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The present classification of spiriferids should be considered as stage, summarizing our knowledge and identifying critical questions, the investigation of which is essential for further advancement of knowledge about spiriferid systematics a nd their paths of evolution.

E.A. Ivanova, 1959

On the History of Systematics and the Evolution of the Brachiopod Order Spiriferida from the Carboniferous of Eastern Europe

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Abstract—This work presents a revision of the history of the systematics of the order Spiriferida. Main directions of evolution of the major groups of Carboniferous spiriferids are identified and the corresponding changes in the composition of the superfamilies Martinioidea Waagen, 1883 and Spiriferoidea King, 1846 are recognized. The family Brachythyrididae Fredericks, 1924 including the subfamilies Brachythyridinae Fredericks, 1924, and Skelidorygminae Carter, 1994, was assigned to the superfamily Martinioidea. The family Angiospiriferidae Legrand-Blain, 1985, with the subfamilies Angiospiriferinae Legrand-Blain, 1985, Brachythyrininae Waterhouse, 2004, and Choristitinae Waterhouse, 1968, was recognized within the superfamily Spiriferoidea. The superfamily Neospiriferoidea Waterhouse, 1968 was established with the families Imbrexiidae Carter, 1992, Neospiriferidae Waterhouse, 1968, Trigonotretidae Schuchert, 1893, and Spiriferellidae Waterhouse, 1968

Keywords: Brachiopoda, order Spiriferida, evolution, system, Carboniferous, Eastern Europe

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INTRODUCTION

The analysis of a data set on morphology and shell interior of the Carboniferous spiriferids of Eastern Europe obtained as a result of the revision of all presently known names of this brachiopod group (Poletaev, 2018) has led the author to the conclusion that the hierarchy of the characters used in *Treatise* (Carter et al., 2006) to distinguish some taxa above genus level in the systematics of the Order Spiriferida needs refinement. In particular, to determine the generic composition of the family Choristitidae, priority was given to characters of the external shell morphology, i.e., serration of the area, type of costation, microornamentation, and in the shell interior, to the absence of the delthyrial plate and presence of vascular system. At the same time, little consideration was given to a role of specific adminicula in *Choristites* Fischer de Waldheim, 1825, which is the type genus of the family designated by its author (Waterhouse, 1968). As a result, the subfamily Choristitinae, as it was accepted in *Treatise*, included many genera, the internal structure and external morphology of which were remotely similar to those of the type genus. There are many similar cases. In the author's opinion, this is because determination of the hierarchy of the characters of higher-rank taxa almost disregarded the role of phylogeny and evolutionary history of particular spiriferid lineages, i.e., the methods employed by Russian authors for building the system, which is surely one of the major challenges of paleontology.

Therefore, the aim of the present study is to analyze major trends in the history of the development of the spiriferid systematics and to identify the pathways of the evolution of external morphology and shell interior of these benthic organisms due to changes in ecology and community structure of their living environment. This concerns spiriferids overall, but primarily the systematics of the spiriferids that occurred within the boundaries of the East European biogeographic province throughout the Carboniferous. The end result of this work is the author's proposed refinement of the criteria for identifying taxa within the order Spiriferida, which is reflected in changes in the ranks of these taxa and in the emendation of a substantial part of contemporary spiriferid systematics.

The foundations of the spiriferid systematics were laid by Waagen (1883), who placed brachiopods with a spiral brachidium into the suborder Spiriferacea, including the families Atripidae, Nucleospiridae, Athyridae, and Spiriferidae. In the family Spiriferidae King, 1846, Waagen distinguished four subfamilies:

Suessiinae Waagen 1883 (genera *Suessia* Eudes-Deslongchamps, 1855, *Cyrtina* Davidson, 1858, *Spiriferina* d'Orbigny, 1847);

Delthyrinae Waagen 1883 (genera *Syringothyris* Winchell, 1863, *Cyrtia* Dalman, 1828, *Spirifer* Sowerby, 1816);

Martiniinae Waagen, 1883 (genera *Martinia* McCoy, 1844, *Martiniopsis* Waagen, 1883); and Reticulariinae Waagen, 1883 (genera *Reticularia* M'Coy, 1844, *Ambocoelia* Hall, 1860).

Exactly this system was used by Tschernyschew (1902) to describe brachiopods of the Upper Carboniferous (now largely of the Lower Permian) of the Urals and Timan. Subsequently, a major step forward for the systematics of the Carboniferous spiriferids of Russia was made by Fredericks (1919, 1924). Importantly, he developed the work of Tschernyschew on the role of the apical apparatus in spiriferid systematics, and elaborated it further into his own systematics, in which he used a combination of seven types of external morphological characters and ten types of shell interior characters. As a result Fredericks identified at least 50 possible formal combinations for the Carboniferous and Permian spiriferids, some of which corresponded to the previously known genera, but more than half he identified as new genera. He grouped genera of the family Spiriferidae into six subgroups, to which another three and one not yet clearly defined were added later (Fredericks, 1926). Overall, the spiriferid system proposed by Fredericks in 1926 was as follows:

Family **Spiriferidae King, 1846**

Subfamily **Martiniinae Waagen, 1883**

Type genus *Martinia* McCoy, 1844

Genera: *Martinia* McCoy, 1844 (type species *Spirifer glaber*, Sowerby, 1820),

Elina Fredericks, 1919 (type species *Spirifer rectangulus* Kutorga, 1844),

Ambocoelia Hall, 1860 (type species *Orthis umbonata* Conrad, 1842),

Moumina Fredericks, 1919 (type species *Martinia incerta* Tschernyschew, 1902),

Paulonia Nalivkin, 1925 (type species *Spirifer ranovensis* Peetz, 1893),

Ella Fredericks, 1918 (type species *Martinia simensis* Tschernyschew, 1902),

Squamularia Gemmellaro, 1899 (type species *Spirifer rostrata* Kutorga, 1844).

Subfamily **Brachythyrinae Fredericks, 1919**

Type genus not indicated.

Genera: *Brachythyris* McCoy, 1844 (type species *Spirifera ovalis* Phillips, 1836),

Anelasma Ivanov, 1925 (type species *Spirifer strangwaisi* Verneuil, 1845),

Eliva Fredericks, 1919 (type species *Spirifer lyra* Kutorga, 1844).

Subfamily **Munellinae Fredericks, 1919**

Type genus *Munella* Fredericks, 1919

Genera: *Munella* Fredericks, 1919 (type species *Spirifer nikitini* Tschernyschew, 1902),

Martinuopsis Waagen, 1883 (type species *Martinuopsis inflatum* Waagen, 1883),

Eoreticularia Nalivkin, 1918 (type species *Delthyris indifferens* Barrande, 1848),

Guerichella Packelmann, 1913 (type species *Spirifer* (*Guerichella*) *angustisellatus* Paeckelmann, 1913),

Elivella Fredericks, 1919 (type species *Martinuopsis baschkirica* Tschernyschew, 1902),

Elivina Fredericks, 1919 (type species *Spirifer tibetanus* Diener, 1897),

Reticulariopsis Fredericks, 1916 (type species *Spirifera elliptica* Phillips, 1836).

