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Research article

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New and revised taxa of Carboniferous spiriferides (Brachiopoda, Spiriferida) from the Donets Basin (Ukraine) and South Urals (Russia)

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Abstract. The brachiopods *Meristorygma donakovae* Poletaev, 2018, *Johnsoniana* nom. nov. from Mississippian strata of the Urals and *Betaneospirifer stepanovi* Poletaev, 2015 from Gzhelian rocks of the Urals are re-described. *Tiramnia davidi* sp. nov. from the Bashkirian of the Donets Basin (Ukraine) is newly described. Revision of available data shows that the revised genus *Verneuilia* Hall & Clarke, 1893 belongs to the family Elythyridae Gourvennec, 1994 of the superfamily Martinioidae Waagen, 1883. The genera *Johnsoniana* nom. nov., *Changshunella* Sun *et al.*, 2004 and possibly *Minythyra* Branton, 1984 belong to the family Oceaniidae Poletaev, 2015 of the superfamily Paeckelmanelloidea Ivanova, 1972. The importance of characters such as denticulation of the hinge line of the interarea and type of vascular impression in the diagnosis of higher spiriferid taxa is shown.

Keywords. Carboniferous, Brachiopoda, Spiriferida, Donets Basin, South Urals.

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Introduction

Carboniferous brachiopods from the Urals and the Donets Basin have been studied with varying intensity since the middle of the 19th century. During the 20th century, the most representative studies of the taxonomy of Carboniferous brachiopods of the Urals were the works of Yanishevsky (1900, 1910, 1918), Chernyshev (1902), Gerasimov (1929), Einor (1936, 1957), Semikhatova (1941a, 1941b), Stepanov (1948), Barkhatova (1970), Kalashnikov (1974, 1980) and Nalivkin (1979). They and their students Mironova (1967), Alexandrov & Einor (1979, 1996), Donakova (1983) and others continued these studies in the late 20th century.

At the beginning and especially in the middle of the 20th century, works on Late Palaeozoic brachiopods from the carbonate and coal-bearing deposits of the Donets Basin were published by Lebedev (1913), Lisitsyn (1925), Ilovajsky (1929) and Licharev (1938). Since the middle of the 20th century, the most representative works in the taxonomic study of brachiopods from Carboniferous strata of the Donets Basin were monographs and articles by Rotai (1931, 1951) and Aisenverg (1950, 1951) and Aisenverg &

Poletaev (1971, 1983). Since the end of the last century, the present author has extended this work (Poletaev 1975, 1998, 2008, 2013, 2015, 2017, 2018, 2022).

Significant revisions of the East European Carboniferous Spiriferida Waagen, 1883 from the Donets Basin and the Urals have been published in local journals (e.g., Poletaev 2009, 2015, 2017) and in an atlas (Poletaev 2018), but only in Russian. All these publications remained poorly accessible and almost unknown to the scientific community. As a consequence, the recent huge collective review of almost all modern data on the genus composition and biostratigraphic significance of Carboniferous brachiopods of the world (Angiolini *et al.* 2022) rather poorly reflects the currently available data on spiriferids of Eastern Europe, especially of the Urals and Donets Basin. So far, only the revision of Late Palaeozoic spiriferid taxonomy has been published in English (Poletaev 2022). Therefore, the publication of descriptions of new taxa according to currently accepted international standards is still needed. It will ensure the validity of these taxa and the possibility of their wide use in palaeontology and biostratigraphy of the Carboniferous not only in the Urals and Ukraine. These data would be useful not only to revise the systematics of Late Palaeozoic spiriferids of Europe, but also to acknowledge the work of palaeontologists of the past generations.

Material and methods

The studied material is kept in different palaeontological museums in Ukraine, Russia, China, Belgium, Germany and England. Most of the material (about 40 specimens) from the Donets Basin (Ukraine; Fig. 1C–D) has been examined directly from the collections, either visually or by thin section. These include material collected by David Aisenverg (1951) from limestones of the Smolyanyivka Formation (also known as C₂³ or H) of the Donets Basin, eastern Ukraine (Fig. 1A–B). They are stored in the National Museum of Natural History in Kyiv (NMNH 1433 and NMNH 2446 collections).

The examined samples from Bashkortostan (Urals, Russia; Fig. 2) are housed in the Geological Museum of the National Taras Shevchenko University in Kyiv (collection GMNTSU 79). Most of the Ural material is kept in the Centralny Nauchno-Issledovatel'sky Geologo-Razvedochnyi Museum (collection CNIGR) of the All-Russian Geological Institute (VSEGEI), some in the Vsesoiuzny Nauchno-Issledovatel'sky Geologo-Razvedochnyi Institute (VNIGRI) Museum and in the Saint Petersburg Mining University (collection SPGGI 46) in Saint-Petersburg, Russia.

Other specimens have been used thanks to their descriptions and pictures in the articles listed in References. Unfortunately, it is not possible to make better pictures at the moment.

The spiriferid taxonomy of Carter *et al.* (2006) is used in the systematic palaeontology section, except for the diagnosis of the superfamilies Brachythyridoidea Frederiks, 1924 and Paeckelmanelloidea Ivanova, 1972, which are partly modified here.

