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Research paper

New observations on the skeletons of the earliest bryozoans from the Fenhsiang Formation (Tremadocian, Lower Ordovician), Yichang, China

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Abstract

The earliest unequivocal bryozoans occurred in the Fenhsiang Formation (upper Tremadocian, Lower Ordovician) of Yichang, South China, providing important clues about the early evolution of primitive bryozoans. In this study, SEM and EDAX were used to analyze the microstructure of the walls of two bryozoan genera, *Nekhorosheviella* and *Orbiramus*, from the Fenhsiang Formation. All walls of *Nekhorosheviella* and endozonal walls of *Orbiramus* show poor preservation in thin sections, with a granular appearance reflecting extensive neomorphism, whereas exozonal walls of *Orbiramus* are distinctly laminated. These preservational differences may reflect skeletal chemistry, particularly the magnesium content of the calcite. Phosphatic skeletal linings were found to be distributed unevenly in the autozooecia of *Nekhorosheviella*, but were absent in *Orbiramus*.

Keywords: Bryozoa; Fenhsiang Formation; *Nekhorosheviella*; *Orbiramu*; Phosphatic skeleton

1. Introduction

The early fossil record of bryozoans is poorly known. There have been several claims of fossil bryozoans in the Cambrian, but none have survived a close scrutiny. These include most recently described *Pywackia baileyi* Landing in Landing et al., 2010, a phosphatic/phosphatized fossil from the Upper Cambrian of Mexico, which is most probably an octocoral (Taylor et al., 2013). Indisputable bryozoans first appear in the deposits of Early Ordovician age, with all of the orders present by the Middle Ordovician in the Palaeozoic (Taylor and Ernst, 2004). Although yet to be quantified, this taxonomic diversification is paralleled by the evolution of considerable morphological disparity, such that either bryozoans radiated explosively within a short interval of geological time during the Ordovician, or they have a long, 'cryptic' evolutionary history yet to be uncovered.

Almost 130 years ago, 'mural pores', later shown to be 'phosphatic spheroliths' (Oakley, 1934), were reported in the cystoporate bryozoan *Favositella interpuncta* from the Silurian Wenlock Limestone of Dudley (Etheridge and Foord, 1884). Subsequently, diverse types of phosphatic spheroliths and phosphatic skeletal linings have been reported in different Palaeozoic stenolaemates, including Trepostomata, Cystoporata, and Cryptostomata. According to Conti and Serpagli (1988), phosphate in bryozoans provides evidence for bimineralic skeletons in response to particular environmental conditions.

The earliest unquestionable bryozoans, *Nekhorosheviella* and *Orbiramus*, come from the Fenhsiang Formation (upper Tremadocian, Lower Ordovician) of Yichang, South China (Xia et al., 2007), and form the oldest bryozoan reefs (Adachi et al., 2012; Cuffey et al., 2013). Recent studies have shown that diverse phosphatic microproblematica (such as *Fenhsiangia* Long and Burrett, 1989) and the black coral *Sinopathes* Baliński, Sun and Dzik, 2012 occurred in the deposits in which *Nekhorosheviella* and *Orbiramus* were found. In this study, we describe the presence of phosphatic material in the skeletons of

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the earliest bryozoans and interpret its origin and significance for early bryozoan evolution.

2. Materials and methods

The specimens studied here came from the Fenhsiang Formation, *Nekhoroshevielle nodulifera* from the Daping section, and *Orbiramus* sp. from the Chenjiahe section, both in Yichang City, Hubei Province, China. Detailed descriptions of the Fenhsiang Formation can be found in Xia et al. (2007) and Zhang et al. (2009).

For scanning electron microscopy (SEM) and energy dispersive analysis X-ray (EDAX) studies, the bryozoans were embedded in epoxy resin and cut transversely and longitudinally, polished, etched in dilute (5%) acetic acid for several seconds and air-dried. Uncoated etched sections were observed using a LEO 1455-VP scanning electron microscope operating under low vacuum and with a back-scattered electron (BSE) detector. Because the emission that was detected using BSE reflects molecular weight, areas of different composition have different levels of brightness. Compositional analyses were undertaken using an EDX system attached to the same microscope. This enabled spot analyses and mapping of elemental distributions across the sections.

