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The main stages in evolution of Carboniferous Spiriferida and Spiriferinida (Brachiopods) in the paleobasins of Eastern Europe

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Головні етапи еволюції кам'яновугільних Spiriferida та Spiriferinida (Brachiopods) у палеобасейнах Східної Європи

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The twelve temporal intervals during which changes in the generic composition of Carboniferous Spiriferida and Spiriferinida assemblages occurred within the paleobasins of Eastern Europe are established and analyzed. As the most important levels of changes the intervals near Devonian/Carboniferous boundary, in middle Tournaisian and middle Visean, Mississippian/Pennsylvanian, Bashkirian/Moscovian, base of Kasimovian and Carboniferous/Permian boundaries are picked out. The changes of lithological conditions of habitation as the reasons of the morphological evolution of the attachment system in representatives of the superfamilies Spiriferoidea, Paeckelmanelloidea and Brachythyridoidea following the Hangenberg crisis are indicated. The importance of the evolution of the vascular system of the family Angiospiriferidae Legrand-Blain, 1985 for the emergence of the subfamilies Chorisitinae Waterhouse, 1968 and Brachythyrininae Waterhouse, 2004 at the end of the Mississippian is emphasised. It is discussed the scale of the rate of change in the generic composition of Carboniferous spiriferide brachiopods.

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Introduction

Despite the fact that Ch. Darwin laid the foundations of the theory of evolution back in 1859 (Darwin, 1952), the search for specific factors driving directed changes within particular groups of organisms remains highly relevant today.

In the early 21st century, several factors – including the publication of the multi-volume Treatise on Invertebrate Paleontology, Part H, Brachiopoda Revised (Carter et al., 2006; Carter, Remy Gourvennec, 2007) – prompted researchers to re-examine a substantial body of brachiopod material, including Carboniferous spiriferides and spiriferinides housed in museums across Western and Eastern Europe.

The outcomes of this revision, focusing on the species and genus composition of most Carboniferous spiriferides from Eastern Europe and clarifying their internal structure, were published by Poletaev (2018). These findings subsequently enabled the author (Poletaev, 2022) to make slight adjustments to the spiriferids taxonomy presented in the Treatise on Invertebrate Paleontology.

Notably, the genera *Implexina* Poletaev (in Aisenverg and Poletaev, 1971) and *Weiningia* Ching & Liao, 1974 (Ching, Liao, 1974) were reassigned (Poletaev, 2022) to the family Eudoxinidae Nalivkin within the superfamily Ambocoelioidea. The genus *Beschevella* Poletaev, 1975 (Poletaev, 1975) was placed in the family Ingelarellidae of the superfamily Martinioidea, while *Lutuginia* Poletaev, 1997 (Poletaev, 1997) was classified under the subfamily Imbrexiinae within the family Neospiriferidae.

Based on the emergence of a reticular vascular system – first appearing in the early Visean in species of the genus *Angiospirifer* Legrand-Blain, 1985 (Legrand-Blain, 1985) but largely absent in some members of the family Spiriferidae. Poletaev (2009) elevated the rank of the subfamily Angiospiriferinae Legrand-Blain to the family level within the superfamily Spiriferoidea. The newly defined family Angiospiriferidae includes not only Angiospiriferinae but also Choristitinae (previously classified under the family Choristitidae by Carter 2006, In Treatise, p. 1780–1786) and Brachythyrininae, the earliest representatives of which appeared at the end of the Serpukhovian.

A further revision of the species and genus composition of spiriferids in Eastern Europe has enabled the author to correct several earlier taxonomic errors (Poletaev, 2024) and to draw well-supported conclusions regarding the major stages in the development of this brachiopod order during the Carboniferous. It is important to note that spiriferids represent just one – albeit significant – group within a broader fossil fauna. This broader assemblage includes many related groups that were interconnected through biocenotic relationships and underwent nearly synchronous transformations at several critical stratigraphic boundaries.

An analysis of the evolutionary sequence of spiriferides from the late Famennian (Devonian) through to the early Permian reveals a number of distinct stages in their history. These stages are demarcated by twelve transitional stratigraphic levels, each marked by notable changes in the systematic composition of the spiriferides assemblage. These intervals, reflecting both phylogenetic developments and migratory episodes, define the stages in the shared evolutionary history of the benthic biota across three major Eastern European basins: the Foreland Trough of the Western Urals, the Moscow Syneclise, and the Donets Basin. These basins collectively formed a single paleobiogeographic province. In practical stratigraphy, the extinction of certain genera and the emergence of others are crucial indicators for defining the boundaries of regional stratigraphic units and correlating them with the International Chronostratigraphic Scale (ICS).