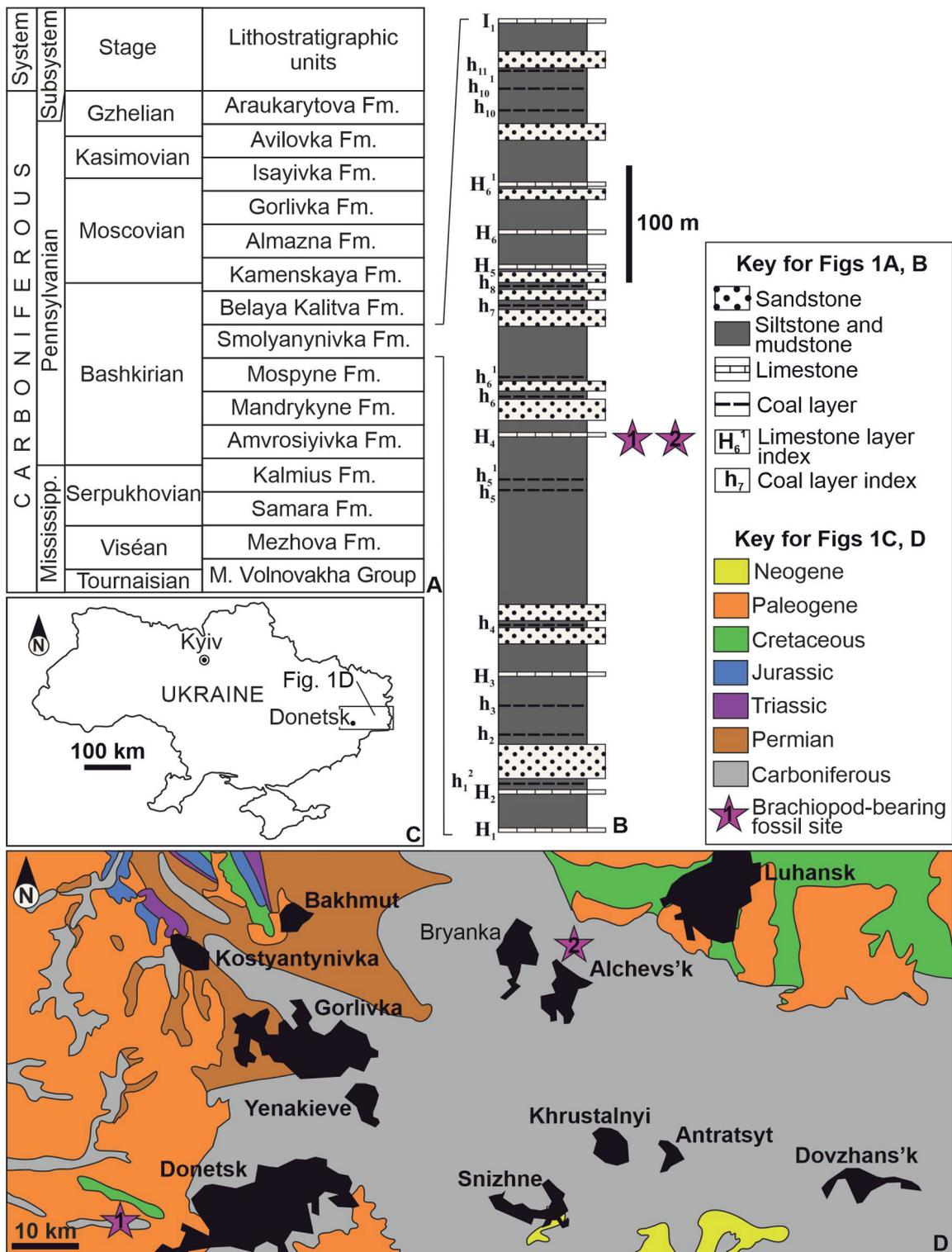


Fig. 1. Geographical and stratigraphic location of the studied spiriferid-bearing localities (marked by stars) in Ukraine. **A.** Carboniferous stratigraphy of the Donets Basin and position of the Smolyanynivka Formation. **B.** Lithologic column of the Smolyanynivka Formation and stratigraphic position of the spiriferid-bearing fossil sites (modified after Nemyrovska *et al.* 2013). **C–D.** Geographical location of the studied spiriferid-bearing localities (1 = Donetsk Region, Khartsis'k District, Vovcha River, Illinka village; 2 = Luhansk Region, Bila River, Gorodyshche village).

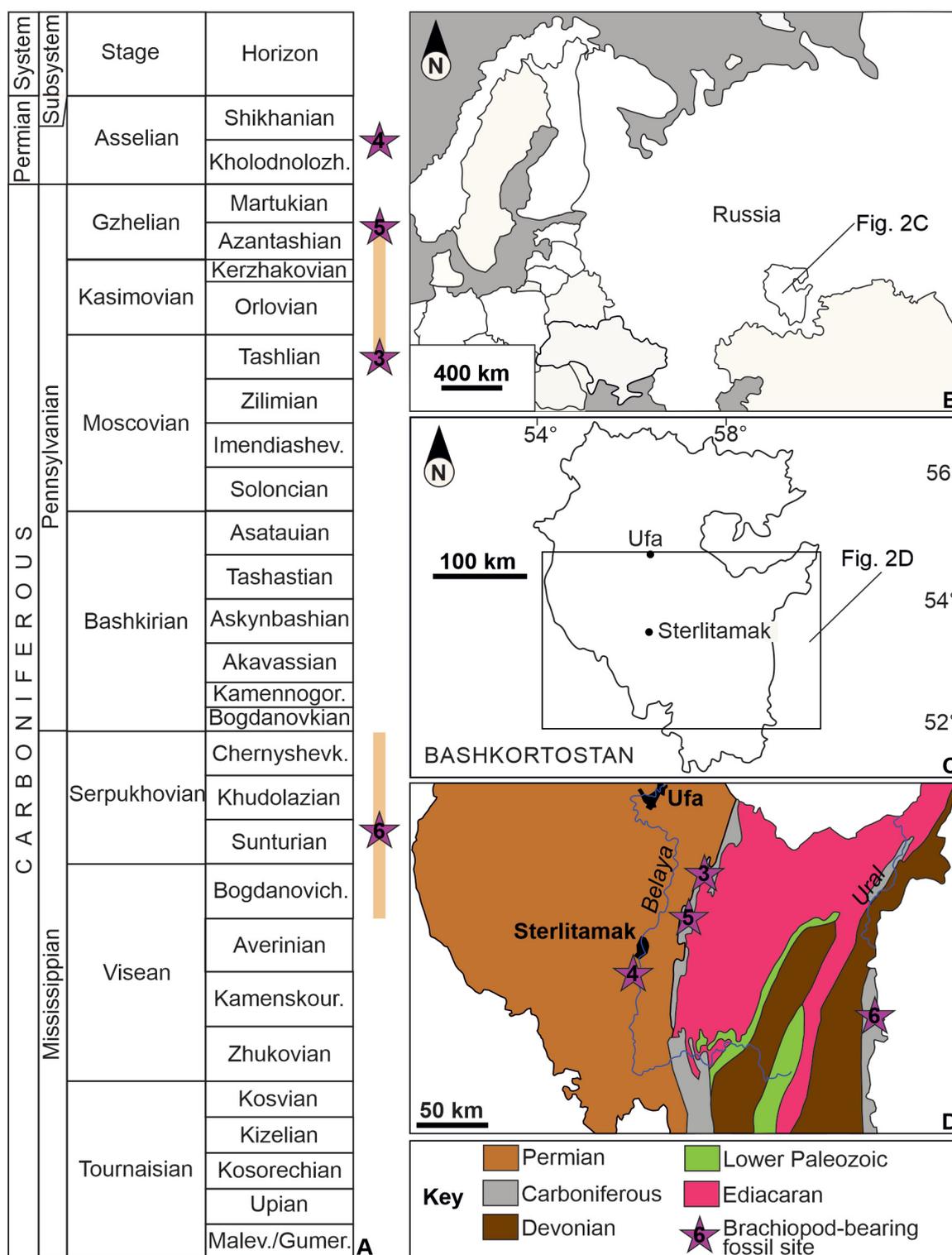


Fig. 2. Geographical and stratigraphic location of the studied spiriferid-bearing localities (marked by asterisks) in Bashkortostan (Urals, Russia). **A.** Carboniferous stratigraphy of the South Urals (modified from Kulagina *et al.* 2009: fig. 2). **B–D.** Geographical location of the studied spiriferid-bearing localities: 3 = the Zilim River, Tash-Asty village; 4 = the Belaya River, Sterlitamak town, Tura Tau and the Yurak Tau Mounts; 5 = the Belaya River, Tabynskoie village, Voskresenka Mount; 6 = the Ural River, Magnitogorsk Region.

Results

Phylum Brachiopoda Duméril, 1806
Classe Rhynchonellata Williams, Carlson, Brunton, Holmer & Popov, 1996
Order Spiriferida Waagen, 1883
Suborder Spiriferidina Waagen, 1883
Superfamily Martinioidea Waagen, 1883
Family Martiniidae Waagen, 1883
Subfamily Martiniinae Waagen, 1883

Genus *Tiramnia* Grunt, 1977

Type species

Martinia uralica Chernyshev, 1902; original designation.

Diagnosis

Shells small to medium-sized, brachythyrid outlines, without plates or septa in either valve; fold and sulcus weakly or moderately developed; furrow in sulcus is very weak or absent. Surface smooth or with the weak, short ribs on anterior edge. Muscle field of ventral valve comparatively large, lanceolate; radial vascular imprints ramiform; axial mantle canal (vascula media) singular.

Included Pennsylvanian species

Arctic Russia, the northern Ural (Chernyshev 1902; Grunt 1977): *Tiramnia uralica* (Chernyshev, 1902), *T. semiglobosa* (Chernyshev, 1902) Permian, Cisuralian; *T. tschaikensis* Grunt, 1977; upper Pennsylvanian, Cape Chaika.

Arctic Canada and Southeastern Alaska (Carter & Poletaev 1998): *Tiramnia waltery* Poletaev, 1998 and *T. grunti* Poletaev, 1998; Pennsylvanian.

Greenland (Grunt 1977): *Tiramnia greenlandica* Grunt, 1977; Permian.

China (Chao 1929): *Tiramnia changchiacouensis* Chao, 1929; Pennsylvanian.

Ukraine (this paper) *Tiramnia davidi* sp. nov., Lower Pennsylvanian.