Subfamily **Elythinae Fredericks, 1919**

Type genus *Spirifer* Sowerby, 1816

Genera: *Eospirifer* Schuchert, 1908 (type species *Spirifer radiatus* Sowerby, 1816),

Spirifer Sowerby, 1816 (type species *Conchiliolites (Anomia) striatus* Martin, 1793),

Choristites Fischer von Waldheim, 1825 (type species *Choristites mosquensis* Fischer von Waldheim, 1825),

Schuchertia Fredericks, 1926 (type species *Delthyris niagarensis* Conrad, 1842),

Neospirifer Fredericks, 1919 (type species *Spirifer fasciger* Keyserling, 1846),

Spirelytha Fredericks, 1919 (type species *Spirifer schei* Tschernyschew, 1902),

Elytha Fredericks, 1918 (type species *Delthyris fimbriatus* Conrad, 1842).

Subfamily **Delthyrinae Fredericks, 1919** (non Waagen, 1883 nec Tschernyschew)

Type genus *Delthyris* Dalman, 1828

Genera: *Munia* Fredericks, 1918 (type species *Munia muni* Fredericks, 1918)

Spiriferellina Fredericks, 1919 (type species *Terebratulites cristatus* Schlotheim, 1816),

Spiriferinaella Fredericks, 1926 (type species *Spiriferina artiensis* Stuckenberg, 1898), *Lytha* Fredericks, 1919 (type species *Spiriferella tschernyschewiana* Fredericks, 1916),

Reticularia McCoy, 1844 (type species *Terebratula? imbricata* Sowerby, 1822),

Reticulariina Fredericks, 1916 (type species *Spiriferina spinosa* Norwood et Pratten, 1855),

Delthyris Dalman, 1828 (type species *Delthyris elevata* Dalman, 1828),

Maia Fredericks, 1919 (type species *Spiriferina ornata* Waagen, 1883),

Spiriferella Tschernyschew, 1902 (type species *Spirifer saranae* Verneuil, 1845).

Subfamily **Cyrtiinae Fredericks, 1919**

Type genus *Cyrtia* Dalman, 1828

Genera: *Cyrtia* Dalman, 1828 (type species *Cyrtia exporrecta* Wahlenberg, 1821),

Cyrtospirifer Nalivkin, 1918 (type species *Spirifer verneuili* Murchison, 1840),

Cyrtella Fredericks, 1919 (type species *Cyrtia kulikiana* Fredericks, 1924),

Spinocyrtia Fredericks, 1916 (type species *Delthyris granulosus* Conrad, 1842).

Subfamily **Syringothyrinae Fredericks, 1926**

Type genus not indicated, may be, *Syringothyris* Winchel, 1863

Genera: *Cyrtinaella* Fredericks, 1916 (type species *Cyrtina biplicata* Hall, 1857),

Cyrtina Davidson, 1858 (type species *Calceola heteroclyta* Defrance, 1828),

Syringothyris Winchel, 1863 (type species *Syringothyris typa* Winchel, 1863),

Davidsonella Fredericks, 1916 (type species *Spirifera septosa* Phillips, 1836),

Spinocyrtina Fredericks, 1916 (type species *Cyrtina hamiltonensis* Hall, 1857),

Squamulariina Fredericks, 1916 (type species *Cyrtina parva* Gürich, 1896),

Cyrtinaellina Fredericks, 1916 (type species *Cyrtina acutirostris* Schumard, 1855).

Subfamily **Spiriferininae Fredericks, 1926**

Type genus apparently *Spiriferina* d`Orbigny, 1847

Genera: *Spiriferina* d`Orbigny, 1847 (type species *Terebratulites rostratus* Schlotheim, 1816),

Mentzelia Quenstedt, 1827 (type species *Spirifer medianus* Quenstedt, 1868).

In 1919, Fredericks proposed the subfamily Brachythyrinae, composed of the genera *Brachythyris* and *Eliva* and then added to it the genus *Anelasma* with the type species *S. strangwaisi* in 1924 (see Fredericks, 1919, 1924). As *Anelasma* was found to have been preoccupied as the name of genus, in 1929 Fredericks replaced it with *Brachythyrina* Fredericks, 1924 without, however, having indicated a type species for the subfamily Brachythyrinae. In fact, this subfamily remained a nomen dubium (Fredericks, 1929).

Enormous contribution to the improvement of the spiriferid system was made after World War II by Ivanova (1959). In the 35 years since the establishment of the spiriferid system by Fredericks, the number of the known genera increased more than fourfold, while the system proposed by Ivanova's predecessors and contemporaries had itself become more complex. Ivanova developed and published her own spiriferid system. Three superfamilies, namely, Spiriferinacea, Spiriferacea, and Delthyriacea were recognized in the new system based on distinctions in the types of the apical apparatus and pathways of the phylogenetic development of representatives of the order Spiriferida. Overall, the system, embracing approximately 180 listed genera, was rather clearly represented at the level of families and subfamilies in the figure (Ivanova, 1959, text-fig. 9) reproduced below (Fig. 1).

It should be emphasized that Ivanova was the first to recognize two major trends in the evolution of Late Paleozoic spiriferids, on the scheme and in the description of the superfamily Spiriferacea. The first is the emergence in some taxa of imprints of the vascular system in the Carboniferous, due to which the ovarian markings scattered in the majority of spiriferids across the entire interior surface of the ventral valve began concentrating around the muscle area; the second is the development in a number of taxa of transverse grooves and a serrated hinge line on the ventral area.

In the 1959 scheme (Ivanova, 1959), these differences are taken into account in recognizing the two subfamilies Spiriferinae and Brachythyrinae in the family Spiriferidae. The subfamily Brachythyrinae included the genera *Choristites*, *Choristitella* A. Ivanov et E. Ivanova, 1937, *Purdonella* Reed, 1944, *Brachythyris*, *Ella*, and *Brachythyrina* and provisionally the genera *Odontospirifer* Dunbar, 1955, *Sergospirifer* Ivanova, 1952, and *Eochoristites* Chu, 1933. The type genus of the subfamily, however, continued to be undefined, which means that the subfamily Brachythyrinae in fact remained a nomen dubium.

After having analyzed the systems of his predecessors, Waterhouse (1968) presented his own views on the spiriferid system. He distinguished a new subfamily in the family Spiriferidae, Neospiriferinae, with the type genus *Neospirifer* Fredericks, 1924, and the subfamilies Spiriferillinae with the type genus *Spiriferella* Tschernyschew, 1902 and Choristitinae with the type genus *Choristites* in the family Brachythyrididae.

