A new Byronia species from the Late Ordovician of Estonia

Olev Vinn^a, Kalle Kirsimäe^a, Luke A. Parry^b and Ursula Toom^c

^a Department of Geology, University of Tartu, Ravila 14A, 50411 Tartu, Estonia; olev.vinn@ut.ee, kalle.kirsimae@ut.ee

^b Department of Earth Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK; lp13932@bristol.ac.uk

^c Institute of Geology, Tallinn University of Technology, Ehitajate tee 5, 19086 Tallinn, Estonia; ursula.toom@ttu.ee

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Abstract. A new species of a possible thecate scyphozoan *Byronia jaegeri* sp. nov. is described from the late Katian of Estonia. This new taxon is distinct as it lacks the longitudinal ornamentation present in other *Byronia* species. *Phosphanullus* is a phosphatic attachment disk, which has been considered to be a junior synonym of *Byronia*. We report qualitative energy dispersive analysis and scanning electron microscopy of the composition of *B. jaegeri*, demonstrating that the tube is organic in composition and has a lamellar microstructure. The compositional differences of *Phosphanullus* and *Byronia* do not support their synonymy. It is likely that *Phosphanullus* belongs to a closely related but distinct phosphatic group of thecate scyphozoans, due to their morphological similarity, but differing composition.

Key words: Cnidaria, Scyphozoa, microstructure, tube composition, Ordovician, Baltica.

INTRODUCTION

Byroniids are an order of tube-shaped fossils that have a stratigraphic range from the Cambrian to Permian (Bischoff 1989). Their composition is believed to be variable, with both phosphatic and organic tubes included within the group (Bischoff 1989). Tubes of byroniids were attached to the substrate by a small disk-shaped holdfast (generally 0.1 to 0.8 mm in diameter, Holmer 2004). The phosphatic attachment disks are known as Phosphanullus Müller, Nogami & Lenz 1974, but this genus has been considered to be a junior synonym of Byronia Matthew (Bischoff 1989). Phosphatic attachment discs that can be assigned to 'Phosphanullus' have been described from the Ordovician of Estonia (Öpik 1930). Öpik (1930, p. 31, fig. 11, pl. 5.2) illustrated and described the occurrence of numerous attachment discs presumably belonging to Byronia universalis from the Kukruse Regional Stage (Sandbian) in northern Estonia (Holmer 2004). In the Kukruse Regional Stage, numerous B. universalis discs and tubes were found attached to dorsal valves of the discinid brachiopod Schizotreta, but identical attached phospahtic discs have also been reported occurring on trilobites and other types of brachiopods from the same stratigraphic level in northern Estonia (Öpik 1930; Holmer 2004).

Byronia is a cosmopolitan genus known from North America, Europe, Australia and Antarctica (Wrona 2004). Byroniids have been affiliated with various animal groups but most commonly referred to some kind of tube-forming worms (Holmer 2004). Bischoff (1989) analysed

the phylogenetic affinities of byroniids in detail and came to a conclusion that the tube and attachment disks of byroniids are most similar to the attached thecae of the polypoid stage of coronate scyphozoans. Byronida has recently been considered as an entirely extinct order of thecate scyphozoans (Bischoff 1989; Holmer 2004; Wrona 2004; van Iten et al. 2014;). The earliest thecate medusozoan polyps, including conulariid-like small shelly fossils, Byronia, Hyolithellus and Sphenothallus are known from the strata of Terreneuvian age (e.g. Zhu et al. 2000; van Iten et al. 2010, 2014). Tubes that are similar to the Phanerozoic thecate medusoids are also known from the Ediacaran of Brazil (Corumbella and a possible conulariid), making them a rare instance of a group that is known from both sides of the Ediacaran-Cambrian boundary (van Iten et al. 2014).

The aim of the paper is to (1) describe the new species of *Byronia* and (2) discuss the tube composition and microstructure of *Byronia*.