Remarks

Tiramnia Grunt, 1977 differs from *Martinia* M'Coy, 1844 by the presence of a ramified vascular system; *Tiramnia* differs from *Jilinmartinia* Li & Gu, 1980 by having single (connected) vascula media rather than paired vascula developed in the ventral interior of the latter. *Tiramnia* differs from the somewhat similar *Postamartinia* Wang & Yang, 1993 by having round, elongated, but not transverse shells, by the absence of low ribs on the flanks, and by a much shorter tongue of sulcus.

Tiramnia davidi sp. nov.

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Fig. 3

Martinia (Pseudomartinia) sp. A. – Aisenverg 1950: 137, pl. 2 figs 9–10.

Martinia (Pseudomartinia) sp. – Aisenverg 1951: 43, pl. 11 fig. 2.

Martinia balkhashica – Poletaev 2008: 28, pl. 1 figs 1–5.

Tiramnia sp. – Poletaev 2018: 23, pl. 13 figs 6–10.

non *Martinia balkhashica* – Beznosova 1968: 191, pl. 29 fig. 15.

Diagnosis

Medium-sized shell with angular edges of trough-shaped anterior part of sulcus of the ventral valve and a shallow furrow along axis of fold distinctly limited in the anterior part of the dorsal valve.

Etymology

Named in honor of David E. Aisenverg, who first distinguished this species.

Material examined

Holotype (Fig. 3A)

UKRAINE • Donetsk Region, Khartsis'k District, Vovcha River, Illinka village; late Bashkirian Smolyanynivka Formation, H₄ limestone layer; Aisenverg 1951 Coll.; NMNH 1433/85.

Paratypes (Fig. 3B–E)

UKRAINE • 12 specs; Luhansk Region, Bila River, Gorodyshche village; late Bashkirian, Smolyanynivka Formation; stratigraphic interval between the H₃ limestone layer to the H₆ limestone layer; Poletaev 2018 Coll.; NMNH 2446/102 to 2446/113.

Description

Medium-sized shell (24 mm wide, 23 mm long and 17 mm thick in the holotype), rounded pentagonal in outline and rather strongly and uniformly biconvex in lateral profile; hinge line shorter than the largest width at mid shell. Umbonal part of ventral valve broad, well-developed, with steep lateral slopes. Cardinal extremities rounded. Beak is well developed, inclined, projecting above hinge line. Ventral interarea short, narrow, triangle, smooth. Sulcus distinctly developed, rather wide, shallow with weak axial groove and trough-like tongue; uniplicate anterior margin with distinctly angular margins of tongue at junction with lateral slopes. Dorsal valve somewhat less convex than ventral one. Dorsal umbo

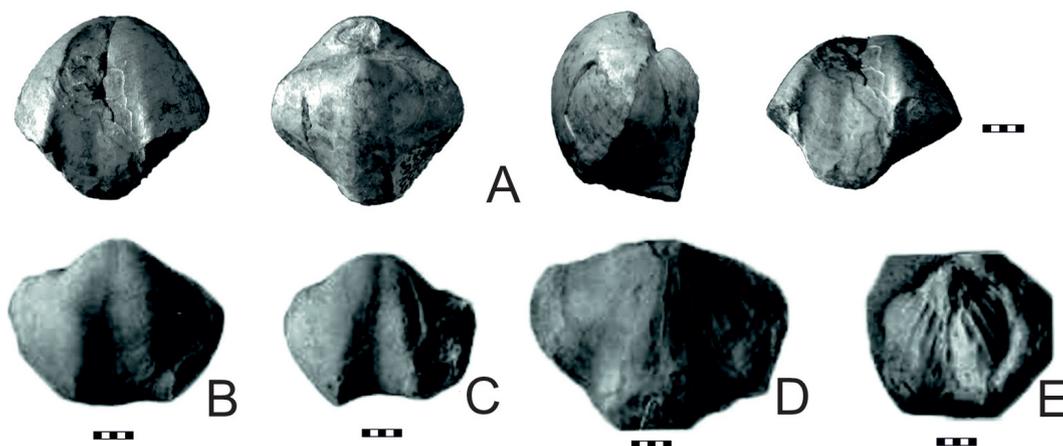


Fig. 3. *Tiramnia davidi* sp. nov. from the Donets Basin (Ukraine). Pennsylvanian, Bashkirian. **A.** Holotype NMNH 1433/85 (Aisenverg 1951 Coll.) Donetsk Region, Illinka village; ventral, dorsal, lateral and anterior views (copy from Aisenverg 1951: pl. 11 fig. 2). **B–C.** Paratypes NMNH 2446/102, NMNH 2446/103 (Poletaev 2018 Coll.) Luhansk Region, Bila River, Gorodyshche village; ventral views (copy from Poletaev 2018: pl. 13 figs 8–9). **D.** Paratype NMNH 2446/104 (Poletaev 2018 Coll.) same locality; dorsal view (copy from Poletaev 2018: pl. 13 fig. 7). **E.** Paratype NMNH 2446/105 (Poletaev 2018 Coll.) same locality; internal view of the ventral valve (copy from Poletaev 2018: pl. 13 fig. 10). Scale bar units = 1 mm.

small, well expressed. Fold broad, indistinct in posterior part, but distinctly developed in the anterior part, where its slopes fall steeply. Fold also bears a slight median furrow. Shell surface mostly smooth, weak lines of growth are visible, and rare traces of short weak radial ribs near the anterior commissure. Microsculpture not observed on the specimens. Internal structure of the ventral valve with subrhombic deepened muscular imprints in the umbonal region, as well as traces of single axial and several ramiform lateral imprints of the vascular system (see Fig. 3E).

Remarks

The new species differs from other known species of *Tiramnia* in having a more pronounced sulcus with a trough-like profile of the tongue and a distinct fold with a median groove. Based on morphological similarity and close geological age, the specimens under study were previously assigned to the Bashkirian *Martinia balkhashica* Beznosova, 1968 from eastern Kazakhstan (Poletaev 2008). However, the holotype of *M. balkhashica* has an interior with twin *vascula media* (Beznosova 1968: pl. 29 fig. 16), which clearly shows that the Kazakh species belongs to *Jilinmartinia*. Other representatives of *Tiramnia*, similar to *T. semiglobosa*, differ from the new species by the rounded contours of the shells, sometimes drop-shaped, with an elongated ventral apex, a weak, poorly defined sulcus, often with a median groove. *Martinia buckmani* Yanishevsky, 1918 from the late Serpukhovian of Central Asia and early Bashkirian of the Donets Basin and the Urals is very similar to the new species. However, *M. buckmani* is distinguished by its smaller size, swollen shell with a strongly protruding and wrapped apical part of the ventral valve, and apparently by its internal structure. *Tiramnia davidi* sp. nov. differs from *Postmartinia juresanensis* (Stepanov, 1948) from the Pennsylvanian of Bashkortostan by the angular rather than rounded lateral profile of the clearly limited anterior end of the sulcus and its much less developed continuation (tongue), as well as by its stratigraphic and geographic occurrence.

Superfamily **Brachythyridoidea** Frederiks, 1924

Diagnosis emended

Outline commonly ovate; hinge line shorter than width, weakly denticulated; cardinal extremities rounded; lateral slopes usually with few simple coarse ribs or with numerous flat bifurcated ribs. Microornament absent or weakly developed. Delthyrium partially covered by deltidium or stegidial plates; subdelthyrial plates absent; ventral adminicula absent; vascular imprints pinnate or ramiform; miophragm or septum in ventral valve usually absent. Dorsal adminicula and crural plates absent.