The next big step forward in the systematization of the order Spiriferida, in which the number of genera already amounted to at least 300, was a system proposed by Ivanova (1972).

While proceeding with the development of phylogenetic principle of building the system, she used types of microornamentation in addition to internal structure of the shells to justify the establishment of the

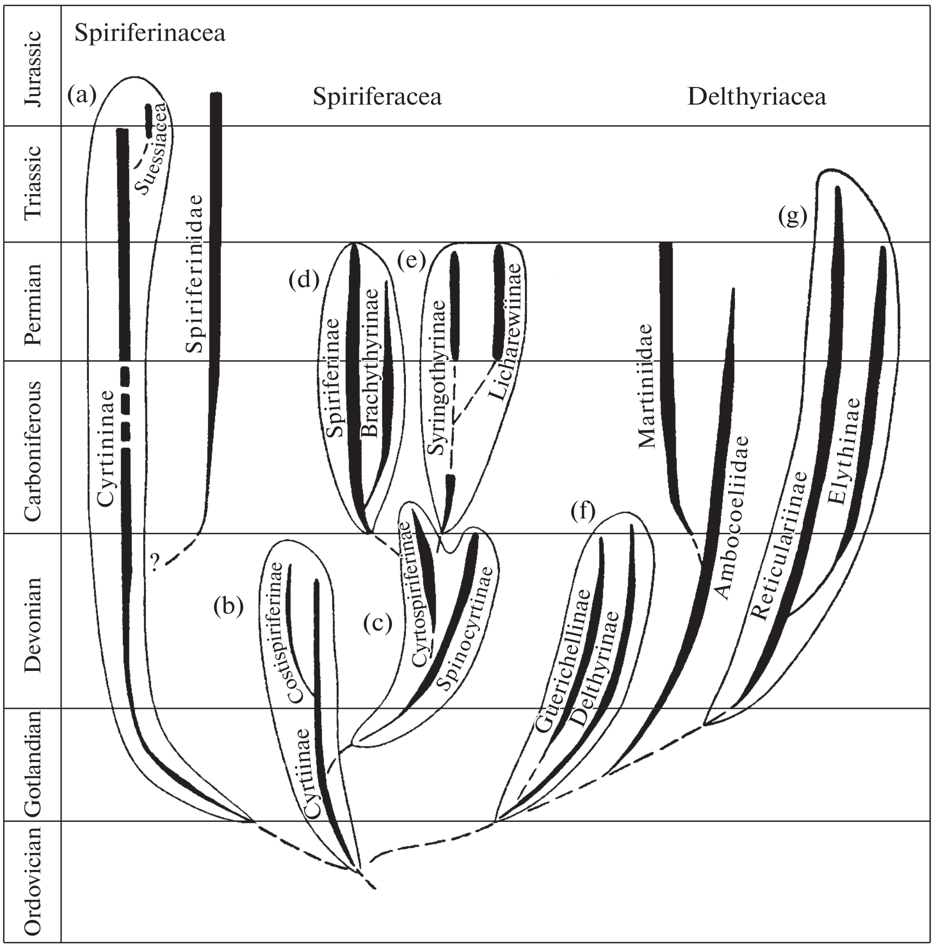

Fig. 1. A scheme of phylogenetic development of representatives of the order Spiriferida (after Ivanova, 1959). Thin lines delineate families: (a) Cyrtinidae; (b) Cyrtiidae; (c) Cyrtospiriferidae; (d) Spiriferidae; (e) Syringothyridae; (f) Delthyridae; and (j) Reticulariidae. Subfamily Verneuiliinae is not included in the scheme.

higher taxa. The rank of the three former superfamilies was raised to suborder; the ranks of their subordinate taxa were changed accordingly. In the suborder Spiriferidina of the Upper Paleozoic spiriferids, Ivanova distinguished the superfamilies Spiriferacea (including the families Spiriferidae, Brachythyrididae, and Choristitidae), and Syringothyridacea (families Syringothyrididae and Paeckelmanellidae). The superfamily Spiriferidinacea composed of the families Spiriferinidae and Spiriferellinidae was established in the same suborder. The superfamilies Martiniacea with the families Ambocoeliidae and Martiniidae were placed in the suborder Delthyrididina, as well as Reticulariacea composed of the families Reticulariidae and Elythidae (Fig. 2).

The work by Ivanova (1972) was the first to designate the genus *Brachythyris* as the type genus of the family Brachythyrididae. Her brief characteristic of the now available family Brachythyrididae emphasizes two trends clearly identifiable in its phylogenesis. One of them is the step-by-step evolution of the vessel (vascular) system, while another is associated with reduction of a number of the internal structures until they completely disappear. According to Ivanova (1972), evolution of representatives of the superfamily Martiniacea, which had emerged at the beginning of the Devonian, is marked by pedogenesis particularly evident in the Ambocoeliidae. The family Martiniidae is characterized by the primitive (pinnate) vascular system, foveolate punctures, smooth area, and neotenic (primarily brachithyridic) shell shape. Smooth shapes with reduced microsculpture largely belong to subfamily Martiniinae; while laterally plicated forms, with acicular microsculpture, were earlier isolated into the independent subfamily Ingelarellinae (see Campbell, 1959).

Carter (1974) published an article reporting two new subfamilies Strophopleurinae (with the type genus *Strophopleura* Stainbrook, 1947) and Prospirinae (with the type genus *Prospira* Maxwell, 1954) in the family Spiriferidae King. He conditionally assigned the genus *Brachythyrina* to Prospirinae. Additionally, that paper described several new genera, including the genera *Meristorygma* Carter, 1974 and

