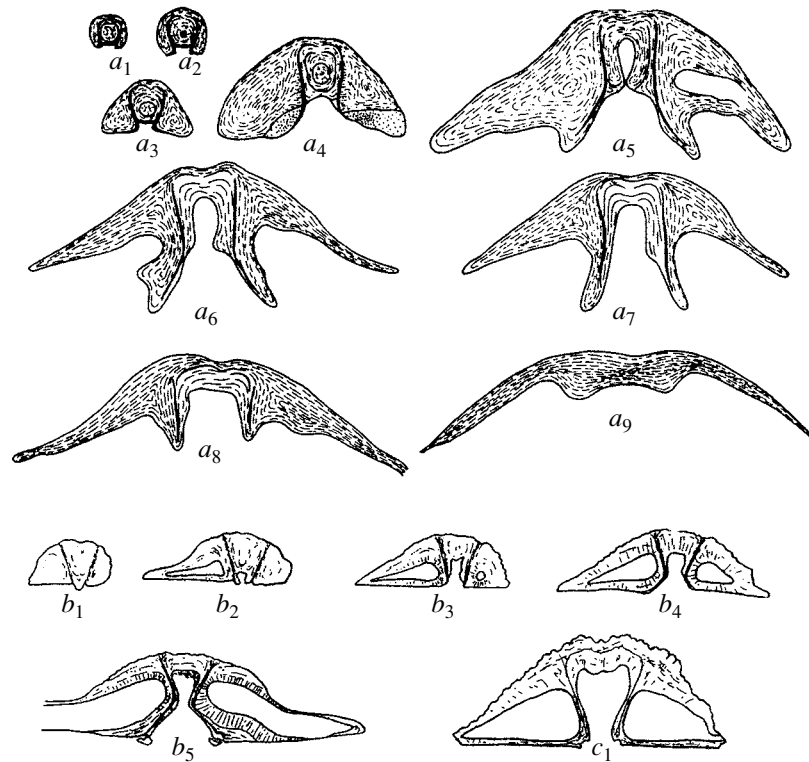


Fig. 2. Scheme of the ventral valve interior (in a series of fine cross sections): (a₁–a₉) *Mesochorispira ussuilensis* sp. nov. (= *Spirifer striatus* sensu Nalivkin and Fotieva, 1973, fig. 7; specimen no. 87/579); (b₁–b₅, c₁) *Spirifer striatus* Martin (from Harrington and Leanza, 1952, figs. 1, 2; specimens nos. B. 90.560 and B. 46.915).

Unispirifer theodorovichi (pars): Nalivkin, 1979, p. 136, pl. 51, figs. 1–3 (non: pl. 52, fig. 1; pl. 53, fig. 1).

Palaeochoristites konincki: Nalivkin, 1979, p. 140, pl. 50, figs. 2–4; pl. 56, fig. 1.

Etymology. From the Ussuli River in Bashkiria.

Holotype. TsNIGR Museum, no. 193/10124, complete but slightly damaged shell; Bashkiria, Ussuli River; Lower Carboniferous, Upper Tournaisian Substage, Kizel Horizon (Nalivkin and Fotieva, 1973, pl. 20, fig. 1).

Description (Figs. 2a₁–2a₉). The shell is medium-sized or large, transversely extended, and strongly biconvex (the ventral valve is 1.2–1.5 as convex as the dorsal valve). The adult shell is half as thick as the shell width. The shell shape changes from semicircular in young specimens to rounded pentagonal in adults. The ears are poorly developed. The sulcus and fold are well pronounced but moderately developed, and as ribbed as the lateral sides. The anterior margin is uniplicate.

The ventral valve ranges from semicircular to sub-pentagonal and strongly inflated, with the greatest convexity near the midlength of the valve. The umbo is small and low, becoming strongly curved in adults. The umbonal angle is 130–160°. The ears are from rectangular to slightly elongated, and slightly rounded in adult shells. The greatest width is at the hinge line; in

young shells, the width-to-length ratio is approximately 2, while in adult and senile shells, it is at most 1.5. The ventral area is up to 8–10 mm high, flattened, and curved only under the umbo, with parallel margins and obliquely cut ends. Its surface is ornamented with longitudinal growth lines and with coarser transverse grooves under the superficial layer. The delthyrium is open and close to an equilateral triangle in shape. The sulcus starts in the umbo as a poorly pronounced groove and gradually widens and deepens towards the anterior margin where it terminates in a short and rounded linguiform extension. The edges of the transverse profile of the sulcus lack sharp bends at the axial line and boards. The slopes of the sulcus decrease in steepness in the anterior region of the valve. The sulcus of the adult shells has 14 to 16 ribs. All the ribs, except for the median rib, are produced by bifurcation (sometimes repeated) of two or three rib pairs positioned symmetrical to the median rib. These rib pairs are separated from the ribs bordering the sulcus at the early developmental stages. The closest to the median paired ribs are the first to appear in the ontogeny, they are usually followed by the bifurcating median and, then the second, and sometimes the third pair of symmetrical ribs separates from the lateral ribs and branches to cover the entire slopes of the sulcus with ribs. Some ribs on the sulcus slopes also bifurcate near the umbo and, rarely, in the anterior region of the valve, but they