Remarks

The presence of a denticulated hinge line in the ventral interarea of *Spirifera ovalis* Phillips, 1836 has not yet been demonstrated, but this character has been found and is supported by some other data. Angiolini *et al.* (2011: 71) revised the Carboniferous brachiopod fauna from historical sections in England. As a result, they established the genus *Latibrachythyris* Angiolini *et al.*, 2011. The type species of *Latibrachythyris* is *Spirifer pinguis* Sowerby, 1821 and has a denticulated hinge line. Carniti *et al.* (2022: 865) attributed *Spirifer crassus* de Koninck, 1883 to *Latibrachythyris* and, following Angiolini *et al.* (2011), also *Spirifer rotundatus* Sowerby, 1825. There is no doubt that the authors' definitions of these species are correct, but the exact definition of some *Brachythyris*-like genera is problematic. An examination of the brachiopod collections of de Koninck (1883, 1887) at the Royal Belgian Institute of Natural Sciences in Brussels, Belgium, in 1992 showed that specimens of *Spirifer subrotundatus* M'Coy, 1844 (sensu de Koninck, 1887) have a primary median costa in the sulcus and a distinct short septum in the ventral valve. Therefore, this species must now be assigned to *Phragmobrachythyris* Poletaev 1999 from the family Skelidorygmidae Carter, 1994 (Carter & Gourvenec 2007). A correct genus definition of all *Brachythyris*-like spirifers is only possible by using serial cross sections of the apical part of the shell. The data presented above have shown that *Latibrachythyris* has a weakly denticulated hinge line and *Phragmobrachythyris* has

a miophragm or septum in the ventral valve. Altogether, these data do not allow to assign the families Brachythyrididae Frederiks, 1924 and Skelidorygmidae to the superfamily Martinoidea Waagen, 1883, as I had done earlier (Poletaev 2022).

Stratigraphic distribution

Late Devonian to Permian.

Family **Brachythyrididae** Fredericks, 1924

Diagnosis

Primary median costa in sulcus absent.

Stratigraphic distribution

Late Devonian (Famennian) to Permian (Lopingian).

Genus *Meristorygma* Carter, 1974

Type species

Meristorygma arctica Carter, 1974; original designation.

Diagnosis

Medium-sized shell with diverse outline; fold and sulcus moderately developed. Well-defined sulcus with two, rarely four primary ribs and median furrow; uniplicate anterior commissure usually with subquadrate tongue; fold with three distinct ribs; the central with weakly furrow. Ribs on sides are few and weak. Hinge line of short, smooth ventral interarea non-denticulated. Ventral adminicula and dorsal crural plates are absent; vascula ramose, radially arranged with a pair of strong vascular media, which correspond to the pair of costae in the sulcus. Microornament is absent.

Species included

Arctic Canada and southeastern Alaska (Carter 1974: 674): *Meristorygma arctica* Carter, 1974; Pennsylvanian.

Russia, Northern and Polar Ural (Kutorga 1844; Kalashnikov 1980): *M. panduriformis* (Kutorga, 1844); upper Pennsylvanian–Lower Permian; *M. pajkchoica* Kalashnikov, 1980; Moscovian.

South Ural (Bashkortostan) and Middle Asia (Yanishevsky 1900; Poletaev 2018): *M. gracilis* (Yanishevsky, 1900) upper Serpukhovian–lower Bashkirian; (this paper) *M. donakovae* Poletaev, 2018; uppermost Viséan–Serpukhovian, Magnitogorsk district.

Ukraine, Donets Basin (Rotai 1951; Poletaev 2018): *M. miussensis* (Rotai, 1951) upper Bashkirian; *M. postgracilis* (Rotai, 1951); Moscovian.

Remarks

The analysis of the ventral valve of the natural mould of *Meristorygma arctica* (Carter & Poletaev 1998) has shown that the species has a ramose, radially arranged vascular system with a twin of strong vascular media, in contrast to *Brachythyris ovalis* (Phillips, 1836), which has a weak, simple, pinnate vascular system. The variability of the vascular system of related taxa may mostly be the result of evolution (Lazarev & Poletaev 1982).

Meristorygma donakovae Poletaev, 2018
Fig. 4A

Meristorygma donakovae Poletaev, 2017: 74 (nom. nud.).
Meristorygma donakovae Poletaev, 2018: 88, pl. 112 fig. 3.

Spirifer sp. – Yanishevsky 1900: 150, pl. 1 fig. 7.
Spirifer aff. *gracilis* – Yanishevsky 1910: 96, pl. 12 fig. 17.
Brachythyris integricostus – Donakova 1983: pl. 2 figs 6–7.

Diagnosis

Transversely-ovate shell with one to two pairs of ribs in the sulcus, small rounded tongue and relatively broad, scanty ribs on the lateral slopes.

Material examined

Holotype (Fig. 4)

RUSSIA • South Urals, Magnitogorsk region, right bank of Ural River; Kizil Formation, upper Visean and Serpukhovian; Donakova 1983 Coll.; CNIGR Museum 12065/8.

Paratypes

RUSSIA • 2 specs; same data as for holotype; CNIGR 12065/9, 12065/10.

Additional material

RUSSIA • 20 specs; same data as for holotype; CNIGR 12065.

Description

Shell small to medium-sized; ventral valve with transversely-ovate outline, approximately equidimensional (holotype with length 26 mm, width 28 mm, thickness 18 mm), thin-walled. Hinge margin shorter than greatest width; interarea low, triangular, anacline to apsacline, smooth. Sulcus moderately developed, well delineated, with median furrow and two, rarely four primary ribs arising from parietal ribs. Anterior margin uniplicate with a small rounded tongue. Ribs on lateral slopes are few (5–7), well expressed. Dorsal valve oval in outline, almost such convex as ventral valve. Fold with three distinct ribs, of which two lateral ribs weakly bifurcate; interspaces between ribs broad. Surface of ribs smooth with concentric traces of growth. Ventral adminicula absent. Features of vascular system not established.

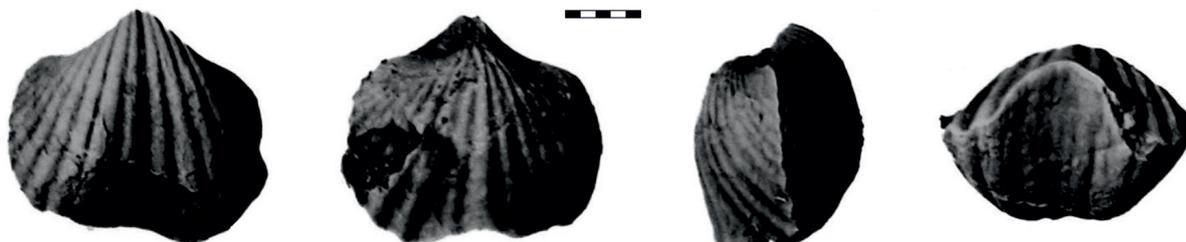


Fig. 4. *Meristorygma donakovae* Poletaev, 2018 from South Urals (Russia). Mississippian. Holotype CNIGR Museum 12065/8 (Donakova 1983 Coll.) from Magnitogorsk District; ventral, dorsal, lateral and anterior views (copy from Poletaev 2018: pl. 112 fig. 3). Scale bar units = 1 mm.

Remarks

This species differs from *Meristorygma arctica* by wider transversely oval outlines of the shell and a short, rounded tongue with a pair of weak additional ribs on its slopes, whereas *M. arctica* has a long, flat and subquadrate tongue with a pair of ribs. *Meristorygma donakovae* differs from the geographically and stratigraphically closest species *M. gracilis* by wider and less numerous ribs on the lateral slopes of both valves. The specimens examined resemble *M. postgracilis* in outline and rib pattern, but the latter has a narrower shell, more frequent bifurcation of the ribs in the sulcus, and a subquadrate tongue. *Meristorygma parva* (Rotai, 1951) differs in small size and low total number of ribs (not more than eight); *M. miussensis* and *M. panduriformis* in contrast are much larger and have very rare bifurcation of ribs in the sulcus.

Superfamily Spiriferoidea Waagen, 1883
Family Trigonotretidae Schuchert, 1893
Subfamily Neospiriferinae Waterhouse, 1968

Genus *Betaneospirifer* Gatinaud, 1949

Type species

Spirifera moosakhailensis Davidson, 1862: 28; original designation.