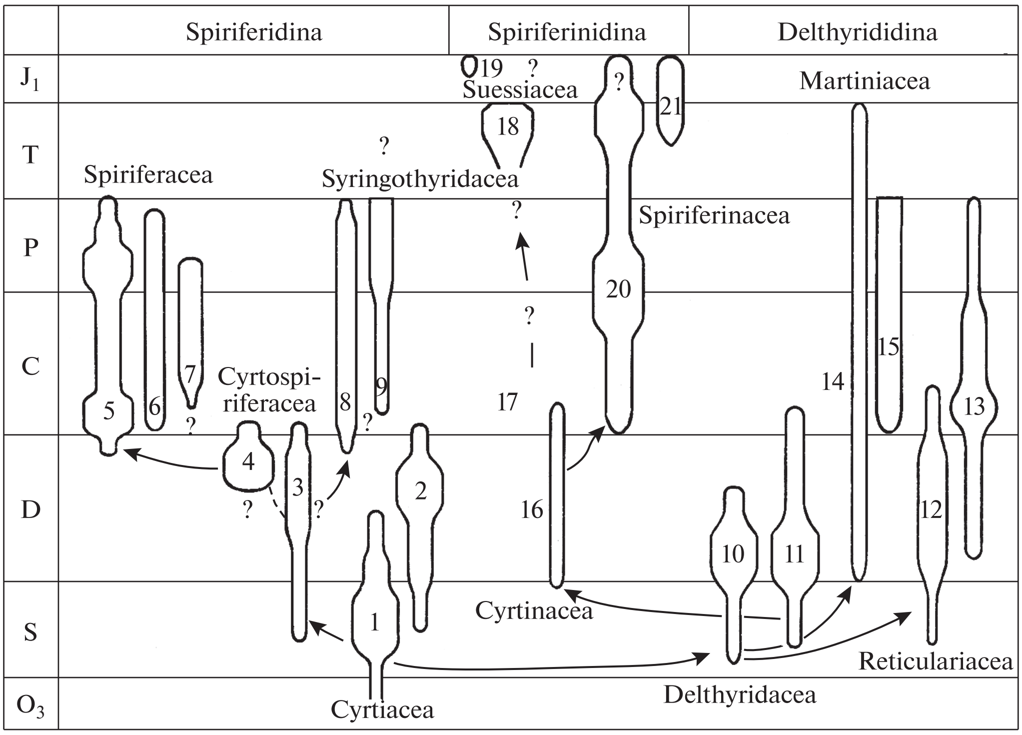

Fig. 2. Scheme of phylogenetic development of representatives of the Spiriferida (after Ivanova, 1972). Families: (1) Cyrtiidae, (2) Costispiriferidae, (3) Spinocyrtiidae, (4) Cyrtospiriferidae, (5) Spiriferidae, (6) Brachythyrididae, (7) Choristitidae, (8) Syringothyrididae, (9) Paeckelmanellidae, (10) Guerichellidae, (11) Delthyrididae, (12) Reticulariidae, (13) Elythidae, (14) Ambocoeliidae, (15) Martiniidae, (16) Cyrtinidae, (17) Davidsoninidae, (18) Laballidae, (19) Suessiidae, (20) Spiriferellinidae, and (21) Spiriferinidae. Width of figures indicates the number of genera: under three for the minimal, four to six for medium-sized and 7 to 15 for the maximum.

Skelidorygma Carter, 1974, which Carter classified in the family Brachythyrididae, as well as providing a detailed description of the type species of the genus *Imbrexia* Nalivkin, 1937.

A long overdue monograph by D.V. Nalivkin came out in 1979, where he presented his own interpretation of the systematics of the order Spiriferida (Nalivkin, 1979). More likely than not, his system had been developed even before the publication of spiriferid system by Ivanova (1972), but took into account the systems of a number of authors published in 1965 (Moore, 1965). Nalivkin was the first to distinguish three suborders Spiriferidina, Retziidina, and Athyrididina in the order Spiriferida. Fourteen families (including two new ones) and one new subfamily were established by Nalivkin in the suborder Spiriferidina:

Cyrtospiriferidae H. et G. Termier, 1949 (type genus *Cyrtospirifer* Nalivkin, 1918)

Spinocyrtiidae Ivanova, 1959 (type genus *Mucrospirifer* Grabau, 1931)

Syringothyridae Fredericks. 1926 (type genus *Syringothyris* Winchell, 1863)

Spiriferidae King, 1846 (type genus. *Spirifer* Sowerby, 1816)

Choristitidae Nalivkin, 1979 (type genus *Palaeochoristites* Sokolskaja, 1941)

NB: The family Choristitidae was distinguished by Waterhouse in 1968 with the type genus *Choristites*; the genus *Palaeochoristites* was later recognized as the type genus of the family Palaeochoristitidae (Carter et al, 1994).

Brachythyrididae Fredericks, 1924 (type genus *Brachythyris*);

Verneuiliidae Schuchert et Le Vene, 1929(type genus *Verneuilia* Hall et Clarke, 1894);

Bashkiriidae Nalivkin, 1979 (type genus *Bashkiria* Nalivkin, 1979);

Costispiriferidae H. et G. Termier, 1949 (type genus *Costispirifer* Cooper, 1942);

Eudoxiniinae Nalivkin, 1979 (type genus *Eudoxina* Fredericks, 1929);

Cyrtinidae Fredericks, 1912 (type genus *Cyrtina* Davidson, 1858);

Spiriferinidae Davidson, 1884 (type genus *Spiriferina* Orbigny, 1847);

Ambocoeliidae George, 1931 (type genus *Ambocoelia* Hall. 1860);

Reticulariidae Waagen, 1883 (type genus *Reticularia* McCoy, 1844);

Martiniidae Waagen, 1883 (type genus *Martinia* McCoy, 1844).

Both Nalivkin and Ivanova link the family Brachythyrididae to the type genus *Brachythyris*, which, according to data of the former, emerges in the Upper Devonian and is represented by several species in the Tournaisian of the Urals and North America and the Viséan of Europe. Nalivkin, however, continues to assign to Brachythyrididae the genus *Brachythyrina*, featuring the developed vascular system and, based on the internal structure, definitely inconsistent with the type genera of the family Brachythyrididae and subfamily Prospirinae, in which Carter had included genus *Brachythyrina* (Carter, 1974).

Legrand-Blain et al., 1984 gave special attention to this in the study of representatives of genus *Brachythyrina*. First of all, Legrand-Blain noted that the ramiformed vascular system in *Brachythyrina* emerges earlier in the mid-Serpukhovian or probably before that, rather than at the Mid-Carboniferous boundary as was considered by Lazarev and Poletaev (1982). Based on the morphology of the species of *Brachythyrina* from the "Kulm" of the Pyrenees, in 1984 Legrand-Blain distinguished the new subgenus *Brachythyrina* (*Anthracothyrina*) Legrand-Blain, 1984. One year later, she published the results of her study of topotypes of the "*Spirifer trigonalis* Martin" group from the Upper Viséan and Lower Serpukhovian of Scotland (Legrand-Blain, 1985). This group of taxa, sharing common external characters, shows high variability of the internal structures; in other words, is a "zone of bifurcation". Of these representatives, Legrand-Blain distinguished two morphs; specifically, one without dental plates and another with short or primordial dental plates. Note that based on the photographs of beaks' sections presented in monograph by S.V. Semikhatova (1941), these plates featured prismatic layers and a Choristite-type structure. Metaphorically speaking, it is conceivably "milk teeth" of the future choristites. The studies of Legrand-Blain showed that another branch of spiriferids, similarly possessing ramified vascular markings and missing dental plates, emerged almost contemporaneously with protochoristites within the *Spirifer trigonalis* group in the Late Viséan and Early Serpukhovian. Legrand-Blain combined both morphs to the new genus *Angiospirifer* Legrand-Blain, 1985 with the type species *Spirifer trigonalis* Martin, 1809 and distinguished a new subfamily Angiospiriferinae, which, in addition to *Angiospirifer*, included the genera *Brachythyrina*, *Prochoristitella* Legrand-Blain, 1969, *Kinghiria* Litvinovich, 1966, ?*Quizhouspirifer* Xian, 1983, and ?*Subspirifer* Shan et Zhao, 1981. In my opinion, the probability of the origin of angiospiriferids from early spiriferids is supported by data of M.E. Yanishevskii (1935), giving evidence of developmental instability of dental plates and barely noticeable vascular system in *Spirifer greberi* Schwetzov, 1925. Forms morphologically similar to angiospirifers, lacking not only the dental plates, but also vascula traces, had earlier been isolated into the genus *Eobrachythyrina* (Lazarev and Poletaev, 1982) and classified under subfamily Spiriferinae. There is no doubt that the genus *Angiospirifer* became a progenitor of two strong branches and, subsequently, two leading groups of spiriferids of the Middle-Upper Carboniferous of Easton Europe.