GEOLOGICAL BACKGROUND

The Ordovician sequence of Estonia is relatively complete, but compressed. It is represented mostly by carbonate rocks except for the terrigenous Lower Ordovician part of the sequence. A shallow epicontinental sea covered the area of modern Estonia (Fig. 1) in the Late Ordovician. Limestones are the most common rocks in the Late Ordovician of Estonia. They are exposed in northern Estonia, forming a wide belt from the Narva

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River in the east to Hiiumaa Island in the west (Nestor & Einasto 1997). During the Ordovician Baltica drifted from the southern high latitudes to the tropical realm (Torsvik et al. 2012), which caused a drastic climatic change on the palaeocontinent. The climatic changes resulted in an increased sedimentation rate of carbonates. Finally, deposits that are characteristic of an arid and tropical climate appeared in the Estonian Late Ordovician sequence (Nestor & Einasto 1997). These types of tropical deposits were lacking in the Early and Middle Ordovician when Baltica was situated in a temperate climate zone (Jaanusson 1973). The appearance of stromatoporoids, tabulate corals and reefs marked the warming of the climate in the early Katian. These fossil groups and reefs became prevalent in the Hirnantian (Nestor & Einasto 1997).

MATERIALS AND METHODS

Two *Byronia* tubes were collected by Dr Jaak Nõlvak from the Pirgu Regional Stage (upper Katian) of the Pärnu-6 and Laeva-18 drill cores (Fig. 1). Small pieces were removed from one tube for scanning electron microscopy (SEM). The SEM imaging and analysis of samples was performed on a variable pressure Zeiss EVO MA15 SEM equipped with the Oxford X-MAX energy dispersive detector (EDS) system and Aztec Energy software for element analysis. The outer surface of the tubes and freshly broken pieces perpendicular to tube wall bedding were studied in uncoated and coated state, with the coated samples prepared by depositing a 5 nm thick Pt conductive layer using a Leica EM SCD 500 high-resolution sputter.

SYSTEMATIC PALAEONTOLOGY

Phylum CNIDARIA? Class, Order and Family uncertain Genus *Byronia* Matthew, 1899

Type species. Byronia annulata Matthew, 1899.

Byronia jaegeri sp. nov. Figures 2A–F, 3

Holotype. Almost complete tube GIT 494-25.

Paratype. Partially preserved tube GIT 494-17.

Type horizon. Pirgu Regional Stage, upper Katian.



Fig. 2. *Byronia jaegeri* sp. nov. tubes from the Pirgu Regional Stage, upper Katian of Estonia. **A**, GIT 494-25, general view, Pärnu drill core; **B**, GIT 494-25, detailed view of perpendicular ornamentation; **C**, GIT 494-17, general view, Laeva drill core; **D**, GIT 494-25, detailed view of perpendicular ornamentation; **E**, GIT 494-25, longitudinal section showing lamellar microstructure; **F**, GIT 494-25, transverse section showing lamellar microstructure.



Fig. 3. Composition of Byronia jaegeri sp. nov. tubes. Cps, counts per second.

Type locality. Pärnu-6 drill core.

Derivation of name. In honour of Dr Manfred Jäger (Rosenfeld, Germany) for his contribution to knowledge of taxonomy and ecology of various tubeworms.

Diagnosis. Tubes completely covered with well-developed and regular perpendicular annulation without any longitudinal ornament. Annuli have the shape of rounded symmetrical curves in longitudinal section. Tubes have organic composition and lamellar microstructure.

Material. One complete and one partially preserved tube.

Description. Black coloured gently curved tubes with a very low rate ($\sim 5^{\circ}$) of apertural expansion. Tubes are completely covered by well-developed and relatively regular perpendicular annulation. Annuli lack sharp edges. They have the shape of rounded symmetrical waves in longitudinal section. The development of annuli varies even within close distance. In general the annuli are larger and better developed near the aperture than at the beginning of the tube. There are 15 to 17 annuli per 1 mm near the tubes aperture. Annular crests are not usually much thinner than the interspaces between the annular crests. The interspaces between annular crests are slightly concave. The tube surface is smooth between the annuli and devoid of any microrelief. The tube wall is thin, 20 µm thick between the annuli and up to 45 µm thick at the annular crests. Tube thickness does not increase notably towards the aperture. The tube wall is composed of thin lamellae of various thickness (5–10 μ m). The lamellae are continuous through the annuli. Tube ultrastructure is homogeneous as observed by SEM. Tubes are not mineralized and have a completely organic composition.

Remarks. The new species is most similar to *B. mirrabookaensis* Bischoff, 1989, especially in its annular crests, but differs distinctly from the Australian species *B. mirrabookaensis* in having a smaller number of annular crests per 1 mm and a larger tube. The new species differs from *B. universalis* in the organic composition of the tube and much better developed perpendicular ornamentation (Holmer 2004, p. 220, fig. 22.3C). The new species also resembles *B. annulata* Matthew, 1899 (see Howell 1962, p. W163, fig. 104-1-1; Kozlowski 1967, fig. 3B) but differs in the lack of fine longitudinal striae.