Diagnosis

Shells relatively thick-walled, medium to large in size; with transverse outlines; cardinal extremities from weakly rounded to mucronate or alate; ventral area triangular or trapezoidal with subparallel lower and upper edges, usually apsacline; hinge line denticulate; lateral slopes moderately or sharply folded, covered with numerous fasciculated almost uniform in width ribs, microornament regularly imbricate. Ventral valve has short deltidial plate, composed of short, rapidly diverging adminicula and dental flanges.

Remarks

The remark in the description of *Betaneospirifer* (Carter *et al.* 2006: 1790) “The validity of this genus is contingent on confirmation and completion of the diagnosis of *Neospirifer*” was related to the error in the choice of the lectotype of *Spirifer fasciger* Keyserling, 1846 as the type species of *Neospirifer* Frederiks, 1924. The revision of Keyserling’s (1846) collection published by Poletaev (1997) showed that the specimen SPGGI 129/46, chosen by Archbold & Thomas (1984) as the lectotype of *Spirifer fasciger*, most probably does not belong to the real syntypes of this species, because its image is missing among the primary good quality drawings of Keyserling’s specimens. In addition, this specimen does not show any characters of the species and has to be rejected as lectotype. Specimen SPGGI 128/46 has been proposed (Poletaev 1997) as neolectotype of *Spirifer fasciger* (not paralectotype as decided by Carter *et al.* 2006: fig. 1185, 1b–c). It is the “ragged” ventral valve, which has an ovate overline, a few weak radial plicae on the flanks, and obviously belongs to Neospiriferinae. This ventral valve was first shown in dorsal view by Poletaev (1997) and has a very unusual type of short triangular ventral area and a trace of a deltidial plate. The difference between the confirmed type species of *Neospirifer* and *Spirifera moosakhailensis*, the type species of *Betaneospirifer*, is obvious. The genus *Neospirifer* includes only the type species and some closely related species from the Productus Limestone (Late Permian) of Salt Range (Pakistan), described by Reed (1944: 678) and Waterhouse (2004: 1–265). Most of the thick-walled species of Neospiriferinae with long, trapezoidal ventral area belong to *Betaneospirifer* and other neospiriferid genera.

Distribution

Carboniferous (late Moscovian) to Early Permian of Russia and Pakistan.

Betaneospirifer stepanovi Poletaev, 2018
Fig. 5A–C

Betaneospirifer stepanovi Poletaev, 2017: 74 (nom. nud.).

Betaneospirifer stepanovi Poletaev, 2018: 84, pl. 110 figs 3–5.

Spirifer (*Spirifer*) *fasciger* var. *sterlitamakensis* – Stepanov 1948: 41, pl. 7 fig. 12.

Neospirifer sterlitamakensis – Mironova 1967: 43, pl. 4 fig. 6. — Lapina 1975: 191, pl. 85 fig. 2. —
Alexandrov & Einor 1979: 75, pl. 28 fig. 18.

Diagnosis

Small shells with transverse outline; hing line short; cardinal extremities rounded or orthogonal; three to four folds on each side of ventral valve; ribs relatively few, narrow, forming fascicles.

Material examined

Holotype (fig. 5A)

RUSSIA • Bashkortostan, Belaya River, Tabynskoie village, Voskresenka Mountain; Gzhelian; Mironova 1967 Coll.; CNIGR Museum 8491.48.

Paratypes

RUSSIA • 1 spec.; Urals, Bashkortostan, Belaya River, Tabynskoie village, Voskresenka Mountain; Gzhelian; Stepanov 1948 Coll.; VNIGRI Museum 163 • 5 specs; Bashkortostan, Zilim River, Tash-Asty village; upper Moscovian; Alexandrov and Einor 1979 Coll.; GMNTSU 79.226 (fig. 5B).

Description

Shell small to medium in size (15–30 mm in width), transversely oval in outline; hinge line slightly shorter than greatest width. Ventral valve evenly convex with a well-delineated umbo; has three to four longitudinal plicae on each side. Apex beak-shaped, curved above the hinge line. Ventral interarea triangular, apsaclin. Cardinal extremities small, obtuse or rounded. Sulcus deep, sharply expressed, pointed, forming a small tongue at the anterior margin, three ribs on each slope of sinus and one along axis. On the sides narrow simple radial ribs, collected in four bundles of three ribs each, separated by sharp intervals. The outer peculiarities of the dorsal valve (main axial fold and four folds on each side)

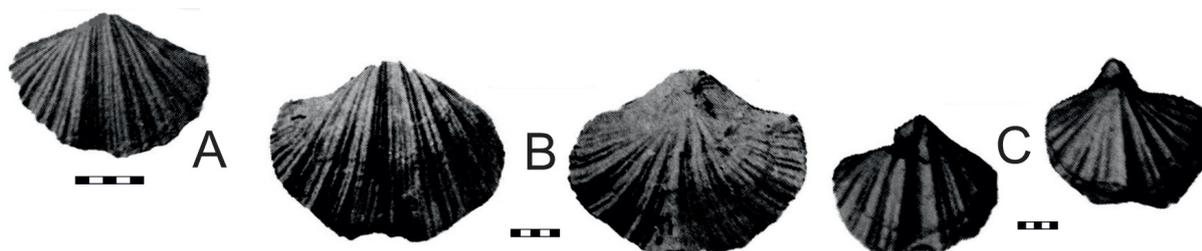


Fig. 5. *Betaneospirifer stepanovi* Poletaev, 2018 from Bashkortostan (Urals, Russia). **A.** Holotype CNIGR 8491/48 (Mironova 1967 Coll.) from Tabynskoie; ventral view (copy from Mironova 1967: pl. 4 fig. 6). **B.** Paratype GMNTSU 79/226 (Alexandrov & Einor 1979 Coll.) from Tash-Asty; ventral and dorsal views (copy from Alexandrov & Einor 1979: pl. 28 fig. 18). **C.** Paratype VNIGRI 163 (Stepanov 1948 Coll.) from Tabynskoie village; ventral and dorsal views (copy from Stepanov 1948: pl. 7 fig. 12). Scale bar units = 1 mm.

are well visible on the well safed paratype of the species. Inner structure of the shell is few investigated. Ventral valve has a pair of long thin dental plate.

Remarks

Betaneospirifer stepanovi differs from *B. sterlitamakensis* (Gerasivov, 1929) by its suboval shell, much shorter hinge margin, rounded cardinal extremities, and by the essential difference in stratigraphic distribution. The stratigraphic range of *B. stepanovi* includes the late Pennsylvanian, but the range of *B. sterlitamakensis* is Early Permian (Asselian and early Sakmarian). The specimens examined differ greatly from the other species of *Betaneospirifer* in their small size as well as geographic and stratigraphic distributions. It is likely that the studied specimens represent the oldest (Late Pennsylvanian) species of the genus *Betaneospirifer*.

Stratigraphic and geographic range

Late Moscovian and Late Pennsylvanian; South Urals, Russia.

Superfamily **Paeckelmanelloidea** Ivanova, 1972

Diagnosis (emended)

Moderately to strongly transverse shell with maximum of width at hinge line; flanks usually with simple ribs, rarely smooth; stratigraphically younger forms sometimes with bifurcations; fold and sulcus smooth or with median rib in sulcus and on fold, more rarely multicostate or with pair of opposed plica on both valves; ventral interarea usually moderately to very high, often catacline to procline or weakly apsacline; hinge line denticulate; microornament usually consisting of capillae and anteriorly free growth lamellae; dental adminicula usually present; vascular markings simple, radial; crural plates and dorsal adminicula lacking; ctenophoridium present.