do not form bundles. The total number of ribs on the ventral valve of adults (including the sulcus ribs) is up to 70. In the anterior margin, the ribs are from 0.5 to 1.5–2 mm wide.

The ribs are flattened circular in cross section, separated from each other by relatively narrow and shallow grooves, and have microornamentation of concentric growth lines and hardly visible fine radial striae.

The dorsal valve is almost semicircular. The dorsal umbo is small and low. The posterior margin is almost straight. The area is low and almost linear. The notothyrium is open, wide and obtuse-angled at the top. The curvature and convexity of the dorsal valve changes slightly in ontogeny, unlike the convexity of the ventral valve, which strongly increases with the shell growth, changing from 0.9 in the young to 0.5 in adults. The fold is relatively low, gently rounded, and clearly outlined laterally by grooves, which are somewhat deeper than the grooves between the ordinary ribs. The ribs of the dorsal valve are similar to the ribs of the ventral valve in number, width, frequency of bifurcation, and microornamentation.

Measurements, mm. According to the figures published by Nalivkin and Fotieva (1973) and Nalivkin (1979), the shells of *M. ussuilensis* sp. nov. are up to 80 mm wide, 55–57 mm long, and 40–41 mm thick. The ventral area is up to 8–9 mm high.

Inner structures. The interior of the ventral valve of *M. ussuilensis* sp. nov. is well illustrated by the serial fine sections in the paper of Nalivkin and Fotieva (1973) (Fig. 2). A short delthyrial plate is buried in the strongly developed shell thickening in the umbonal region. This plate is duplicated by the secondary shell layer in the form of a false delthyrial plate. The ventral adminicles are relatively short, only slightly projecting beyond the hinge line, almost as high as the delthyrial keels, and diverge to the shell bottom at an angle of 10–12°. Other structures of the ventral valve and the interior of the dorsal valve are unknown.

Variability. The age-related changes in the length to width ratio and the width and thickness of young and adult shells were taken into account in the description of the species. In addition, two adult forms are recognized in the material from the Ural Mountains. Besides the typical large shells whose young stages are strongly transversely extended, the Kizel Horizon of the Ural Mountains has yielded smaller specimens with the habitus of adult shells. Some of them were identified by Nalivkin as *Palaechoristites konincki* (Dewalque, 1895). This species has been revised by Sartenaer and Plodowski (2002) and is unambiguously assigned to the genus *Mesochorispira*. The variability in size of adult *M. ussuilensis* sp. nov. are probably connected with variation in habitat conditions.

Comparison. *Mesochorispira* was widespread in the Paleotethys in the terminal Late Tournaisian–Early Visean and formed a series of local species.

M. ussuilensis sp. nov. is most similar in morphology and geographical distribution to *M. ischimica* (Litvinovich) (Litvinovich et al., 1969) from the Early Visean (Ishim Horizon) of northern Kazakhstan and the Sargardon Formation of Central Asia (original observations) and differs in the shorter relative length of adult shells and smaller number of ribs which are therefore wider and more flattened.

The new species differs from *M. konincki* (Dewalque) (Sartenaer et Plodowski, 2002) from the Late Tournaisian of Western Europe in the greater relative width of the shell, less developed umbonal region of the ventral valve, more elongated and slightly pointed ears and, hence, semicircular rather than oviform subsquare (typical for *M. konincki*) outline, and in the considerably smaller adult shells.

The new species differs from *M. grimesi* (Hall, 1858) from the Early Osage of North America (Carter, 1992) in the angular (rather than rounded) ears, the higher ventral area, which usually coincides with the shell's greatest width, the considerably more convex ventral valve in comparison with the dorsal valve, the shallower sulcus, and therefore the more flattened fold and less curved anterior margin.