The aim of this article is on a base of modern Spiriferida and Spiriferinida system and new more correct data about stratigraphic range of spiriferide brachiopods genera to clarify levels of main changes of their assemblies and try to discover the cause.

Results

The onset of the early Tournaisian stage in spiriferides evolution is marked by a level near the Devonian–Carboniferous boundary. Like many such boundaries, this one corresponds with a significant global event – the Hangenberg Crisis. This event, which occurred at the close of the Devonian, involved a dramatic drop in sea levels and a widespread decrease in oceanic oxygen content, leading to an ecological collapse and a major extinction event among benthic faunas (Becker et al., 2016). The initial changes in spiriferid composition began slightly before the officially recognized Devonian–Carboniferous boundary, below the conventionally isochronous level corresponding to the conodont *praesulcata/sulcata* zonal transition (Aretz, Corradini, 2016).

This crisis led to the disappearance of key Devonian superfamilies such as Theodossioidea and

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Cyrtospiriferoidea, including genera such as *Tenisia* Martynova, 1970 (Martynova, 1970) – a likely ancestor of *Eudoxina* Frederiks & Kruglov, 1928 (Frederiks, Kruglov, 1928) – as well as *Cyrtospirifer* Nalivkin, 1924 (in Frederiks, 1924) and *Theodossia* Nalivkin, 1925 (Nalivkin, 1925). Among the once-diverse Devonian ambocoeliids, many genera vanished, though a notable exception was the widespread emergence (epibole) of the enduring genus *Crurithyris* George, 1931 (George, 1931).

This boundary is further defined by the appearance of new taxa such as Paulonia Nalivkin, 1925 (Nalivkin, 1925), along with the genera Eudoxina and Implexina (in Aisenverg and Poletaev, 1971). Among martinioids, Eomartiniopsis Sokolskaya, 1941 (Sokolskaya, 1941) appears, while the superfamily Brachythyridoidea persisted, represented by genera like Brachythyris McCoy, 1844 (McCoy, 1844) and Phragmobrachythyris Poletaev, 1999 (Poletaev, 1999). Within the family Spiriferidae of the superfamily Spiriferoidea, new genera such as Unispirifer Campbell, 1957 (Campbell, 1957) – likely the stem genus for Mississippian spiriferides – emerge alongside Atylephorus Sartenaer & Plodowski, 1996 (Sartenaer, Plodowski, 1996) and Austrochoristites Roberts, 1971 (Roberts, 1971). The latter possibly have migrated from Gondwana's Paleotethyan shores, where it was originally described in the Australian Tournaisian.

Overall, the changes in the spiriferides assemblage across the Devonian–Carboniferous boundary in Eastern Europe were profound (see Figure).

As a result, characteristic spiriferids of the Early Tournaisian in Eastern Europe included abundant *Crurithyris, Eudoxina, Eomartiniopsis,* and occasionally *Austrochoristites,* alongside the widely distributed genus *Punctothyris* Hyde, 1953 (Hyde, 1953), which also appeared in North America during this period.

According to Poletaev (2022), the extinction of dominant Theodossioidea and Cyrtospiriferoidea taxa in the late Devonian and the concurrent rise of evolutionarily adaptive genera from superfamilies such as Spiriferoidea can be attributed to bioecological factors. Afanasieva (2018) observed that the dramatic proliferation of foraminiferal and microbial carbonate production on warm-water shelf shoals during the Early Carboniferous led to thick accumulations of limestone-silt sediments. As result, Devonian cyrtospiriferids, which anchored themselves to relatively firm substrates using a single pedicle, were unable to adapt to these new soft-bottom environments or to die. By contrast, some families within the Spiriferoidea and related groups retained a pedicle during early growth stages and evolved byssus filaments along the anterior margin of the area of ventral valve (Poletaev, 2022). Initially serving a supplementary role, these filaments eventually became the main mode of attachment to soft sediment, allowing these genera to thrive under new environmental conditions and to form the taxonomic foundation of the Carboniferous spiriferid brachiopods radiation – including the involvement of Spiriferoidea (especially Angiospiriferidae), Brachythyridoidea and Paeckelmanelloidea.

The beginning of the second stage of the evolution of spiriferides in the Carboniferous is the middle of the Tournaisian age. This time level is marked by the disappearance of most ancient ambocoeliids, including the genus *Paulonia* and the marker of this stage, the genus *Eudoxina,* which is widespread not only in Eastern Europe (Donets Basin, Urals) but also in Eastern Poland and even North America, as well as the genus *Implexina*, which is characteristic of Eastern Europe. Among the Theodossioidea, the genus *Austrochoristites* disappears, but many new genera appear: the leading genus *Palaeochoristites* and the genus *Ectochoristites*, represented in Donets Basin, Central Asia and Australia. The genus *Kizilia* Nalivkin, 1979 (Nalivkin, 1979) was created among martiniids.

