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Palaeobiogeography and diversification of Tournaisian–Viséan bryozoans (lower–middle Mississippian, Carboniferous) from Eurasia

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ABSTRACT

The Mississippian represented the last diversification event of bryozoans in the Palaeozoic which affected all taxonomic levels. Within the borders of modern Eurasia Tournaisian–Viséan bryozoans are known from 24 areas, with a total of 878 species in 180 genera. Palaeobiogeographical analysis is here made according to the stages and substages of the Tournaisian and Viséan. Six characteristic species were identified for the lower Tournaisian which are distributed in more than one region of the continent, and for the upper Tournaisian there are two such species. Eleven species occur in the narrow stratigraphic interval of the lower Viséan that display a wide geographic distribution within Eurasia, in the upper Viséan there are 14 such species. Analysis of the generic composition showed the closest similarity between Tournaisian bryozoans of Kazakhstan, the Kuznetsk Basin and Eastern Transbaikalia. Significant similarity in the generic composition of Germany, Britain, Ireland and France is observed during the Viséan. Two centres of radiation bryozoans were identified: «Eastern» and «Western».

1. Introduction

Bryozoans are benthic organisms playing important role in marine ecosystems from the Ordovician to the recent. Evolution of the phylum Bryozoa displays several significant diversification and succeeding extinction events, one falling in the Frasnian/Viséan interval. Rise in generic diversity is observed from the end of the Famennian reaching a maximum at the end of Viséan and followed by extinction of several taxa in the Serpukhovian (Ernst, 2013). During Famennian–Viséan ages bryozoans experienced crucial changes in their taxonomic composition (e.g., the rapid appearance of new families and suborders; extinction of Devonian genera and families; change of dominant order). The Mississippian represented the last diversification event of bryozoans in the Palaeozoic.

An analysis of the diversity of orders of Palaeozoic bryozoans, including those from the Carboniferous, was made by Gorjunova et al. (2004). They came to the conclusion that the diversity depends on the developmental phase of the higher taxon (bloom, decline, extinction or origination) under secondary influence of abiotic factors.

General biogeographical analyses have been provided for most of the Palaeozoic. Naimark et al. (1999) suggested that faunal radiations across different regions occurred diachronously, and that endemic species developed in areas that promoted bryozoan habitats rather than in isolated basins. Buttler et al. (2013) have reported on Early Palaeozoic biogeography, and Ross (1982) and Ross and Ross (1985) provided a summary of Late Palaeozoic (Carboniferous–Permian) biogeography, while Ross and Ross (1982) discussed factors that influenced faunal distributional patterns. At the level of the geological period, a number of overviews of bryozoan biogeography throughout the Palaeozoic have been documented either globally or from a more restricted viewpoint geographically or temporally: Ordovician (Ross, 1982; Tuckey, 1990a), Silurian (Tuckey, 1990b; McCoy and Anstey, 2010), Devonian (Bigey, 1985; Tolokonnikova and Ernst, 2010), Carboniferous (discussed below), and Permian (Ross, 1978, 1979; Gilmour and Morozova, 1999).

The first overview of the palaeobiogeography of Carboniferous bryozoans was made by Ross (1981). She analysed generic diversity for 11 regions of the world according to stages of the Carboniferous and discussed changes in the composition of families and orders. Ross reasoned for continuity between Devonian, Carboniferous and Permian bryozoans, and inferred bryozoan diversification and radiation during the Viséan, which was apparently induced by such abiotic factors as fluctuating sea-levels driven by glaciations in Gondwana, and the loss of shallow-water environments due to the closure of the ocean between Euramerica and Gondwana (Ross, 1982). During the Late Carboniferous an increased number of new ecological niches developed due to a gradual warming of the climate that resulted in the origination of some new bryozoan lineages and a pronounced provincialism (Ross and Ross, 1985). However, the second half of the Carboniferous is generally marked by a reduction in taxonomic diversity (Ross, 1981). McKinney

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(1993) documented the distribution of the distinctive fenestrate *Archimedes* from the Carboniferous of North America and argued that changes in its life-history during that period resulted in a change in its distribution from shallow water shelf areas during the early Carboniferous to deeper basinal facies towards the end of the Carboniferous.

On account of their richness and abundance in marine deposits, it has been recognised that bryozoans have a considerable potential for use in stratigraphy (e.g., Nekhoroshev, 1925; Bancroft, 1987). Their wide distribution is ensured by passive dispersion of larvae with current system or floating objects (for example, seaweeds, pumice). As all living organisms, development and diversity of bryozoans depend on abiotic and biotic factors. The most limiting ones for the development of the colonies of modern bryozoans are water temperature, salinity, food supply, substrate and predation (Taylor and Larwood, 1990). It can be inferred that the same factors had similar effects on bryozoans during the Mississippian.

During the last few decades a considerable volume of new data on Carboniferous bryozoans has been obtained for Eurasia (e.g., Yang et al., 1988; Wyse Jackson, 1996; Ernst, 2005), while for other continents such data are scarce. During this time, bryozoan taxonomy has been revised significantly and new information on bryozoan distributions have been obtained. For other continents such as North America a number of monographic and other taxonomic studies have appeared (Snyder, 1991a,b; Gilmour and McColloch, 1995) but studies carried out in the late 1890s and first half of the twentieth century require reassessment. Furthermore, understanding of the stratigraphical framework for some regions in Eurasia has been improved. This increase in data has permitted this new compilation to document in considerable detail the palaeobiogeography of bryozoans of Eurasia during Tournaisian–Viséan time which was an important stage in the development of the phylum Bryozoa.