Remarks. *M. ussuilensis* sp. nov. was for some time identified with Visean *Spirifer striatus* Martin (Archbold and Thomas, 1984). The new species differs from the latter species in the ribbing pattern, the wider, more flattened ribs which do not form bundles as a result of bifurcation (*S. striatus* has more convex, angular, and repeatedly bifurcating ribs up to the formation of bundles). Fine serial sections show that the representatives of these two genera are quite similar in the shell interior, although they differ considerably in the angle of convergence of the ventral adminicles in the dorsoventral direction. According to Harrington and Leanza (1952), in *S. striatus* (specimens nos. B. 90560, B. 46915, and B. 90562), this angle is up to 40°, while in *M. ussuilensis* (Fig. 2) and *M. grimesi* (Poletaev, 1999), it does not exceed 25°. Therefore, specimen no. B. 289, whose interior in cross sections was also published by Harrington and Leanza (1952), probably belongs to *Mesochorispira* rather than to *Spirifer*.

Occurrence. Middle and southern Ural Mountains, Bashkiria; Lower Carboniferous, Upper Tournaisian, Kizel Horizon.

Material. More than thirty variously preserved specimens.

Subfamily Purdonellinae Poletaev, 1986

Genus *Podtsheremia* Kalashnikov, 1966

Podtsheremia duplicicosta triplicicosta Poletaev, subsp. nov.

Plate 8, figs. 1–3

Spirifer duplicicostus: *Atlas of Index Fossils* ..., 1941, p. 112, pl. 26, fig. 3.

Etymology. From the typical triple branching of ribs.

Holotype. CMNS, no. 2446/84, complete adult shell; southern Ural Mountains, Uvel'ka River; Lower Carboniferous, Serpukhovian Stage (Pl. 8, fig. 2).

Description. The shell is medium-sized or large, transversely subrhombic, with rounded lateral sides and cardinal angles. The hinge line is considerably shorter than the greatest width. The ventral area is widely triangular and concave. The delthyrium is almost equilateral and open. The area height is about one-fifth of the ventral valve length. The ventral area is two or three times as high as the dorsal area. The notothyrium is obtuse-angled at the top.

Both valves are moderately and uniformly convex. The sulcus and fold are well developed and moderately wide. The sulcus is relatively shallow, bordered gently laterally, and fluently curved in profile. The linguiform extension is short but the anterior margin is distinctly uniplicate. The fold is relatively low, rounded in profile, and sharply bordered laterally.

The ribs covering the entire shell surface are smooth, relatively narrow, and usually grouped on lateral sides in bundles of three ribs. The bundles start directly from the umbo. Each lateral side of the adult shell bears up to 23 ribs. The sulcus and the fold bear 10–12 ribs each.

Inside the ventral valve, the dental plates are thin, short, slightly diverging anteriorly, and connected under the umbo by a short delthyrial plate. The secondary thickening of the valves is poorly developed. Inside the dorsal valve, the lamellar cardinal process and short hanging crural plates are developed.

Measurements, mm. The largest syntypes are up to 50 mm wide, 40 mm long, and 27–29 mm thick. Their hinge line is 35–36 mm long and the area is 7–8 mm high.

Comparison. The new subspecies differs from the most similar in habitus nominal subspecies *P. duplicicosta duplicicosta* (Phillips) (Davidson, 1857) mainly in the trifurcating (rather than bifurcating) and, hence, narrower ribs, which are more densely spaced on the lateral sides of the shells of the same size.

Remarks. In the relatively large sample of *P. duplicicosta triplicicosta* subsp. nov., some specimens have a lot of bifurcating ribs, while *P. duplicicosta duplicicosta*, has the trifurcating ribs. However, in the new subspecies, the trifurcating ribs obviously

prevail, while, in the nominal subspecies, the bifurcating ribs predominate.

Occurrence. Southern Ural Mountains, Bashkiria; Lower Carboniferous, Serpukhovian Stage; Novaya Zemlya Archipelago; Lower Carboniferous, Upper Visean Stage.

Material. Thirty-six well and satisfactory preserved specimens from the type locality.

Genus *Purdonella* Reed, 1944

Purdonella kalashnikovi Poletaev, sp. nov.

Plate 8, figs. 4–7

Purdonella nikitini elongata (pars): *Atlas of fauna and flora ...*, 1979, p. 87, pl. 30, figs. 3 and 4 (non 5); pl. 36, fig. 4 (non 5).

Etymology. In honor of Nikolai Vlasovich Kalashnikov.

Holotype. CMNS, no. 2446/96, complete adult shell; Polar Ural Mountains, Chaika Cape; Upper Carboniferous, Kazimovian Stage.