Among the spiriferids, the genus *Mesochorispira* Carter, 1992 (Carter, 1992) (important for interregional and intercontinental correlation, appears, widely represented in North America, Asia (China, Kuzbass, Central Asia, Kazakhstan), the western Urals, Western Europe (Belgium) and even Australia. At this time, the genus *Anthracospirifer* Lane, 1963 (Lane, 1963), represented by many species, may have originated in North America and later appeared in Eastern Europe as an emigrant. At the beginning of the second stage, according to I.M. Garan (1970), the genus *Imbrexia* Hall, 1858 (Hall, 1858) – the oldest representatives of the Neospiriferidae appears in the Urals. It is widely represented in the North American Tournaisian. At the end of the stage (Kosvinian time), there are the genera *Podtsheremia* Kalaschnikov, 1966 (Kalaschnikov, 1966) and *Ala* Nalivkin, 1979 (Nalivkin, 1979) in the subfamily Purdonellinae in the Urals, as well as the first representatives of the genus *Skelidorygma* Carter, 1974 (Carter, 1974) in the superfamily Brachythyridoidea.

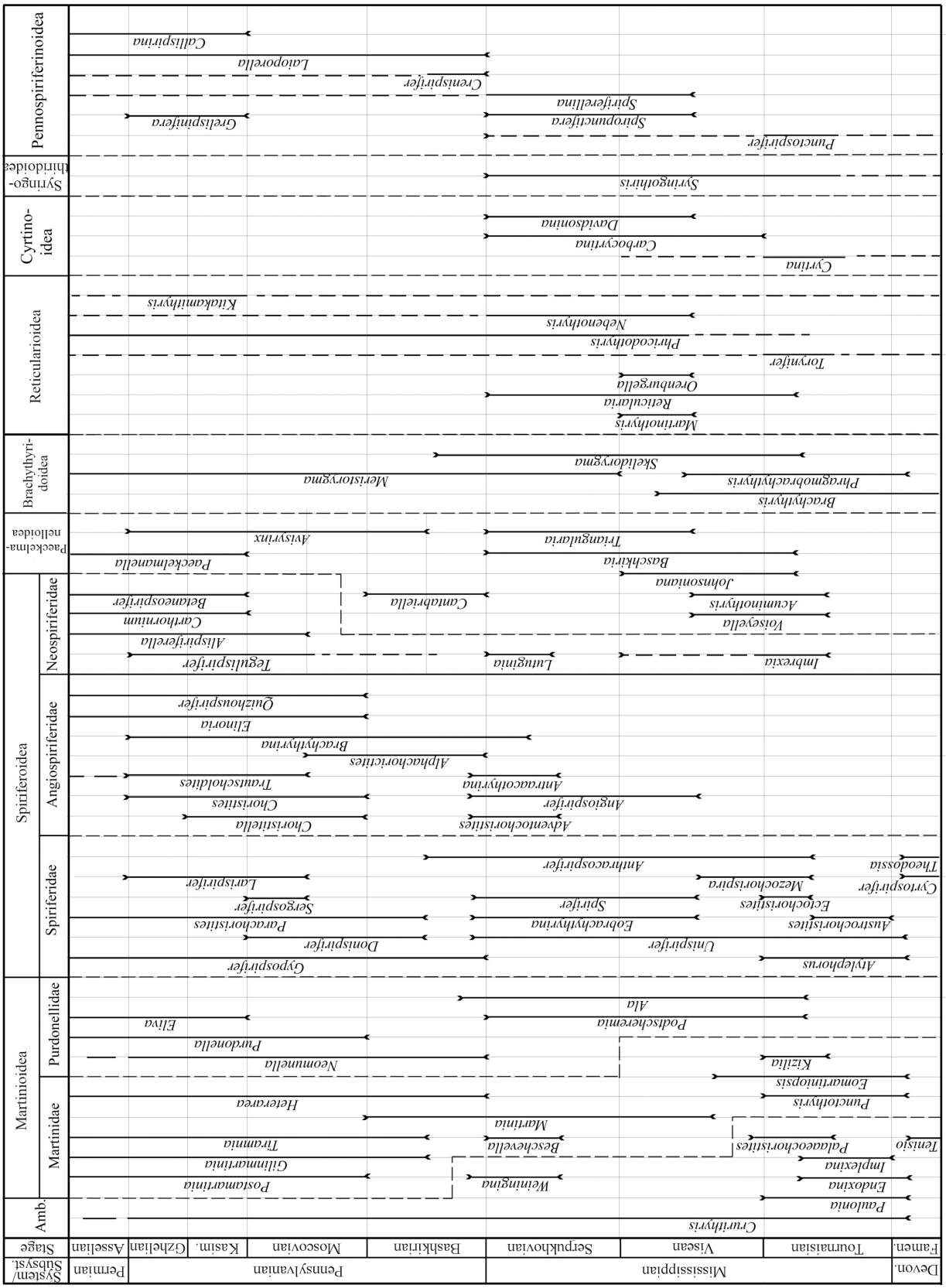

Figure. Scheme showing the stratigraphic distribution of Spiriferida and Spiriferinida genera within the superfamilies Theodossioidea, Cyrtospiriferoidea, Ambocoelioidea, Martinioidea, Spiriferoidea, Paeckelmanelloidea, Brachythyridoidea, Reticularioidea, Cyrtinoidea, and Pennospiriferinoidea in the Carboniferous of Eastern Europe. Abbreviations: Amb. = Ambocoelioidea; Devon. = Devonian; Famen. = Famennian; Kasimov = Kasimovian

At the end of the late Tournaisian stage of spiriferides development, almost globally distributed representatives of the superfamily Paeckelmanelloidea, the genera *Voiseyella* Roberts, 1964 (Roberts, 1964) and *Acuminothyris* Roberts, 1963 (Roberts, 1963), as well as the genera *Bashkiria* Nalivkin, 1979 (Nalivkin, 1979), known only in Europe, and the genus *Johnsoniana* Poletaev, 2024 (Poletaev, 2024), typical for the Johnsonianidae nom. now. (new name for preoccupied Oceaniidae (Poletaev, 2024), first appeared in Eastern Europe. The spiriferids of the superfamily Reticularioidea in the Late Tournaisian Stage of Bashkiria (southwestern Urals) include such well-known genera as *Phricodothyris* George, 1932 (George, 1932), *Reticularia* McCoy, 1844 (McCoy, 1844), and in the southeastern Urals the genus *Torynifer* Hall, Clarke, 1894 (Hall, Clarke, 1894), which is widespread in North America and Asia. The final part of the Tournaisian Stage in the Donets Basin is characterized by a short-term migration of brachiopods from Western Europe and possibly the Mississippian Basin. At the same time, the occurrence of representatives of the Order Spiriferinida of the superfamilies Cyrtinoidea, Syringothyridoidea and Pennospiriferinoidea in the sections of the predominantly northern part of Eastern Europe and the Urals was recorded as part of the persistent and cosmopolitan genera *Cyrtina* Davidson 1859 (in Davidson, 1858–1863), *Syringothyris* Winchell, 1863 (Winchell, 1863) and *Punctospirifer* North, 1920 (North, 1920).

The beginning of the Early Visean stage of spiriferides evolution roughly corresponds to the boundary of the Tournaisian and Visean Stages. This level is characterized primarily by the disappearance of a significant part of the spiriferids genera that arose in the Late Devonian or mid-Tournaisian. At this boundary, the genera *Implexina* among the ambocoeliids and *Palaeochoristites* among the Theodossioidea disappear, as well as the genus *Kizilia* among the ancient martiniids; the Tournaisian genera *Ectochoristites* and *Atylephorus* disappear among the spiriferids, as well as the genus *Imbrexia* among the neospiriferids. During the next early Visean stage, the genera *Crurithyris, Eomartiniopsis, Podtsheremia* and *Ala*, as well as the genera *Brachythyris, Skelidorygma, Mesochorispira* and *Anthracospirifer* continue to exist. Some of these genera existed in the sections potentially, i.e. were absent in the assemblage, but reappeared higher up the section. In general, spiriferids occupied an insignificant place in the early Visean brachiopod assemblage, since it was clearly dominated by numerous Rugosochonetidae. This was probably a consequence of paleogeographic and ecological restructuring of the benthos environment due to continental conditions in the central part of the East European Platform at the end of the Tournaisian and in the first half of the Visean.