The next stage of the development of the spiriferid system is reflected in a major paper by four authors (Carter et al., 1994), based on which an updated and comprehensively illustrated spiriferid system, presented 12 years later in the modern edition of *Treatise* (Carter et al., 2006; Gourvennec and Carter, 2007). It is presented below.

Order Spiriferida King, 1846

Suborder Spiriferidinae Waagen, 1883

Superfamily Cyrtioidea Fredericks, 1924 (Upper Ordovician–Lower Devonian)

Families: Cyrtiidae Fredericks, 1924; Hedeinopsidae Gourvennec, 1990.

Superfamily Adolfioidea Sartaener, 1966 (Upper Silurian–Upper Devonian)

Families: Adolfiidae Sartaener, 1966; Echinospiriferidae Liashenko, 1973.

Superfamily Theodossioidea Ivanova, 1959 (Lower Devonian – Lower Carboniferous)

Families: Theodossiidae Ivanova, 1959; Ulbospiriferidae Johnson et Carter, 1994 (composed of subfamilies: Ulbospiriferinae Johnson et Carter, 1994 and Palaeospiriferinae Carter, Johnson et Hou, 1994); Palaeochoristitidae Carter, 1994.

Superfamily Cyrtospiriferoidea Termier et Termuer, 1949 (Lower–Upper Devonian)

Families: Spinocyrtiidae Ivanova, 1959; Cyrtospiriferidae Termier et Termier, 1949 (composed of subfamilies: Cyrtospiriferinae Termier et Termier, 1949 and Cyrtiopsinae Ivanova, 1972).

Superfamily Ambocoelioidea George, 1931 (Upper Silurian–Permian)

Families: Ambocoeliidae George, 1931 (composed of subfamilies: Ambocoeliinae George, 1931; Rhynchospiriferinae Paulus, 1957); Lazutkiniidae Johnson et Hou, 1994; Eudoxinidae Nalivkin, 1979; Verneuiliidae Schuchert, 1929.

Superfamily Martinioidea Waagen, 1883 (Silurian–Permian)

Families: Tenellodermidae Carter, Johnson et Gourvennec, 1994; Elythynidae Gourvennec, 1994; Martiniidae Waagen, 1883 (composed of subfamilies: Martiniinae Waagen, 1883; Eomartiniopsinae Carter, 1994; Elivellinae Carter 1994); Crassiumbellidae Carter, 2006; Ingelarellidae Campbell, 1959 (composed of subfamilies: Ingelarellinae Campbell, 1959; Notospiriferiinae Archbold et Thomas, 1986; Glendoniinae Clarke, 1992); Gerkispiridae Carter, 1985; Perissothyrididae Carter, 1994.

Superfamily Spiriferoidea King, 1846 (Upper Devonian–Upper Permian)

Families: Spiriferidae King, 1846 (composed of subfamilies: Spiriferinae King, 1846 and Prospirinae Carter, 1974; Sergospiriferinae Carter, 1994; Purdonellinae Poletaev, 1986); Choristitidae Waterhouse, 1968 (composed of subfamilies: Angiospiriferinae Legrand-Blain, 1985; Choristitinae Waterhouse, 1968; Tangshanellinae Carter, 1994); Imbrexiidae Carter, 1992; Trigonotretidae Schuchert, 1893 (composed of subfamilies: Neospiriferinae Waterhouse, 1968 и Trigonotretinae Schuchert, 1893); Spiriferellidae Waterhouse, 1968.

Superfamily Paeckelmanelloidea Ivanova, 1972 (Upper Devonian–Permian)

Families: Strophopleuridae Carter, 1974 (composed of subfamilies: Strophopleurinae Carter, 1974; Bashkiriinae Nalivkin, 1979; Pterospiriferinae Waterhouse, 1975); Paeckelmanellidae Ivanova, 1972 (composed of subfamilies: Paeckelmanellinae Ivanova, 1972 and Scenesiinae Carter, 1994.

Superfamily Brachythyridoidea Fredericks, 1924 (Upper Devonian–Permian)

Families: Brachythyrididae Fredericks, 1924; Skelidorygmidae Carter, 1994.

Suborder Delthyridina Ivanova, 1972

Superfamily Delthyridoidea Phillips, 1841 (Silurian–Carboniferous)

Families: Delthyrididae Phillips, 1841 (composed of subfamilies: Delthyridinae Phillips, 1841; Howelellinae Johnson et Hou, 1994); family Hesterolitidae Termier et Termuer, 1949 (composed of subfamilies: Hesterolitinae Termier et Termuer, 1949 and Fimbrispiriferinae Pitrat, 1965); Acrospiriferidae Termier et Termier, 1949; Cyrtinopsidae Wedekind, 1926; Mucrospiriferidae Boucot, 1959.

Superfamily Reticularioidea Waagen, 1883 (Silurian–Upper Permian)

Families: Reticulariidae Waagen, 1883 (composed of subfamilies: Reticulariinae Waagen, 1883; Reticulariopsinae Gourvennec, 1994; Rhenothyridinae Gourvennec, 1994; Obesariimae Gourvennec, 1994; Eoreticulariinae Gourvennec, 1994); Xenomartiniidae Havlicek, 1971; Thomasariidae Cooper et Dutro, 1982; Elythidae Fredericks, 1924 (composed of subfamilies: Elythinae Fredericks, 1924, Martinothyridinae Carter, 1994, Phricodothyridinae Caster, 1939, Toryniferinae Carter, 1994, Anomaloriinae Cooper et Grant, 1976).

Order Spiriferinida Ivanova, 1972

Suborder Cyrtinidina Carter et Johnson, 1994

Superfamily Cyrtinoidea Fredericks, 1911 (Lower Devonian–Lower Carboniferous)

Families: Cyrtinidae Fredericks, 1911; Komiellidae Johnson et Blodgett, 1993.