Family **Oceaniidae** Poletaev, 2015

Diagnosis

Small or very small-sized, transverse, ventribiconvex shell; smooth and with two simple or compound opposed plica, dissected median parts of both valves on three parts. Fold and sulcus rarely have median opposite ribs; ventral interarea high or very high, flat, catacline or procline with strong vertical crenulations; hinge line denticulate; narrow and high delthyrium partly covered by pseudodeltidium; ornament of growth lamella only; ventral interior with low dental flanges; dorsal with ctenophoridium and short crural base.

Genera included

Johnsoniana nom. nov., possibly *Minythyra* Brunton, 1984, *Changshunella* Sun *et al.*, 2004.

Remarks

The history of closely related genera and species previously included in the family Verneuliidae (Schuchert in Schuchert & Le Vene, 1929) is long and confusing. Hall & Clarke (1893) established the genus *Verneulia*, which included two species: *Spirifer cheiropteryx* d'Archiac & de Verneuil, 1842 from the Late Devonian of Germany and *Spirifer oceani* d'Orbigny, 1850 from the Viséan of Belgium. These species, according to the authors of the genus, share common characters: the shell is equibiconvex with each valve "divided externally by two strong divergent ridges into three depressed areas, one central and two lateral" (Hall & Clarke 1893: 58). Schuchert & Le Vene (1929) placed *Verneulia* in a new subfamily and in the family Verneuliidae of the suborder Spiriferidina (Schuchert in Schuchert & Le Vene 1929).

Tiazheva (1960) established *Nuguschella* Tiazheva, 1960 from the Middle Devonian of the Urals, whose type species *Nuguschella polita* Tiazheva, 1960 has a cruralium. The genus was placed in the family Verneuliidae by Ivanova (1960: 272) and Pitrat (1965: H727), but they considered the systematic position of the family uncertain. Ivanova (1960) placed *Verneulia* separately in association with the “plicate ambocoeliids”.

Nalivkin (1979: 143) described *Verneulia oceani* from the late Tournaisian of the Urals as a member of the family Verneuliidae and confidently assigned this family to the suborder Spiriferidina. Wang *et al.* (1966) and Zhang *et al.* (1983) also examined members of the Verneuliidae, but assigned them to the family Cyrtinidae Frederiks, 1911 on the basis of internal characters. Brunton (1984: 101) selected specimen B7923 as the neotype among three Belgian topotypes from the NHM collection. He described and illustrated it for the first time as a neotype of *Verneulia oceani*. He re-established the family Verneuliidae, in which he included the new Visean genus *Minythyra*, but retained for *Verneulia* its Devonian type species *Spirifer cheiropteryx*. Brunton (1984) doubtfully placed the family Verneuliidae in the superfamily Reticulariacea Waagen, 1883.

Gourvenec (1994: 576) was the first to show pictures of the holotype of *Verneulia cheiropteryx* and some topotypes of *V. oceani*. He emphasised the presence of a strong vertical crenulation on the interarea of *V. oceani* in contrast to *V. cheiropteryx* and concluded: “Detailed study of the available material now allows a clear definition and differentiation of the species *cheiropteryx* and *oceani*.” (Gourvenec 1994: 581). He considered the superfamily Spiriferacea rather than Reticulariacea as the higher taxon for *Verneulia*. At the same time, Blodgett & Johnson (1994) described a new species *Verneulia langenstrasseni* from the Middle Devonian of Alaska and placed the family Verneuliidae, including the genera *Verneulia*, *Minythyra* and *Nuguschella*, in the superfamily Ambocoelioidea George, 1931. Carter *et al.* (1994) supported this view.

Sun *et al.* (2004) described a new genus *Changshunella* whose type species *C. yangi* Sun *et al.*, 2004 had a clearly denticulated hinge line and lacked dental plates. In order to place this genus in the family Verneuliidae, the authors extended the family diagnosis by combining the characters of *Changshunella yangi* and “*Verneulia*” *oceani*, which are absent in the Devonian type species of *Verneulia*. Sun *et al.* (2004) also failed to determine the superfamilial assignment of the family Verneuliidae and suggested that a new superfamily should be distinguished. Johnson (Carter *et al.* 2006: 1746) strongly disagreed with the extension of the family diagnosis and wrote: “The Visean species *V. oceani* (d’Orbigny) from Belgium is not congeneric with the type species, bearing strong dental flanges, a finely striated cardinal process, lacking crural plates, in having a clearly denticulate ventral interarea with wide perideltidial areas, and possibly a weakly capillate microornament. It belongs in the Spiriferoidea.” He concluded that these species should not only be placed in different genera, but also in other superfamilies. However, Johnson (Carter *et al.* 2006: 1746) did not attempt to identify or describe the new genus he had actually discovered. Poletaev (2015: 17) established the new genus *Oceania* with *Spirifer oceani* d’Orbigny, 1850 as the type species. At the same time, he proposed to establish the new family Oceaniidae with the type genus *Oceania* and, together with *Minythyra*, to place this family in the superfamily Paeckelmanelloidea. However, the genus name *Oceania* was already used by Péron & Lesueur (1810) and the family Oceaniidae was established by Eschscheltz (1829). Both the genus and family names proposed by the author in 2015 are thus preoccupied (junior homonymy). Consequently, the genus with *Spirifer oceani* as type species is here renamed as *Johnsoniana* nom. nov. and remains type genus of the family Oceaniidae.

Mottequin & Poty (2022) revised old European collections of brachiopods from the historical type locality of Visé, outlining the more correct geographic and stratigraphic positions of this fauna (including the age of “*V.*” *oceani*) as latest Warnantian (Late Asbian) and published an image of the topotype

of “*V.*” *oceani* (Mottequin & Poty 2022: fig. 11j). Wang *et al.* (2023) published the results of their research on the Spiriferidae King, 1946 fauna of the Frasnian (Late Devonian) Refrath Formation in the Bergisches Land of Germany, another historical type area for Western European Devonian fauna. They published the first transverse serial sections of two topotypes of *Verneulia cheiropteryx*, showing short dental plates and illustrating the ctenophoridium in the ventral valve. They also showed the absence of denticles on the hinge line of the ventral interarea, the crural base and short crus in the dorsal valve, rounded cardinal extremities of mature *Verneulia cheiropteryx* and flank plications in young specimens. These are absent in the type species of *Johnsoniana oceani*.

Wang *et al.* (2023) proposed an emended diagnosis of the genus *Verneulia* and included short dental plates in the ventral valve of *V. cheiropteryx*, but not the denticulated hinge line of *V. oceani*. It remains unclear why Wang *et al.* (2023) did not exclude *Spirifer oceani* from *Verneulia*, as its internal structure does not correspond to the revised diagnosis of the genus. They excluded *Verneulia langenstrasseni* from *Verneulia* because its internal structure does not correspond to the emended diagnosis of the genus. In my opinion, this species, together with *Nugushella* Tiazheva, 1960, should have been included under the new generic name in the group of so-called “plicated amboceleids” listed by Ivanova (1960), only without *Verneulia*. The main difference between the internal structures of the Late Devonian (middle Frasnian) *Verneulia cheiropteryx* (according to Wang *et al.* 2023) and the Visean “*Verneulia*” *oceani* (according to Gourvenec 1994) confirms the necessity to separate the genus *Johnsoniana* nom. nov. I agree with Wang *et al.* (2023) that *Verneulia* cannot be placed in the Ambocoelioidea. The type species of *Verneulia* has been well distinguished and described by Gourvenec (1994) and Wang *et al.* (2023). Obviously, this genus has weakly plicate flanks, well-developed dental plates and lack of median septum in the ventral valve, non-denticulated hinge line, knob-like ctenophoridium and pair of short plate-like crural bases in the dorsal valve as well as microornament (after Gourvenec 1994: pl. 1 fig. 6) with very fine, regularly spaced growth lines and randomly arranged tiny pits. All these data allow, in my opinion, to place *Verneulia* in the family Elythyridae Gourvenec, 1994 of the superfamily Martinioidae.