The beginning of the late Visean stage of spiriferides evolution is the mid-Visean level, which is characterized by the extinction of the previously widespread genus *Mesochorispira* and the last representatives of the genus *Eomartiniopsis*, as well as *Voiseyella*, and at the end of the stage, probably, the genera *Brachythyris* and *Phragmobrachythyris*. But the main thing is that at this milestone, a significant renewal of the Early Carboniferous spiriferides assemblage of Eastern Europe occurred, associated not only with phylogeny but also with the migration of benthic fauna as a result of the significant transgression of Paleotethys waters to the Russian Platform. At the beginning of the late Visean substage, typical representatives of the widespread in the Carboniferous genus *Martinia* McCoy, 1844 (McCoy, 1844) first appeared among the Martinioidea, and among the Spiriferidae – Sowerby, 1816 (in Sowerby 1815–1818), as well as representatives of the genus *Eobrachythyrina* Lazarev, Poletaev, 1982 (Lazarev, Poletaev, 1982). It should be noted that in addition to the type species *Spirifer striatus* Martin, 1809 (Martin, 1809), only one other species, *S. kozhimicus* Kalashnikov, 1974 (Kalashnikov, 1974), is known from Eastern Europe. All other numerous species of '*Spirifer*' cited in the literature belong to other known, and possibly still unknown, genera of spiriferids. Together with the genus *Spirifer*, the evolution of the vascular system of spiriferids of the group '*S. trigonalis*' (by Semikhatova, 1941) resulted in the first representatives of the new, in the author's opinion (Poletaev, 2022), family Angiospiriferidae – the genus *Angiospirifer* Legrand-Blain, 1985 (Legrand-Blain, 1985), but more details will be given below. At the same time, the genus *Triangularia* Poletaev, 2001 (Poletaev, 2001) appears among the Paeckelmanellidae, and the genera *Martinothyris* Minato, 1953 (Minato, 1953), *Orenburgella* Pavlova, 1969 (Pavlova, 1969) and *Nebenothyris* Minato, 1953 among the Reticularioidea, as well as in the superfamily Suessioidea – the genus *Davidsonina* Schuchert & LeVene, 1929 (Schuchert, LeVene, 1929), and among the Pennospiriferinoidea – the genera *Spiropunctifera* Ivanova, 1971 (Ivanova, 1971) and *Spiriferellina* Fredericks, 1924 (Fredericks, 1924).

Along with the new genera, such genera as *Crurithyris, Eomartiniopsis, Podtsheremia, Ala, Brachythyris, Skelidorygma*, and *Anthracospirifer* continue to exist (sometimes potentially) in the late Visean spiriferids assemblage of the Carboniferous of Eastern Europe.

The beginning of the next early Serpukhovian evolutionary stage in the development of spiriferids roughly corresponds to the beginning of the Serpukhovian and is determined mainly by the disappearance of many spiriferides genera. At this stage, such small genera as *Imbrexia, Acuminothyris, Johnsoniana, Martinothyris, Orenburgella*, and *Cyrtina*, which are not numerous in terms of the number of species, disappear from the Eastern European Carboniferous spiriferides assemblage. However, in the southeastern Urals, the first representatives of the genus *Meristorygma* Carter, 1974 (Carter, 1974), which was widespread in the Pennsylvanian and even in the Permian, appears. In general, the assemblage of the early Serpukhovian stage of spiriferides evolution in Eastern Europe, which was dominated by various Angiospiriferidae, is somewhat impoverished compared to the previous and subsequent stages. However, it potentially contained the genera *Podtscheremia, Ala, Skelidorygma, Unispirifer, Eobrachythyrina, Angiospirifer, Bashkiria, Triangularia, Anthracospirifer*, as well as representatives of Reticularioidea, Cyrtinoidea, Pennospiriferinoidea, etc.

The onset of the late Serpukhovian stage in the evolutionary history of Carboniferous spiriferides in Eastern Europe approximately corresponds to the beginning of the Protvinian time in the stratotype region of the Serpukhovian Stage. Slightly above this level – i.e., at the start of Novolubian time in the Donets Basin – the last representatives of the genus *Bashkiria* disappeared. However, at the same stratigraphic level, the genus *Eobrachythyrina*, along with several endemic genera with short stratigraphic ranges, emerged in the Donets Basin. These include *Beschevella* and *Lutuginia.*

One of the most significant events in the evolution of the Carboniferous system in Europe during the late Serpukhovian was the establishment of the subfamily Angiospiriferinae by M. Legrand-Blain (1985), within the family Spiriferidae. This subfamily initially included the genera *Angiospirifer* and *Anthracothyrina* (Legrand-Blain et al., 1984). Later, Carter et al. (1994) and Carter (2006) reassigned the Angiospiriferinae, along with several genera of Brachythyrininae, to the family Choristitidae Waterhouse, 1968 (Waterhouse, 1968).