Superfamily Suessioidea Waagen, 1883 (Lower Carboniferous–Lower Jurassic)

Family Davidsoninidae Ivanova, 1972 and three families during the Mesozoic Era

Superfamily Spondylospiroidea Hoover, 1991 (Upper Triassic)

Suborder Spiriferinidina Ivanova, 1972

Superfamily Syringothyridoidea Fredericks, 1926 (Upper Devonian–Upper Permian)

Families: Syringothyrididae Fredericks, 1926; Dimegelasmidae Carter, 1994; Licharewiidae Slyusareva, 1958.

Superfamily Pennospiriferinoidea Dagis, 1972 (Upper Devonian–Lower Jurassic)

Families: Punctospiriferidae Waterhouse, 1975; Spiropunctiferidae Carter, 1994; Reticularinidae Waterhouse, 1975; Paraspiriferinidae Cooper et Grant, 1976; Spiriferellinidae Ivanova, 1972; Pennospiriferinidae Dagis, 1972, and several other families from the Mesozoic.

Note that the major Carboniferous representatives of the superfamily Spiriferoidea are characterized by striated microornamentation, occurrence of delthyrial plates, ovarian markings evenly scattered across the interior surface of the ventral valve or less commonly concentrating around the muscle area, as well as transverse grooves, and serration of the area margin. Characteristically, the area of the multiple Carboniferous representatives of the superfamily Martinioidea, which appears to be more "ancient" than the spiriferoids, as well as ambocoeliids and brachythyridids, remained "smooth" or weakly striated. In these spiriferinids, the vascular system was generally more primitive (pinnate). Representatives of the families Imbrexiidae and Trigonotretidae, having emerged during the Carboniferous, are characterized by the development of free growth lamellae (imbricated microsculpture) and multiple ramifications (bunching up) of ribs. The Carboniferous is also the time when substantial evolution takes place of representatives of superfamilies Paeckelmantlloidea and Reticularioidea, which are characterized by complex acicular microsculpture of the shell surface, as well as of the members of superfamily Pennospiriferinoidea, with porous shell walls. Overall, the spiriferid system represented above is destined to live long, since it is based on direct revision of the type material of the genera carried out by the most experienced professionals. This does not, however, preclude some revisions and additions. In particular, a paper of Waterhouse (2004), concerned with stratigraphy and fossil remains (largely of brachiopods) of the Permian and Triassic of the Himalayas was published in 2004 almost contemporaneously with the spiriferid system of the four abovementioned authors. In his work, the author presented his own point of view on the system of the Late Paleozoic spiriferids composed of three superfamilies: Spiriferoidea, Paeckelmanelloidea, and Brachythyridoidea from the perspective of one of the best experts on the Permian–Triassic fauna of southeastern paleobiochore. The systematic composition of these superfamilies (after Waterhouse, 2004) is presented below:

Superfamily Spiriferoidea King, 1846

Families: Spiriferidae King, 1846 (composed of subfamilies: Spiriferinae King, 1846 and Gypospiriferinae Waterhouse, 2004); Neospiriferidae Waterhouse, 1968 (composed of subfamilies: Imbrexiinae Carter, 1994, Neospiriferinae Waterhouse, 1968, Kaninospiriferinae Kalaschnikov, 1996, Fusispiriferinae Waterhouse, 2004);

Trigonotretidae Schuchert, 1893 (composed of subfamilies Sergospiriferinae Carter, 1994; Angiospiriferinae Legrand-Blain, 1985—tribes Angiospiriferini Legrand-Blain, 1985, Georginakingini Waterhouse, 2004, subfamily Trigonotretinae Schuchert, 1893—tribes Trigonotretini Schuchert, 1893, Grantoniini Waterhouse, 2004, and subfamily Costuloplicinae Waterhouse, 2004); Choristitidae Waterhouse, 1968 (composed of subfamilies Prospirinae Carter, 1974; Choristitinae Waterhouse, 1968, and Purdonellinae Poletaev, 1986); Spiriferellidae Waterhouse, 1968 (composed of subfamilies Spiriferellinae Waterhouse, 1968, Hunzininae Angiolini, 2001, and Elivininae Waterhouse, 2004).

Superfamily Paeckelmannelloidea Ivanova, 1972

Family Strophopleuridae Carter, 1974 (subfamily Pterospiriferinae Waterhouse, 1975)

Superfamily Brachythyridoidea Fredericks, 1924

Families: Brachythyrididae Fredericks, 1924 (composed of subfamilies Brachythyridinae Fredericks, 1924 and Pustuloplicinae Waterhouse, 2004); Brachythyrinidae Waterhouse, 2004; Skelidorygmidae Carter, 1994 (composed of subfamilies Skelidorygminae Carter, 1994 and Tangshanellinae Carter, 1994).

A closer look at the proposed system reveals substantial differences from the system presented in *Treatise* (Carter et al., 2006). In particular, the new subfamily Gypospiriferinae is included in the family Spiriferidae in the superfamily Spiriferoidea; Neospiriferinae is raised to a family, in which the subfamily Imbrexiinae was placed. The subfamilies Sergospiriferinae and Angiospiriferinae are included in the composition of the family Trigonotretidae. The subfamilies Prospirinae and Purdonellinae are classified in the family Choristitidae. The new family Brachythyrinidae with the type genus *Brachythyrina* is distinguished in the superfamily Brachythyridoidea. The subfamily Tangshanellinae is included in the composition of the family Skelidorygmidae. Like to any other system, the described system of spiriferids is relatively subjective and not every new development can be accepted. In my opinion, the recognition by Waterhouse of the family Brachythyrinidae and the subfamily Gypospiriferinae is the most essential for the Carboniferous spiriferid system.

The Atlas of Carboniferous Spiriferids of Eastern Europe was published in 2018 (Poletaev, 2018). It presents findings of a revision at species and genus level of the spiriferid system developed by several generations of paleontologists over 200 years of the study of this group of brachiopods in European Russia and the Soviet Union. The author believed that the major innovations that governed the main direction of the evolution of Carboniferous spiriferids were the development in some taxa at the very end of the Devonian of the so-termed "serration" of hinge margin of the ventral area, as well as the emergence in the beginning of the Carboniferous, and further amplification (increasing complexity), of the vascular system in a number of major spiriferid groups of Eastern Europe (Poletaev, 2017). As was already mentioned, this tendency was noted by Ivanova as early as in 1959 (Ivanova, 1959).

Emergence of serrated margin of the ventral area appears to be related to the described (Afanasjeva, 2014, 2018) adaptation of the majority of the Carboniferous spiriferids to attachment of the shells to relatively soft substrate using filaments similar to byssus. Yakovlev (1908) was the first to suggest that the means of attachment of brachiopods to the substrate may lead to formation of species and genera. Many genera of Carboniferous spiriferids differed in their attachment from Devonian and more ancient representatives of the order, which were commonly attached to hard substrates by a pedicle often surrounded by a pedicle sheath. It is entirely possible that the pedicle sheath of the Devonian spiriferids transformed into the system of stegidial plates, typical of many genera of Carboniferous spiriferids with a serrated area. Formation of the characteristic "serration" of the hinge margin of the ventral area is explained herewith for the first time by the fact that strands, similar to a byssus, produced by the active mantle margin are located in a relatively uniform series along the area margin, like chonetid spines (Poletaev, 2013), rather than at the corners of the area as was previously presumed by Ivanova (1949) (Fig. 3).