2. Geological setting

According to the International Stratigraphic Time, the Tournaisian and Viséan belong to the Mississippian — the lower part of the Carboniferous system (Cohen et al., 2013). The lower limit of the Tournaisian is dated as 358.9 ± 0.4 Ma, and the Viséan ranges from 346.7 ± 0.4 Ma to 330.9 ± 0.2 Ma; the duration of the Tournaisian is 12.2 Ma and of the Viséan 15.8 Ma.

The territory of modern Eurasia is built up of many continental blocks and oceanic depressions, which were situated in different hemispheres during the Mississippian (Stampfli et al., 2013). The northern part of Eurasia belonged to Laurasia, and the southern part to Gondwana. According to existing palaeogeographical reconstructions, continuous climatic cooling and aggregation of the terrains of Laurasia occurred at the beginning of the Carboniferous (Scotese, 2001).

3. Materials and methods

Within the area of modern Eurasia, bryozoans of Tournaisian–Viséan age are known from 24 areas. Tournaisian bryozoans have been reported from Germany, Ireland, Poland, the Donetsk Basin, Nakhichevan (or Transcaucasia in text below), Kazakhstan, Russia (Southern Urals, Eastern Transbaikalia, Kurgan area, Russian Platform, Kuznetsk Basin), Mongolia and China. Viséan bryozoans are known from Ireland, Germany, Britain, Spain, France, the Donetsk Basin, Poland, Russia (Middle and Northern Urals, Eastern Transbaikalia, Kurgan area, Russian Platform, Kuznetsk Basin, Northeast), Afghanistan, Uzbekistan, Iran, Turkmenistan, Kazakhstan, Mongolia, China and Japan.

The current levels of information on the bryozoan faunas from these territories are disproportional. Successive following one another complexes were described from the lower Tournaisian–upper Viséan deposits of Kazakhstan, Mongolia, Eastern Transbaikalia and the Kuznetsk Basin (Nikiforova, 1948, 1950; Nekhoroshev, 1953, 1956; Trizna, 1958; Plamenskaya, 1964; Troitzkaya, 1975; Plamenskaya, 1983; Gorjunova, 1985; Popeko, 2000; Ariunchimeg, 2010). This has allowed regional correlation between these areas and the establishment of biostratigraphical units (beds with bryozoans) for Mongolia and bryozoans zones for Eastern Transbaikalia which are utilized for local correlation (Popeko, 2000; Ariunchimeg, 2010).

On other regions bryozoans have been described from segmental stratigraphical levels, and this has resulted in difficulties in their analysis and interregional correlation on the coeval deposits. The scheme of the Mississippian deposits of Eurasia is shown in Table 1. Asterisks mark levels for which the exact temporal distribution of the bryozoans is unknown, or bryozoan records are associated with certain biostratigraphical zones. Grey shadowing marks intervals from which bryozoans are unknown.

In the lower–middle Mississippian deposits of Eurasia records of 878 species belonging to 180 genera have been databased for this study. They represent 41 families in 4 orders (Table 2). Unfortunately, no detailed information about the stratigraphical distributions of the majority of species is known. For many species, the range covers a stage or even two. Therefore, it was only possible to use the following intervals for palaeobiogeographical comparisons: lower Tournaisian, upper Tournaisian, undivided Tournaisian, lower Viséan, upper Viséan, and undivided Viséan.

Palaeobiogeographical analysis was carried out using an unweighted pair-group average method (UPGMA) in which clusters are joined based on the average distance between all members in the two groups (Hammer et al., 2001). Similarity was measured using the Jaccard similarity coefficient for absence–presence data (Jaccard, 1901). This coefficient measures similarity between sample sets, and is defined as the size of the intersection divided by the size of the union of the sample sets. Cluster analysis was performed using PAST software version 1.97 (Hammer et al., 2001). Palaeogeographical distribution of bryozoan genera was shown using of Principal Coordinates analysis performed in PAST. Only species with adequate taxonomic description were utilized for the analysis, whereas those species with inadequate descriptions, without illustrations or originally left in open nomenclature were ignored.

4. Palaeobiogeography of Tournaisian bryozoans

At the end of the Famennian, bryozoans show intensive diversification at the species and genus levels (Tolokonnikova and Ernst, 2010; Ernst, 2013). A significant number of taxa which appeared at the end of the Devonian continued their existence or even flourished in the Early Carboniferous. The Devonian/Carboniferous boundary is marked by an increase in extinction rates of bryozoans (Ernst, 2013). In the Early Carboniferous bryozoans showed a marked increase in morphological specialization, especially among members of the orders Fenestrata and Cryptostomata. A similar trend is also observed in the brachiopods. The Strunian (latest Famennian) brachiopods have a characteristic aspect of a transitional fauna consisting of a minority of Devonian to prevalent Carboniferous forms (Conil et al., 1986). Analyses of brachiopod fauna from southern China reveal that after a decline in the generic diversity at the Devonian–Carboniferous boundary, the Early Tournaisian fauna shows slight impoverishment (Sun and Baliński, 2011). In the middle Tournaisian brachiopods experienced an explosive increase in diversity at the generic level. The brachiopods constitute a fully recovered high diversity fauna consisting of forms representing a wide spectrum of attachment strategies as well as highly specialised forms adapted to special kinds of ecological niches. Shen et al. (2006) in an analysis of brachiopod diversity of the same region suggest that this recovery occurred slightly later during the Serpukhovian. Similar patterns of diversification in the Mississippian have been noted in Argentina where the number of bivalve genera doubled between the Early and Late Carboniferous while brachiopods have shown a more than six-fold increase in generic diversity (Sterren and Cisterna, 2010). With regard to crinoids, 69 genera are known in the