Considering the priority of the appearance of a specific type of vascular system in the genera *Angiospirifer*, *Brachythyrina* and later *Adventochoristites* Poletaev, 2012 (Poletaev, 2012), Poletaev (2022) raised Angiospiriferinae to family rank as Angiospiriferidae. This family comprises the subfamilies Angiospiriferinae Legrand-Blain, 1985; Choristitinae Waterhouse, 1968 and Brachythyrininae Waterhouse, 2004 (Waterhouse, 2004) – genera that played a dominant role in Pennsylvanian spiriferids assemblages not only in Europe but also in Asia.

Concurrently, the first representatives of the genera *Tegulispirifer* Poletaev, 2000 (Poletaev, 2000) and *Gypospirifer* Cooper, Grant, 1976 (Cooper, Grant, 1976) – the latter likely a descendant of *Unispirifer* – appeared among the Spiriferidae in the Donets Basin. The late Serpukhovian spiriferids assemblage also included many genera that had persisted for extended periods within the system but had already reached the end of their evolutionary trajectories. In the Urals and Central Asia, for example, the final representative of the family Eudoxinidae, the genus *Weiningia*, disappeared at the Mississippian–Pennsylvanian boundary.

The subsequent Early Bashkirian stage marks a major stratigraphic and geohistorical boundary between the Mississippian and Pennsylvanian subsystems of the Carboniferous. At this boundary, the most significant reorganization of the spiriferides taxonomic structure occurred, driven by both ecological and phylogenetic factors. This restructuring was linked to global climatic changes – specifically, widespread glaciation across Gondwana, which triggered a sharp eustatic sea-level fall and a global, albeit short-lived, marine regression (Veevers, Powell, 1987). The resulting reduction of shelf areas and accompanying ecological changes led to the extinction of numerous 'archaic' superfamilies such as Amborcoelioidea (excluding *Crurithyris*), Cyrtinoidea, and Zuessioidea, including the loss of genera like *Carbocyrtina* Ivanova, 1975 (Ivanova, 1975) and *Davidsonina* Schuchert 1929 (in Schuchert, Le Vene, 1929).

At the same level, several characteristic Mississippian genera – *Eobrachythyrina*, *Spirifer*, *Podtsheremia*, *Ala*, along with the later forms *Angiospirifer* and *Unispirifer* – also vanished. In addition, genera such as *Bashkiria*, *Triangularia*, *Reticularia*, *Nebenothyris*, as well as representatives of *Syringothyris*, *Punctospirifer*, and *Spiropunctifera*, are no longer recorded in Carboniferous assemblages of Eastern Europe beyond this boundary. In the Donets Basin, the endemic genera *Beschevella* and *Lutuginia* also disappeared at this point.

Only a few spireferides genera successfully crossed the Mississippian–Pennsylvanian boundary, including *Martinia*, *Skelidorygma*, *Meristorygma*, *Gypospirifer*, *Anthracospirifer*, *Spiriferellina*, *Phricodothyris*, and *Adventochoristites*as well as *Brachythyrina*, which had appeared near the end of the late Serpukhovian. Subsequently, *Adventochoristites* and *Anthracothyrina* disappeared in the early Bashkirian stage.

Thus, near the Mississippian–Pennsylvanian boundary, nearly three quarters of the early Carboniferous genera within the Eastern European *spiriferides* assemblage disappeared (see Figure). However, new genera appeared, or the successors of genera that emerged during the late Mississippian began to flourish. Among the *martiniids* and *purdonellids*, in addition to *Martinia* and *Skelidorygma*, the genera *Heterarea* Cooper & Grant, 1976 (Cooper, Grant, 1976) and *Neomunella* Ozaki, 1931 (Ozaki, 1931) were the first to cross the boundary between the subsystems. Representatives of the genus *Gypospirifer* became widespread among the *Spiriferidae*, while the genus *Alphachoristites* Gatinaud, 1949 (Gatinaud, 1949) appeared within the family *Angiospiriferidae*, with numerous species playing a leading role in the *Bashkirian* spiriferids assemblages of the Old World. At this stage in spiriferides evolution, the genus *Cantabriella* Martínez-Chacón & Río-García, 1987 (Martinez-Chacon, Río-García, 1987) emerged among the *Paeckelmanelloidea* in the Urals, and genera *Crenispirifer* Stehli, 1954 (Stehli, 1954) and *Laioporella* Ivanova, 1975 (Ivanova, 1975) among the *Pennospiriferinoidea* appeared in the Donets Basin. Hypothetically, the Bashkirian spiriferides assemblage of Eastern Europe also included the long-ranging genera *Kitakamithyris* and *Torynifer*, though these were represented only intermittently across their stratigraphic range.