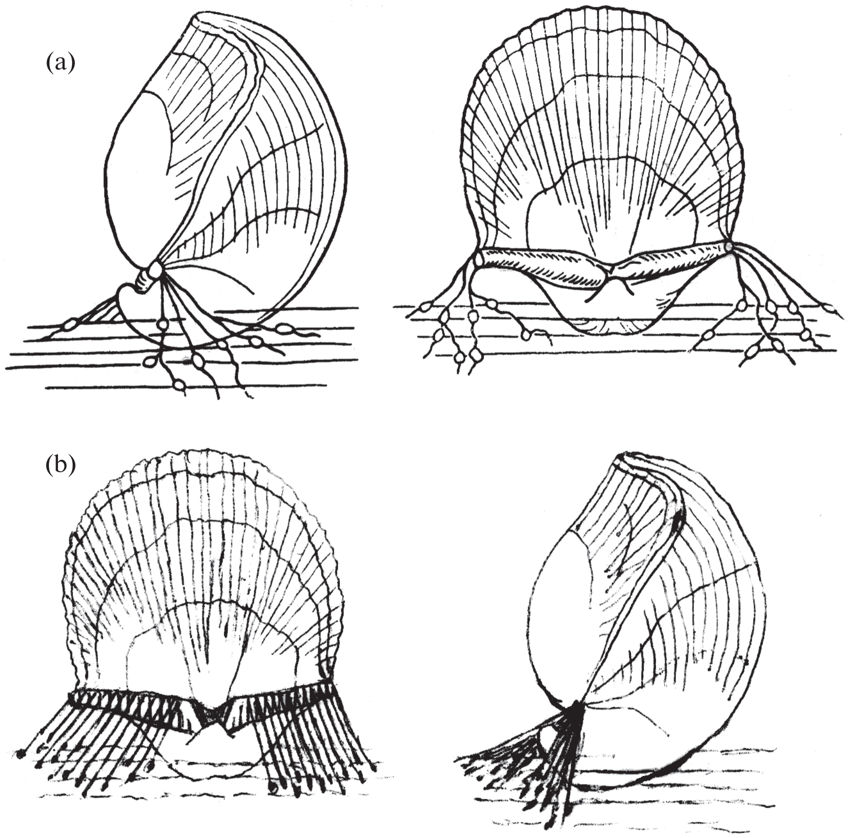

Fig. 3. Types of attachment of spiriferids with the transverse-grooved ventral area: (a) after Ivanova, 1949; (b) after Poletaev, 2013).

The number of these strands at the ends of the area increases as it grows in width, while as the area grows in length, the notches in the hinge margin of area where the strands protrude outside, form the well-known transverse grooves on its surface. Absence of the grooves characterizes the so-called interarea, which evolved at initial stages of ontogeny when the shell was attached by a pedicle (before the loss of the latter). Since the grooves become covered by periostracum as the area grows, they are sometimes inconspicuous, which occasionally caused confusion in the generic assignment of the genus in some morphologically similar species, e.g., *Palaeochoristites cinctus* (Keyserling, 1846) and *Mesochorispira konincki* (Dewalque, 1895).

As previously mentioned (Ivanova, 1959; Poletaev, in press), gradual development and amplification of vascular system played a substantial role in evolution of a significant proportion of the Carboniferous spiriferids of Eastern Europe. In my opinion, during the Viséan, the main lineage of the Early Carboniferous spiriferids (of the genus *Unispirifer* Campbell, 1957), gave rise to a branch with a ramified vascular system, which while gradually evolving in the Late Viséan and Early Serpukhovian, gave rise to the two most widely represented spiriferid groups in the Pennsylvanian of Eastern Europe, North America, and South China, namely, brachythyrins and choristites. Considering the importance of the emergence and increasing complexity of the vascular system of the leading East European groups in the phylogeny and evolution of Carboniferous spiriferids, Poletaev (2018) raised the rank of the subfamily Angiospiriferinae to the family and combined the families Angiospiriferidae and Choristitidae into the superfamily Angiospiriferidoidea, after having separated it from the superfamily Spiriferoidea. The composition of the family Choristitidae (sensu Poletaev, 2018) included the Late Serpukhovian genus *Adventochoristites* Poletaev, 2012 (Poletaev, 2012), which became extinct at the beginning of the Bashkirian Stage, as well as the largely Bashkirian genus *Alphachoristites* Gatinaud, 1949, and Moscovian–Late Carboniferous genera *Choristites*, *Trautscholdites* (Ustritsky, 1967), and *Choristitella*. Representatives of the family Choristitidae did not continue beyond the Carboniferous-Permian boundary. Some authors identified, as Early Permian choristites, the externally similar large representatives of the genus *Parachoristites* Barchatova, 1970, which belong to family Spiriferidae based on their shell interior and may possibly be the direct descendants of the genus *Spirifer*.

In 2020, the author (Poletaev, 2020) submitted a monograph taking into account the proposed changes in spiriferid system of the East European Carboniferous compared to the system published in *Treatise* (Carter et al., 2006). Specifically, the family Eudoxinidae additionally included the genera *Implexina* Poletaev, 1971 and *Weiningia* Ching et Liao, 1974 due to the similarity of the internal structure of these genera with the genus *Eudoxina*, which is the type genus for the family. The most significant were changes in the superfamilies Martinioidea, Spiriferoidea, and Brachythyrididoidea. The families Brachythyrididae and Skelidorygmidae were included in the superfamily Martinioidea, since representatives of both families featured a smooth, triangular shape of the shell similar to Martinioidea and a relatively short area in the absence or primitive vascular system. With some degree of confidence, the same superfamily additionally included family Purdonellinidae. The genus *Beschevella* Poletaev, 1975 earlier tentatively classified within the family Martiniidae was assigned to the family Ingelarellidae, based on its microsculpture.

Overall, the changes proposed by the author in the spiriferid system of the Carboniferous of Eastern Europe resolve into the following: superfamily Brachythyridoidea is excluded from suborder Spiriferidinae, while the families Brachythyrididae and Skelidorygmidae, which composed the latter, became members of superfamily Martinioidea.