Description (Pl. 8, fig. 7). The shell is large and biconvex, with the ventral valve one and a half or twice as convex as the dorsal valve. The ventral valve and the shell are elongated and pear-shaped throughout the ontogeny. The ventral umbo is strongly elongated and beak-shaped. The greatest width and the greatest thickness are near the shell midline or closer to the anterior margin. The length of the hinge line is at most two-thirds of the greatest shell width. The cardinal ends are clearly rounded. The ventral area is triangular at all developmental stages, flatly concave, with the apical angle about 90°. The height of the ventral area is about one-seventh of the valve length. The margins of the area are separated from the palintrope by a poorly pronounced rib. The delthyrium is open; its apical angle is 35°. The sulcus is moderately narrow and shallow, with a groove on the bottom, and bordered weakly laterally. The anterior commissure is uniplicate. The linguiform extension enlarges with growth.

The dorsal valve outline varies from rounded to transversely oviform. The dorsal umbo is short and slightly projecting. The fold is weakly bordered, hardly visible in the posterior region of the valve, and gradually widening and rising anteriorly, although remaining rounded.

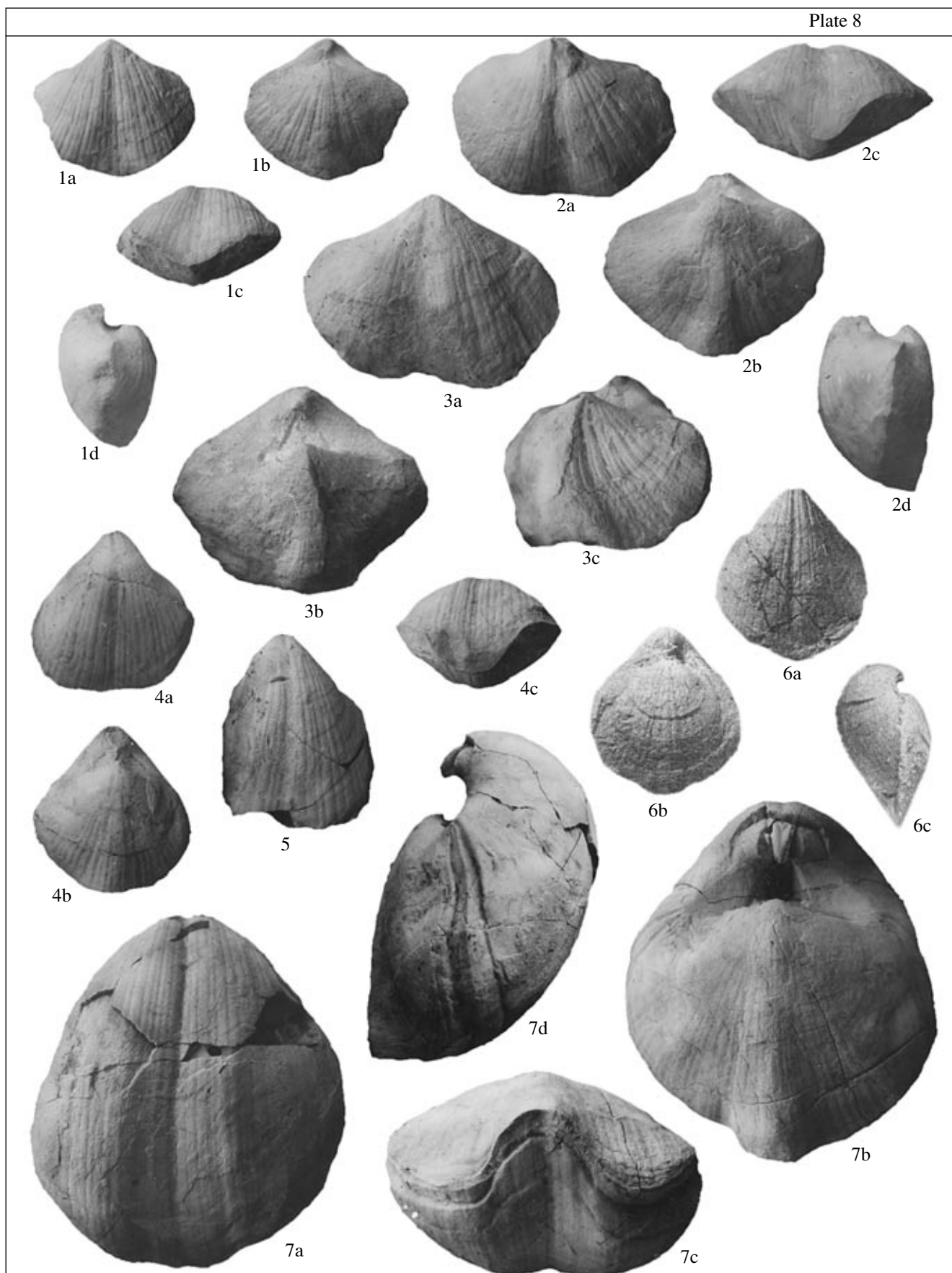
Explanation of Plate 8

All sizes are natural.