3. Systematic description

Class Stenolaemata Borg, 1926
Order Trepostomata Ulrich, 1882
Suborder Esthonioporina Astrova, 1978
Family Orbiporidae Astrova, 1978

Genus *Nekhorosheviella* Modzalevskaya, 1953

Type species: *Nekhorosheviella cribrosa* Modzalevskaya, 1953, Vazalemmask beds (D3), Middle Ordovician, Vazalemmask, Estonia.
Diagnosis: Colonies irregularly massive, some with thick, irregular branches; maculae with clusters of macrozooecia. Autozooecia not differentiated into endozone and exozone. Apertures irregularly polygonal, arranged irregularly, walls granular or poorly laminated; boundaries merged. Diaphragms numerous, complete, straight or curved, closely spaced, regular or irregular. Mesopores lacking. Two kinds of exozonal styles: larger styles in autozooecial corners, and smaller styles closely and evenly spaced centred on autozooecial boundaries.
Geologic age and geographic distribution: Late Tremadocian, Early Ordovician, China; late Middle and Late Ordovician, Estonia.

Nekhorosheviella nodulifera Xia, Zhang and Wang, 2007
(Figs. 1 and 2)

Description: Zoaria irregularly nodular or massive, the studied specimen 8 mm high by 9 mm wide, consisting of three growth bands, each band 2–3 mm in thickness. No clear differentiation between exozone and endozone.

Autozooecia bud throughout the colony. Zooecial walls homogenous and indistinctly granular, about 0.02 mm thick with merged boundaries. Diaphragms numerous, straight or slightly curved, spaced 0.02–0.06 mm apart throughout the chambers. Autozooecial apertures subcircular, rounded or irregularly polygonal, and often slightly petaloid due to indentation by styles, 0.10–0.15 by 0.15–0.20 mm in diameter. Styles, numerous, 0.02–0.06 mm in width.
Phosphatic mineralization: Bright outer layers of zooecial walls evident in BSE images of polished sections were shown to be rich in phosphorus using EDX (Fig. 2). These layers correspond to the phosphatic linings described by Conti and Serpagli (1988). Even in the same section, such phosphatic linings are variably developed, more complete examples covering the basal diaphragms and the interzooidal walls, but other examples present only at the bottoms of the autozooecia. Thickness also varies, from <1 μm to almost 20 μm.
Remarks: *N. nodulifera* differs from the type species *Nekhorosheviella cribrosa* in lacking distinct smaller styles and having petaloid autozooecial apertures in tangential section. In addition, autozooecial walls are merged at their boundaries in *N. nodulifera*.
Locality: Daping village, Fenxiang town, Yichang, Hubei. Stored in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, NIGPAS154832.
Occurrence: Fenhsiang Formation, upper Tremadocian, Lower Ordovician.

Genus *Orbiramus* Xia, Zhang and Wang, 2007

Type species: *Orbiramus normalis* Xia, Zhang and Wang, 2007, Fenhsiang Formation, upper Tremadocian, middle Lower Ordovician, Yichang, China.
Diagnosis: Zoaria ramose, often branching dichotomously. Autozooecial apertures subcircular, oval, often petaloid due to indentation by large styles. Mesozooecia and exilazooecia lacking. Exozone and endozone differentiated in autozooecia. Zooecial wall granular in endozone, and distinctly inclined fibrous or lamellate in exozone. Styles developed, situated within walls, often indented apertures giving petaloid appearance. Diaphragms occur at endozone/exozone boundary and in exozone. Lower Tremadocian–Floian, Lower Ordovician, China.
Geologic age and geographic distribution: Late Tremadocian and Floian, Early Ordovician, Hubei and Anhui, China.

Orbiramus sp.
(Fig. 3A–D)

Description: Zoaria ramose, possessing irregularly bifurcating branches, 3 mm in diameter on average. Neither monticules nor maculae are visible on zoarial surfaces.

Autozooecia bud from the axial part of colony, diverge and make an angle of less than 90° with the colony surface. Autozooecial wall thickening in the exozone results in endozone and exozone being conspicuously differentiated; endozonal walls granular or indistinctly fibrous, on average 0.02 mm thick; exozonal walls distinctly lamellar, 0.18 mm thick on average.