The suborder Spiriferidinae included superfamily Neospiriferoidea composed of the families Neospiriferidae (sensu Waterhouse, 2004) and Trigonotretidae, which representatives feature ramified (bunched-up) ribs, plication on surface of the valves, and imbricated microsculpture. Additionally, the family Trigonotretidae (sensu Waterhouse, 2004), representatives of which, in my opinion, feature massive stegidial structure and buttress in apical part of the ventral valve characteristic of the family, was separated from subfamilies Sergospiriferinae and Angiospiriferinae, which lack these characteristic features. The family Angiospiriferidae with the subfamilies Angiospiriferinae, Brachythyrininae, and Choristitinae became a part of superfamily Spiriferoidea as a taxon with representatives featuring a developed vascular system. The family Spiriferidae also included subfamily Gypospiriferinae, representatives of which had emerged approximately at the division between the Mississippian and Pennsylvanian, gradually evolved, and increased in the Early Permian. As a result of isolation of the independent superfamily Neospiriferoidea in suborder Spiriferidinae, superfamily Spiriferoidea remained composed of families Spiriferidae, Prospiridae, Sergospiriferidae, and Spiriferellidae. Additionally, the subfamily Oceaniinae with the type genus *Oceania* (Johnsen et Poletaev, 2015) was included in the superfamily Paeckelmanelloidea as part of the composition of the family Strophopleuridae (Poletaev, 2015).

CONCLUSIONS

To summarize, brachiopods as relatively sedentary benthic organisms are characterized by highly distinctive provincialism of nomenclature and, in part, of taxonomic composition. Therefore, the general spiriferid system published in *Treatise* (Carter et al., 2006) integrates several subsystems, reflecting the specificity of particular. Paleobiochores. One of these, representing most Carboniferous spiriferids of Eastern Europe and including of six superfamilies, is revised by the present author as shown below.

Order Spiriferida King, 1846

Suborder Spiriferidinae Waagen, 1883

Superfamily Theodossioidea Ivanova, 1959

Family Palaeochoristitidae Carter, 1994; (genus *Palaeochoristites* Sokolskaja, 1941).

Superfamily Ambocoelioidea George, 1931

Family Ambocoeliidae George, 1931; (genus *Crurithyris* George, 1931);

Family Eudoxiniidae Nalivkin, 1979; (genera: *Paulonia* Nalivkin, 1925; *Eudoxina* Fredericks, 1929; *Implexina* Poletaev. 1971; *Weiningia* Ching et Liao, 1974).

Superfamily Martiniioidea Waagen, 1883

Family Martiniidae Waagen, 1883;

subfamily Martiniinae Waagen, 1883; (genera: *Martinia* McCoy, 1844; *Tiramnia* Grunt, 1977; *Gilinmartinia* Li et Gu, 1980; *Postamartinia* Wang et Yang, 1993),

subfamily Eomartiniopsinae Carter, 1994; (genera: *Eomartiniopsis* Sokolskaja, 1941; *Heterarea* Cooper et Grant, 1976; *Kizilia* Nalivkin, 1979).

Family Purdonellidae Poletaev, 1986; (genera: *Podtscheremia* Kalashnikov, 1966; *Ala* Nalivkin, 1979; *Eliva* Fredericks, 1924; *Purdonella* Reed, 1944);

Family Ingelarellidae Campbell, 1959;

subfamily Glendoniinae Clarke, 1992; (genus *Beschevella* Poletaev, 1975).

Family Gerkispiridae Carter, 1985; (genus: *Punctothyris* Hyde, 1953);

Family Brachythyrididae Fredericks, 1924;

subfamily Brachythyridinae Fredericks, 1924; (genera: *Brachythyris* McCoy, 1844; *Meristorygma* Carter, 1974; *Ella* Fredericks, 1918),

subfamily Skelidorigminae Carter, 1994; (genera: *Skelidorigma* Carter, 1974; *Phragmobrachythyris* Poletaev, 1999).

Superfamily Spiriferoidea King, 1946

Family Spiriferidae King, 1946;

subfamily Spiriferinae King, 1946; (genera: *Spirifer* Sowerby, 1816, *Ectochoristites* Campbell, 1957; *Unispirifer* Campbell, 1957;

Parachoristites Barchatova, 1970; *Larispirifer* Enokjan et Poletaev, 1970 *Austrochoristites* Roberts, 1971; *Donispirifer* Poletaev, 1985; *Mesochorispira* Carter, 1992),

subfamily Prospirinae Carter, 1974 (several genera outside of biochores),

subfamily Hypospiriferinae Waterhouse, 2004; (genus *Hypospirifer* Cooper et Grant, 1976),

subfamily Sergospiriferinae Carter, 1994; (genera: *Sergospirifer* Ivanova, 1952; *Anthracospirifer* Lane, 1963; *Eobrachythyrina* Poletaev, 1982).

Family Angiospiriferidae Legrand-Blain, 1985;

subfamily Angiospiriferinae Legrand-Blain, 1985; (genus *Angiospirifer* Legrand-Blain, 1985),

subfamily Brachythyrinidae Waterhouse, 2004 (genera: *Brachythyrina* Fredericks. 1929; *Elinoria* Cooper et Muir-Wood, 1951, *Quizhouspirifer* Xian, 1982; *Anthracothyrina* Legrand-Blain, 1984),

subfamily Choristitidae Waterhouse, 1968 (genera: *Choristites* Fisher, 1825; *Choristitella* Ivanov et Ivanova, 1937; *Alphachoristites* Gatinaud, 1949; *Trautscholdites* Ustritski, 1967; *Adventochoristites* Poletaev, 2012).

Superfamily Neospiriferoidea Waterhouse, 1968

Family Imbrexiidae Carter, 1992; (genera: *Imbrexia* Nalivkin, 1937; *Lutuginia* Poletaev, 1997, and others);

Family Neospiriferidae Waterhouse, 1968; (genera: *Neospirifer* Fredericks, 1924; *Betaneospirifer* Gatinaud. 1949; *Tegulispirifer* Poletaev, 2000);

Family Trigonotretidae Schuchert, 1893;

Family Spiriferellidae Waterhouse, 1968; (genus *Alispiriferella* Waterhouse et Waddington, 1982.

Superfamily Paeckelmannelloidea Ivanova, 1972

Family Strophopleuridae Carter, 1974;

subfamily Strophopleurinae Carter, 1974; (genera: *Acuminothyris* Roberts, 1963; *Voiseyella* Roberts, 1964; *Avisyrinx* Martinez-Chacon, 1975; *Cantabriella* Martinez-Chacon, 1987; *Triangularia* Poletaev, 2001),

subfamily Bashkiriinae Nalivkin, 1979; (genus *Bashkiria* Nalivkin, 1979),

subfamily Oceaniinae Poletaev, 2015; (genus: *Oceania* Johnson et Poletaev, 2015).

Family Paeckelmannelidae Ivanova, 1952;

subfamily Paeckelmannelinae Ivanova, 1952 (genus: *Paeckelmannella* Likharev, 1934).

CONFLICT OF INTEREST

The author declares no conflicts of interest.

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