Figs. 1–3. *Podtsheremia duplicicosta triplicicosta* subsp. nov., southern Ural Mountains, Uvel'ka River; Lower Carboniferous, Serpukhovian Stage: (1a–1d) specimen CMNS, no. 2446/83, young shell in four positions; (2a–2d) holotype CMNS, no. 2446/84, shell in four positions; (3a–3c) specimen CMNS, no. 2446/85, adult shell in three positions.

Figs. 4–7. *Purdonella kalashnikovi* sp. nov.: (4a–4c) specimen CMNS, no. 2446/94, complete young shell in three positions; Polar Ural Mountains, Chaika Cape; Upper Moscovian–lowermost Upper Carboniferous; (5) specimen CMNS, no. 2446/95, broken ventral valve; locality and age the same as above; (6a–6c) specimen from the collection of the Geological Faculty of the Kiev State University, without number, complete young shell in three positions; southern Ural Mountains, Voskresensk reef; Upper Carboniferous (*Atlas of Fauna and Flora ...*, 1979, pl. 36, fig. 4); (7a–7d) holotype CMNS, no. 2446/96, shell in four positions; Polar Ural Mountains; Chaika Cape; Upper Moscovian–lowermost Upper Carboniferous.

Plate 8



The shell surface is covered with ribs. The ribs are flattened, with narrow grooves in the intercostal spaces. The two or three closest to the sulcus ribs bifurcate in the umbo. Other ribs more often bifurcate in the posterior third of the valve. The ribs in the anterior margin are usually about 1.5–2 mm wide. Each lateral side has 15 to 18 ribs and the sulcus has about 15 ribs.

The microornamentation is composed of fine concentric growth ridges and coarser and widely spaced projections, which mark the points of arrested growth. The radial microornamentation is unknown because of poor preservation.

Measurements, mm. The largest known specimen (holotype) is 68 mm long, 58 mm wide, and 36 mm thick. Its hinge line is 36 mm long, and the area is 10 mm high.

Inner structure. The shell interior is typical for *Purdonella*: the ventral adminicles are relatively thin, diverge anteriorly at an angle of 15°, and are no more than one-eighth of the valve in length. The secondary thickening of the valves is almost absent. Even in the large shells, the thickness of the shell wall in the umbonal region does not exceed 1.5–2 mm. The muscle field, ovarian impressions, and mantle canal systems are unknown because of poor preservation. In the dorsal umbo, the lamellar cardinal process and short hanging crural plates are developed.

Comparison. The new species differs from the Early Permian (Asselian) *P. nikitini* (Chernyshev) (Chernyshev, 1902) in the elongated shell and narrower and more clearly defined sulcus and fold. These differences are almost unnoticeable in the young specimens but are well developed in adult shells.

Remarks. Early Bashkirian (?) *P. praenikitini* Kalashnikov (Kalashnikov, 1980) and its junior synonym *P. (?) ancestralis* Dedok (Dedok, 1982) from the southern extremity of the Novaya Zemlya Archipelago were conditionally assigned by the authors of the original descriptions to *Purdonella*. However, these species probably belong to *Neomunella* Ozaki, because their adminicles are thin and buried in the secondary shell layer. Nevertheless, the new species differs from the closely set Early Bashkirian *N. ? praenikitini* from the Novaya Zemlya Archipelago in the narrower and more frequently branching ribs, relatively higher ventral area, and, hence, more elongated umbo of adult shells.

I suppose the subspecies (?) *P. nikitini aucta* Einor (*Atlas of Fauna and Flora ...*, 1979) from the Kazimovian (Myachkovo Horizon) and its possible synonyms *P. nikitini* sensu Kalashnikov (Kalashnikov, 1980) from the western slope of the Ural Mountains and *P. nikitiniformis* sensu Prokofiev (non Ozaki) (Prokofiev, 1975) from the Samarskaya Luka should be placed in *Neomunella* as a separate species, *N. aucta* (Einor). This species differs from the new species in the smaller, more rounded, and less convex shell, relatively longer hinge line, and considerably wider and almost non-branching ribs.

Occurrence. Polar Ural Mountains (Chaika Cape) and the southern Ural Mountains (Voskresensk reef); uppermost Middle Carboniferous–lowermost Upper Carboniferous.

Material. Nine well and satisfactory preserved specimens and six fragments of shells from the Chaika Cape.

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