Morphological Evolution of Eurasian Bryozoans during Famennian–Tournaisian

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Received February 13, 2020; revised February 28, 2020; accepted February 28, 2020

Abstract—The main trends in the morphological evolution of bryozoans at the Devonian-Carboniferous boundary were established when studying the Late Devonian—Early Mississippian bryozoans of Eurasia. The diversity of vertical colonies increased from Early Famennian to Late Tournaisian. An increase in their strength occurred by growth of the exozonal skeleton due to the growth of vesicular tissue in cystoporates, thickening of the autozooidal walls in trepostomates, complication of polymorphism in cryptostomates, and thickening of the branches in fenestrates. The most rapid evolutionary changes were observed in rhabdomesine bryozoans of the order Cryptostomata, expressed in the change of the spiral arrangement of autozooids to complex one and a high diversity of heterozooids and styles. The development of keels, nodes, superstructures, acanthostyles, and spines in bryozoans provide protection from predators.

Keywords: Bryozoa, evolution, morphology, Devonian, Mississippian, Eurasia **DOI:** 10.1134/S0031030121010147

INTRODUCTION

From the Ordovician to the present, bryozoans have been widespread worldwide in different aquatic biotopes (Boardman et al., 1983; Hu and Spjeldnaes, 1991; Ma et al., 2015; McKinney and Jackson, 1989). The modular organization of bryozoans and a high degree of adaptation to various habitat environments are considered probable reasons for their long existence (Ernst, 2019; Gorjunova, 1985; Gorjunova et al., 2004). The morphological evolution of these colonial organisms is determined by complex interactions of diverse factors. Among the internal factors are the presence of individual groups at a specific phase of evolutionary development (extensive divergence, acme, degradation or the relict phase) and the way of implementing one or another evolutionary path (aromorphosis, divergence, homeomorphism, and parallelisms) (Gorjunova et al., 2004; Morozova, 2001). On the other hand, the existing constructive morphologies (wall structure, development or absence of heterozooids) were obviously important (Ernst, 2013a, 2013b). The external factors are global processes (transgression-regression, tectonic activity, climate change, etc.), as well as biota interference (competition between bryozoans of different taxonomic orders, competition with other benthic groups, and the influence of predators) (Ernst, 2013a, 2013b). Besides, it is necessary to consider the local factors, such as water temperature and salinity, depth, and substrate characters (Hageman et al., 1998; McKinney and Jackson, 1989; Nelson et al., 1988; Tolokonnikova and Ernst, 2017). The integrated effect of environmental conditions significantly influenced the shape and structure of colonies and caused the appearance or disappearance of specific structural elements.

The purpose of this work is to analyze the morphological changes in bryozoans over 25.5 Ma from the Early Famennian to the Late Tournaisian. The choice of a specific time interval is due to the importance of the organisms under consideration in the evolution.

The process of replacement of Early Paleozoic bryozoan assemblages by Late Paleozoic ones was terminated at the Devonian–Carboniferous boundary; various internal structures appeared and became common in the Carboniferous–Permian genera. Due to the limited information on the findings of Late Devonian-Early Carboniferous bryozoans on other continents, we have only taken data from Eurasia into account.

MATERIAL AND METHODS

The database compiled by the author has served as the factual basis for the analysis of the morphological changes of bryozoans, widespread in the Famennian— Tournaisian deposits of Eurasia. This database includes (1) the data from all available literature sources, (2) data on material redescribed by the author