The next question is what higher taxa could include the genus *Johnsoniana* nom. nov. and some closely related genera?

Moderate to strong transverse contours of valves with high triangular area, acute or mucronate cardinal extremities and denticulate hinge line preclude the assignment of *Johnsoniana* and *Changshunella* to the superfamily Martinioidae. The absence of regular ribs on the flanks, smooth or with high median ridge sulcus and fold bordered by specific opposite plica do not allow to assign both genera to Spiriferoidae, contrary to the opinion of Gourvenec (1994) and Johnson (Carter *et al.* 2006: 1746). On the other hand, most of the main characters of *Johnsoniana* and *Changshunella* in general are very close to or agree with the diagnosis of the superfamily Paeckelmanelloidea (Carter *et al.* 2006: 1812). Sun *et al.* (2004) assumed the same for *Changshunella yangi*, but the presence of unusual opposed ribs on the ventral and dorsal valves of this species led them to reject the assignment of *Changshunella* to Paeckelmanelloidea. The opposite type of plica on both valves of *Changshunella* links this genus to *Verneulia*. On this basis, Sun *et al.* (2004) suggest that the above genera could form their own superfamily, namely Verneulioidae. However, they prefer to include *Changshunella* in their revised family Verneuliidae and maintain the verneuliids as a separate family in the suborder Spiriferidina.

The pentagonal contours and the presence of extraordinary plica-bordered depressions in the central part of both valves of the biconvex shells of “*Oceania*” and *Minythyra* previously seemed to me sufficient to distinguish a new family Oceaniidae (see Poletaev 2015) and to include it very conventionally in the superfamily Paeckelmanelloidea. In fact, the assignment of this family to Paeckelmanelloidea was wrong, because the characters of Oceaniidae included smooth shells, which were not foreseen in the diagnosis of Paeckelmanelloidea by Ivanova (1972). On the other hand, I agree with Sun *et al.*

(2004) and avoid distinguishing a new superfamily. It will be more reasonable to revise the diagnosis of Paeckelmanelloidea to include “rare smooth forms with opposed ribs or plica on both valves”, which will make a valid inclusion of the family Oceaniidae into this superfamily. The family Oceaniidae includes the genera *Jonsoniana*, *Changshunella* and *Minythyra*, each of which has characters of the emended Paeckelmanelloidea. The family excludes *Verneuilia* because it has tooth plates and no denticulate hinge line. The smooth flanks and the opposite ribs or plica on both valves distinguish Oceaniidae from Strophopleuridae and Paeckelmanellidae, because the latter also have a ventral median septum, which is absent in Oceaniidae. Furthermore, the Frasnian (Late Devonian) *Verneuilia* is not less than thirty million years older than the late Tournaisian to Viséan *Johnsoniana* and *Changshunella* and could perhaps be a distant ancestor of the latter genera.

Genus *Johnsoniana* nom. nov.

Type species

Spirifer oceani d’Orbigny, 1849; original designation (by monotypy).

Diagnosis

Shells small to medium-sized, pentagonal or trapezoidal outline with equibiconvex profiles; ventral interarea triangular, medium high, concave only under apex, apsacline to catacline with denticulate hinge line equal to the width of shell; cardinal extremities acute but not mucronate; delthyrium narrowly elongate, triangular, high, partly covered by pseudodeltidium; shallow ventral sulcus and median depression on fold clearly limited by coarse rounded opposite plica, divided each valve into three depressed areas; flank plications absent; anterior commissure subrectilinear. Surface smooth or with concentric wrinkles and obscure irregular radial striae (10–12 per mm). In ventral valve strong deltidial ridges, boarding delthyrium, septum and dental plates absent; in dorsal valve short base of crural plate and flat ctenophoridium. Shell substance impunctate.

Stratigraphic and geographic range

Western Europe (Belgium), Russia, Urals (Bashkortostan); Mississippian, from the Late Tournaisian to Viséan (late Warnantian or late Asbian).

Included species

Type species only.

Johnsoniana oceani (d’Orbigny, 1850)

Fig. 6B–E

Spirifer oceani d’Orbigny, 1850: 149, pl. 38 fig. 29.

Spirifer cheiropteryx – de Koninck 1843: 245, pl. 15 fig. 9. — Quenstedt 1871: 510, pl 53 figs 71–73.

Spirifer oceani – de Koninck 1887: 132, pl. 28 figs 11–16.

Verneuilia oceani – Hall & Clarke 1893: 1–317. — Ivanova 1960, pl. 58 figs 14–15. — Nalivkin 1979:

143, pl. 62 figs 19–24. — Brunton 1984: 101, text-fig. 160. — Gourvenec 1994: 578, pl. 1 figs 7–31.

— Mottequin & Poty 2022: text-fig. 11j.

Oceania oceani – Poletaev 2015: 17–18; 2018: 95, pl. 117 figs 1–7.

Diagnosis

As for genus.

Material examined

Neotype (Fig 6B)

GREAT BRITAIN • Viséan, upper Warnantian (late Asbian); specimen from Davidson Coll., selected by Brunton (1984: 101, fig. 160); NHM B7923.

Paratypes

FRANCE • 2 specs; Viséan; Office National des Collections Paléontologiques (ONCP), University C. Bernard, Lyon; ONCP D306a, ONCP D306e (Fig. 6D–E).

RUSSIA • 17 specs; Southern Urals (Bashkortostan), Ussuily River; upper Tournaisian, Kizelovskian Horizon; Nalivkin 1979 Coll.; CNIGR Museum 3085 (Fig. 6C).

Description

The shell is small with trapezoidal outline; the cardinal extremities are angular but not mucronate. The maximum width coincides with the hinge line. The convexity of the shell is regular but the ventral valve is slightly more convex than the dorsal. The ventral interarea is high, triangular, regularly curved, usually apsacline to catacline; beak is small and curved. The delthyrium is narrow and much higher than the width, the upper half is covered by a convex pseudodeltidium. The surface of the interarea bears strong vertical crenulations that are never branching. These crenulations produce a fine denticulation on the hinge, corresponding to equivalent cupules on the dorsal valve.

The dorsal interarea is very narrow, anacline. The angle between ventral and dorsal interareas is 90°–120°. The ventral sulcus is shallow, widely rounded, tends to become deeper and wider towards the anterior margin. The dorsal sulcus corresponds to the ventral one. The sulci are bordered by low angular plications, that never become carina. The sulci widen regularly during the early stages of growth but bounding plications tend to become parallel or almost convergent. The anterior edge of the plications does not significantly protrude beyond the general anterior outline. The commissure is usually bent towards the ventral valve before abruptly turning towards the dorsal one near the sulci. In this case a more or less developed tongue is present. The flanks are smooth. The microornament consists of faint, regularly spaced growth lines coarser than in *Verneulia cheiropteryx*. In the ventral valve are very long divergent dental flanges, bordering the inner side of the delthyrium (Gourvenec 1994: 580, fig. 2). The teeth are small. In the apical part of the ventral valve sometimes is a short, low, flat median ridge. In the dorsal valve, the very faint striated ctenophoridium is located on an elevated cardinal platform anteriorly and extended by a narrower median shelf at about ¼ of the length of the shell. The ctenophoridium is bounded by weakly developed very short and narrow sockets. Under the sockets are located the narrow, slightly oblique crural bases, supported by small “columnal” thickenings of the shell united the cardinal platform with crural bases and joining them at the floor of the valve. These very poorly developed thickenings do not properly constitute the crural plates or only rudimentary ones. The direction of the spires is approximately parallel to the plications (after Gourvenec 1994: 578).