The beginning of the next stage in spiriferides evolution, which roughly corresponds to the middle of the Bashkirian Stage, is less pronounced than the preceding phase. At this boundary, the last *Skelidorygma* disappear, and the first isolated representatives of evolutionarily advanced genera related to *Brachythyrina*, **–** *Tiramnia* Grunt, 1977 (Grunt, 1977) and *Jilinmartinia* Lee & Gu, 1980 (Lee, Gu, 1980) appear. Within the superfamily Spiriferoidea, the genus *Donispirifer* Poletaev, 2000 (Poletaev, 2000) emerged – characteristic exclusively of the early Pennsylvanian. Among the angiospiriferid brachiopods of the subfamily Choristitinae, the genus *Parachoristites* Barchatova, 1970 (Barchatova, 1970) appeared, likely descended from *Angiospirifer*; it persisted into the early Permian in Eastern Europe, the Arctic, and Central Asia. The genus *Avisyrinx* Martínez-Chacón, 1975 (Martínez-Chacón, 1975) likely originated during the middle Bashkirian. These mostly new genera formed the dominant components of the late Bashkirian stage in the Early Pennsylvanian spiriferide brachiopods evolution of Eastern Europe.

The subsequent evolutionary stage is more significant and, together with other fossil groups, characterizes the beginning of the Moscovian. At this boundary, the last representatives of the once-widespread genus *Martinia* and the less common *Cantabriella* disappear from the Carboniferous spiriferide assemblage. However, *Tiramnia* became widespread among the martiniids, while the genera *Postamartinia* Wang & Yang, 1993 (Wang, Yang, 1993), and *Purdonella* Reed, 1944 (Reed, 1944) also appeared. A major event in the Carboniferous spiriferides evolution of Eastern Europe was the emergence and progressive development of the stratigraphically important genera *Choristites* Fischer de Waldheim, 1825 (Fischer de Waldheim, 1825), *Choristitella* Ivanov & Ivanova, 1937 (Ivanov, Ivanova, 1937), *Elinoria* Cooper & Muir-Wood, 1951 (Cooper, Muir-Wood, 1951), and *Quizhouspirifer* Xian Si-yuan, 1983 (Xian, 1983). Representatives of *Choristites*, alongside foraminifers, bivalves, and corals constituted the core of the benthic macrofauna on the Paleotethys shelf.The phylogenetic development of *Choristites* is reflected in the emergence and successive dominance of three subgenera. Each subgenus is characteristic of a different interval within the Moscovian or late Pennsylvanian. The first representatives of *Choristites* (*Priskites*) likely appeared at the end of the Bashkirian, but this subgenus is mainly associated with the first half of the Moscovian. In the early Moscovian spiriferids assemblage, the abundance of *Ch.* (*Priskites*) exceeded that of *Tiramnia*, *Donispirifer*, *Parachoristites*, *Brachythyrina*, and *Phricodothyris*. This assemblage also included the rarer genera *Crenispirifer* and *Laioporella*.

The subsequent late Moscovian stage in spiriferid evolution in Eastern Europe coincides with an ecological optimum, marked by a substantial sea-level rise, widespread transgression across epicontinental basins (Montañez et al., 2018). As a result, only a small part of the earlier spiriferid brachiopods assemblage disappeared at the onset of this stage, including the last coarse-ribbed *Alphachoristites*, which had been widespread during the Bashkirian. These were replaced – possibly as their descen-

dants – by the genus *Trautscholdites* Ustritski, 1967 (Ustritski, 1967). Typical *Ch.* (*Choristites*) of the *sowerbyi-mosquensis* group became widespread, and the subgenus *Ch.* (*Neochoristites*) emerged, alongside the appearance of new genera such as *Sergospirifer* Ivanova, 1975, *Larispirifer* Enokjan et al., 1986 (Enokjan et al., 1986), and *Alispiriferella* Waterhouse & Waddington, 1982 (Waterhouse, Waddington, 1982). The genus *Tegulispirifer* Poletaev, 2000 also became prominent, completing the assemblage. Most genera that emerged during this interval continued to persist not only through the late Moscovian, but also into the late Pennsylvanian and even the Permian.

The next stage in the evolution of Carboniferous spiriferides roughly corresponds to the beginning of the Kasimovian Age of the Late Pennsylvanian and is marked by the disappearance of the genera *Sergospirifer* and *Donispirifer*, which were characteristic of the late Middle Carboniferous in Eastern Europe. Simultaneously, new genera emerged that shaped the composition of the spiriferides assemblage not only in the late Pennsylvanian of the Eastern European basins but also in the early Permian.