Stratigraphic distribution. Pirgu Regional Stage, upper Katian.

DISCUSSION

Preservation

The tubes of *Byronia jaegeri* are relatively well preserved, showing the original external ornamentation. Tube walls are almost completely compressed, with an

elliptical cross section, showing no signs of plastic deformations, which indicates that the wall was originally rather rigid. However, the lack of well-developed cracks in the tube wall indicates that it originally had certain degree of elasticity. Organic tubes of modern coronate scyphozoans exhibit similar properties to the described *Byronia* tubes. *Byronia* tubes most likely had circular to slightly elliptical cross sections, but the fossil material has been compressed due to burial and compaction.

Structure

The lamellar microstructure of the studied tubes presumably represents the original tube structure. It is possible that the laminae were better developed before the fossilization and that tube microstrucure has somewhat homogenized during diagenesis. It is likely that the laminae were deposited in direction from the exterior inwards, so that the laminae which deposited first form the external part of the tube. The homogeneous tube ultrastructure could be an artefact of the preservation as organic cuticles of various modern invertebrates often have fibrous ultrastructures. Sphenothallus is a phosphatic scyphozoan closely related to Byronia (van Iten et al. 2014) and possesses a similar tube which is also composed of thin lamellae (Vinn & Kirsimäe 2015). Muscente & Xiao (2015) concluded that pristine Sphenothallus tests consist of exteriorly sculptured and interiorly unsculptured organophosphatic lamellae. Conulariids are also phosphatic scyphozoans presumably related to Byronia and Sphenothallus (van Iten et al. 2014). In conulariids the periderm is composed of thin lamellae (van Iten 1991, 1992a, 1992b) and thus in this aspect resembles the theca of Byronia. Ford et al. (2016) found that the conulariid periderm is composed of extremely thin $(0.5-3 \mu m)$, variably distinct microlamellae that alternate from organic-poor to organicrich. These lamellae are slightly thinner than those in Byronia (5–10 µm), but still of comparable thickness.

Internal structures such as peridermal teeth are not visible due to the compression of the tubes. Such structures are present in extant coronate scyphozoans but are only known from fossil material where tubes are three-dimensionally preserved, such as in *Olivooides* (Dong et al. 2013).

Composition

Qualitative EDS elemental analysis of uncoated specimens does not allow us to determine the exact composition of the studied *Byronia* tubes, but the high content of C in the tube wall is indicative of an organic composition. The lack of phosphorus (below detection limit, <0.1 wt%) in the tube wall indicates a non-phosphatic composition of the tube wall (Fig. 3). According to Kozłowski (1967), Mierzejewska & Mierzejewski (1979) and Mierzejewski (1986), tubes of Byronia from the Ordovician of Baltica have an organic composition. This is well in accordance with our observations. The tubes have been compressed following deposition but preserve fine details of the perpendicular ornament, a smooth surface of the tube wall between the perpendicular ridges and lamellar microstructure. These observations support an originally organic tube composition, as diagenetic demineralization of the tube would result in a more porous tube microstructure. In contrast, the phosphatic tubes and attachment disks of Phosphanullus were most likely originally biomineralized as they are known from environments without indications of diagenetic phosphatization of fossils (Öpik 1930). The compositional differences of Phosphanullus and Byronia therefore do not support their synonymy. It is likely that Phosphanullus and Byronia represent closely related lineages of coronate scyphozoans, one with biomineralized tubes and the other with organic ones. Phosphatic tubes are also known in another closely related tubicolous cnidarian -Sphenothallus (Vinn & Kirsimäe 2015). Corumbella werneri from the Ediacaran of Brazil also possesses a lamellar fabric and presumably was organic in composition (e.g. Pacheco et al. 2015).

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Uus Byronia liik Eesti Hilis-Ordoviitsiumist

Olev Vinn, Kalle Kirsimäe, Luke A. Parry ja Ursula Toom

Uus *Byronia* liik *B. jaegeri* sp. nov. on kirjeldatud Eesti Hilis-Ordoviitsiumist. *B. jaegeri* sp. nov. koda on orgaanilise koostisega ja lamellilise ehitusega. Uuel liigil puudub pikisuunaline ornament, mille poolest ta erineb teistest *Byronia* liikidest. *Phosphanullus*'e ja *Byronia* koostise erinevus ei toeta nende perekondade sünonüümideks pidamist.