Remarks

The external appearance of *Johnsoniana oceani* is similar to that of *Verneulia cheiropteryx* (Fig. 6A), but the former can be distinguished by its smaller, less transverse shell outline, lack of mucronation of the cardinal extremities, denticulate hinge line, much narrower sulcus bordered by low angled but never carinate plications. The plications bordering the sulci of *J. oceani* tend to become parallel during adult growth, whereas they are regularly divergent in *V. cheiropteryx*. *Johnsoniana oceani* is distinguished from *V. cheiropteryx* by the absence of short dental plates in the ventral valve. *Johnsoniana oceani* is distinguished from *Changshunella yangi* by the much larger size, lack of prominent median plications in sulcus and opposite rib on dorsal valve, lack of sticks on anterior ends of ribs, bordered sulci. The

type species of *Verneulia* and *Johnsoniana* also differ in the micro-ornamentation of the shell surface: the presence of fine randomly arranged pits on *V. cheiropteryx* and obscure radial striae on *J. oceani*.

Distribution

Calcaire de Visé (Visean) in Belgium; late Tournaisian of the South Urals (Bashkortostan), Russia.

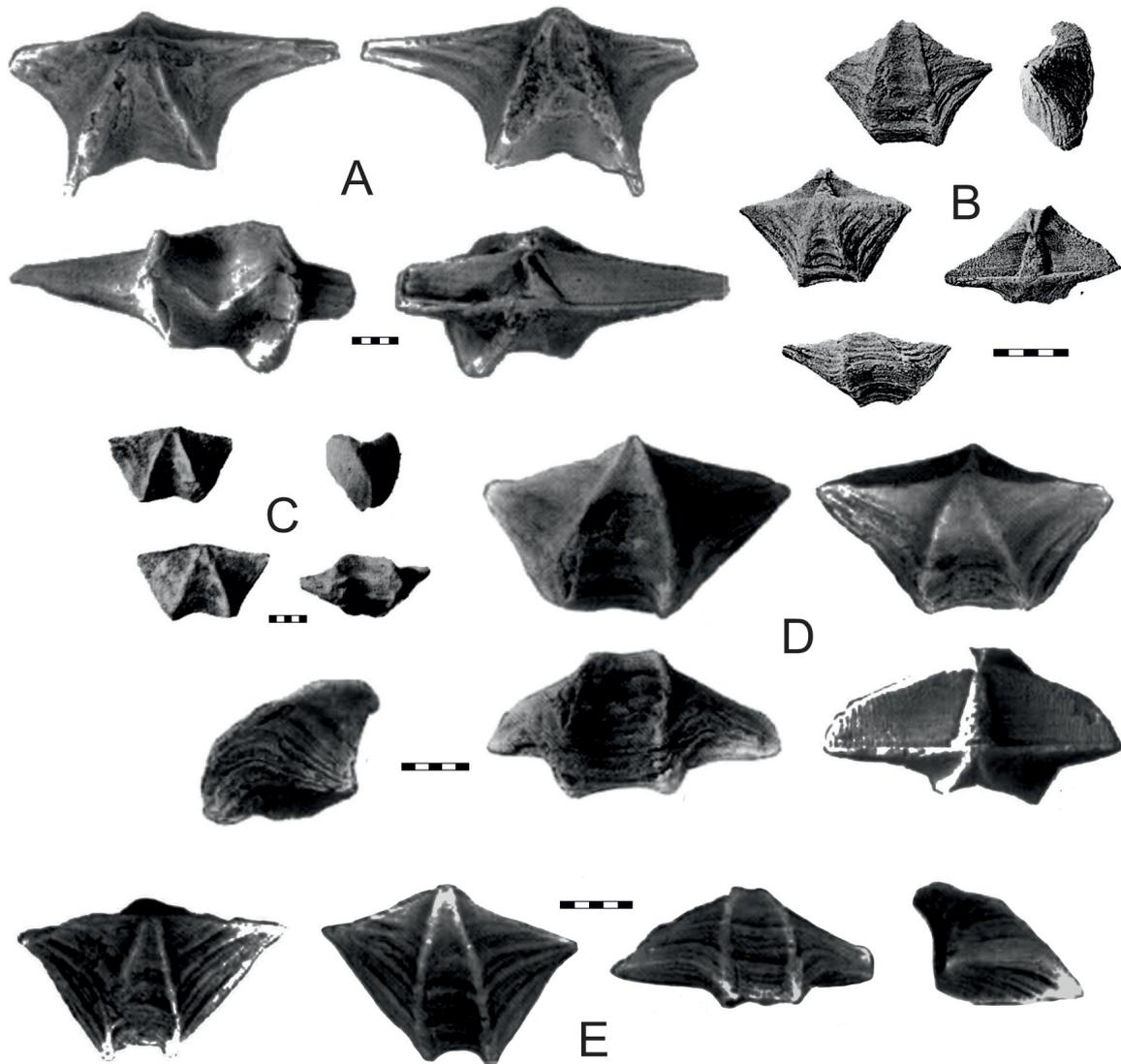


Fig. 6. **A.** *Verneulia cheiropteryx* (d'Archiac & de Verneuil, 1842). Lectotype ONCP D568 (Gourvenec 1994 Coll.) from Refrath (Bergisches Land, Germany). Devonian, Frasnian; dorsal, ventral, anterior and posterior views (copy from Gourvenec 1994: pl. 1 figs 1–5). **B–E.** *Johnsoniana oceani* (d'Orbigny, 1850). **B.** Neotype NHM B7923 (Brunton 1984 Coll.) from Visé (Belgium). Visean; ventral, lateral, dorsal, posterior and anterior views (copy from Brunton 1984: text-fig. 160a–e). **C.** Paratype CNIGR Museum 3085 (Nalivkin 1979 Coll.) from Bashkortostan (Urals, Russia). Upper Tournaisian; ventral, lateral, dorsal and anterior views (copy from Nalivkin 1979: pl. 62 fig. 21). **D.** Paratype ONCP Museum D306a (Gourvenec 1994 Coll.) from Visé (Belgium). Visean; ventral, dorsal, lateral, anterior and posterior views (copy from Gourvenec 1994: pl. 1 figs 11–15). **E.** Paratype ONCP Museum D306e (Gourvenec 1994 Coll.) from same locality; dorsal, ventral, anterior and lateral views (copy from Gourvenec 1994: pl. 1 figs 16–19). Scale bar units = 1 mm.

Discussion

The re-description and re-study of previously briefly described new taxa, published in little-known regional publications, now allows us to complete the characters and justify the validity of *Meristorygma donakovae*, and to describe the new species *Tiramnia davidi* sp. nov. The redescription of *Betaneospirifer stepanovi* is proposed with the arguments of independence of the genera *Neospirifer* and *Betaneospirifer*, based on the very specific characters of the neolectotype of the former (Poletaev 1997) and its clear difference from the holotype of the latter. These data confirmed the validity of *Betaneospirifer*.

The study of the history and interrelationship of some genera previously included in the family Verneuliidae confirms Johnson's (Carter *et al.* 2006: 1746) conclusion about the erroneous unification of species with very different internal structures into one genus *Verneulia*, especially because it is the type genus of the family Verneuliidae. Based on this observation, Poletaev (2015) established a separate new genus *Oceania*, as well as a new family Oceaniidae. The name *Oceania* was preoccupied and is here renamed *Johnsoniana* with *Spirifer oceani* as the type species. The family Oceaniidae is also preoccupied and a special request should be addressed to the ICZN (1999) to further process to its name replacement. It includes, in addition to the type genus *Johnsoniana*, the genera *Changshunella* and *Minythyra*. In order to assign the family Oceaniidae to the superfamily Paeckelmanelloidea, an emendation of the diagnosis of the superfamily has been proposed to include spiriferids with smooth valves and a pair of opposite ribs or plica on both valves. The revised genus *Verneulia* (s. str.) may contain only the type species *Spirifer cheiropteryx* and belongs in my opinion to the family Elythyridae of the superfamily Martinioidae. It is not excluded that Frasnian *Verneulia* could be an ancestor of the Tournaisian-Visean genus *Johnsoniana*. The systematic position of *Nugushella* and "*Verneulia*" *langenstrasseni* is still unclear.

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