Among the martiniids, the last Carboniferous representatives of the family Purdonellidae appear – namely, the genus *Eliva* Fredericks, 1924 (Fredericks, 1924). Among the spiriferids, the earliest representatives of the family Neospiriferidae Waterhouse, 2004 emerged, including the genera *Cartorhium* Cooper & Grant, 1976 (Cooper, Grant, 1976) and *Betaneospirifer* Gatinaud, 1949 (Gatinaud, 1949). The genus *Paeckelmanella* Licharew, 1934 (Licharew, 1934) became widespread during this time, and within the 'porous' spiriferids of the superfamily Pennospiriferinoidea, notable genera such as *Callispirina* Cooper & Muir-Wood, 1951 (Cooper, Muir-Wood, 1951) and *Gjelispinifera* Ivanova, 1975 appeared.

Ecologically, the humid climate of the Moscovian gradually transitioned to arid conditions during the Late Pennsylvanian. Although the extent of epicontinental basins diminished, the composition of the spiriferides assemblage remained largely unchanged. At the onset of the Gzhelian, only the genus *Choristitella* disappeared. The assemblage at this time was dominated by the final species of *Choristites* of the subgenus *Ch.* (*Neochoristites*), along with *Trautscholdites*, new species of *Parachoristites*, and large representatives of *Jilinmartinia* and *Elinoria*. These genera not only defined the character of the Late Carboniferous spiriferid brachiopods association, but also crossed the Permian boundary in their stratigraphic distribution – except for *Choristites*.

This final boundary coincides with the beginning of the Permian period and is associated with continued environmental shifts driven by the final stages of Gondwana's formation, the onset of a major glaciation, and the regression of most epicontinental seas. Exceptions include the northeastern margin of the Russian Platform and Timan, where carbonate sedimentation of the Cisuralian Permian continued. As a result, many genera of martiniids, spiriferids (including neospiriferids and spiriferellids), as well as paeckelmanellids, some reticulariids, and pennospiriferinids, not only survived this transition but flourished. Nevertheless, across much of Eastern Europe, environmental stress in the early Permian triggered a significant and abrupt decline in benthic biota, including many brachiopod genera. The final representatives of the Pennsylvanian genera *Choristites*, *Brachythyrina*, *Larispirifer*, *Gjelispinifera*, *Laioporella*, and *Avisyrinx* disappeared, although some species of *Parachoristites* and possibly *Trautscholdites* persisted. Several genera from the superfamilies Reticularioidea and Pennospiriferinoidea also crossed this boundary and became part of the early Permian spiriferides assemblage, signaling the beginning of a new evolutionary stage for this group.

Conclusions

The results of the author's comprehensive revision of the Carboniferous spiriferides nomenclature of Eastern Europe and the review of the historical development of this order of brachiopods allow the following conclusions to be drawn:

1. The evolution of spiriferides assemblages is a stepwise, intermittently progressive process, which can be understood at three distinct levels:
   - Macro-level: General evolutionary trends in morphological, and physiological traits among representatives of the Spiriferida and Spiriferidina;
   - Meso-level: Uneven, stepwise changes in the composition of orictocenoses at the superfamily, family and genus level;
   - Micro-level: Phylogenetic sequences within individual genera.
2. Key features of higher-level evolutionary trends in Carboniferous spiriferides include:
   a) A shift in the mode of shell attachment to the substrate – from the Devonian's flexible pedicle to the development and eventual replacement by multiple byssus filaments, particularly in the Spiriferidae and Paeckelmanellidae;

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b) A gradual contraction in the area of development of the genetic system, accompanied by the evolution and increasing complexity of the vascular system – from pinnate to reticulate and saccate forms within Angiospiriferidae, from the Visean through to the early Permian.

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Встановлено та проаналізовано дванадцять часових інтервалів, протягом яких відбувалися зміни у родовому складі карбонових угруповань Spiriferida та Spiriferinida в межах палеобасейнів Східної Європи. Як найважливіші рівні змін виділено інтервали на границі девону і карбону, у середині турне і середині візе, поблизу границь міссісіпію і пенсильванію, башкирського і московського, низів касимовського ярусів, а також границі карбону і пермі. Вказано на зміну літологічних умов проживання як причину морфологічної еволюції системи прикріплення у представників надродин Spiriferoidea, Paeckelmanelloidea та Brachythyridoidea після Гангенберзької кризи. Підкреслено значення еволюції судинної системи представників родини Angiospiriferidae Legrand-Blain, 1985 для виникнення підродин Chorisitinae Waterhouse, 1968 та Brachythyrininae Waterhouse, 2004 наприкінці міссісіпію. Обговорюється масштаб швидкості зміни родового складу спіриферид (брахіоподи) карбону.

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