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First record of agglutinated worm tubes from the uppermost Cambrian of Estonia

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ABSTRACT:

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A new species of agglutinated tube, *Cryptosiphon oboloides* sp. nov., is described from the Furongian of Estonia. The agglutinated tubes are composed of pieces of lingulate shells that are placed to form an overall pattern. The studied agglutinated tube strongly resembles cases of modern caddisfly larvae, though we do not suggest any phylogenetic affinity to caddisflies. The tubes originally contained an organic inner lining with a sticky external surface that enabled worms to glue on shell fragments and sand grains. The relatively well-arranged grains in the tube wall suggest that the animal actively assisted in gluing the shell fragments, orienting, and finding the right place for them. It is possible that worms capable of building agglutinated tubes from shell material originated in Baltica and later dispersed to the Armorican Terrane Assemblage and other regions in the Early to Middle Ordovician.

Key words: Agglutinated tubes; polychaetes; brachiopods; sandstones; Furongian; Baltica.

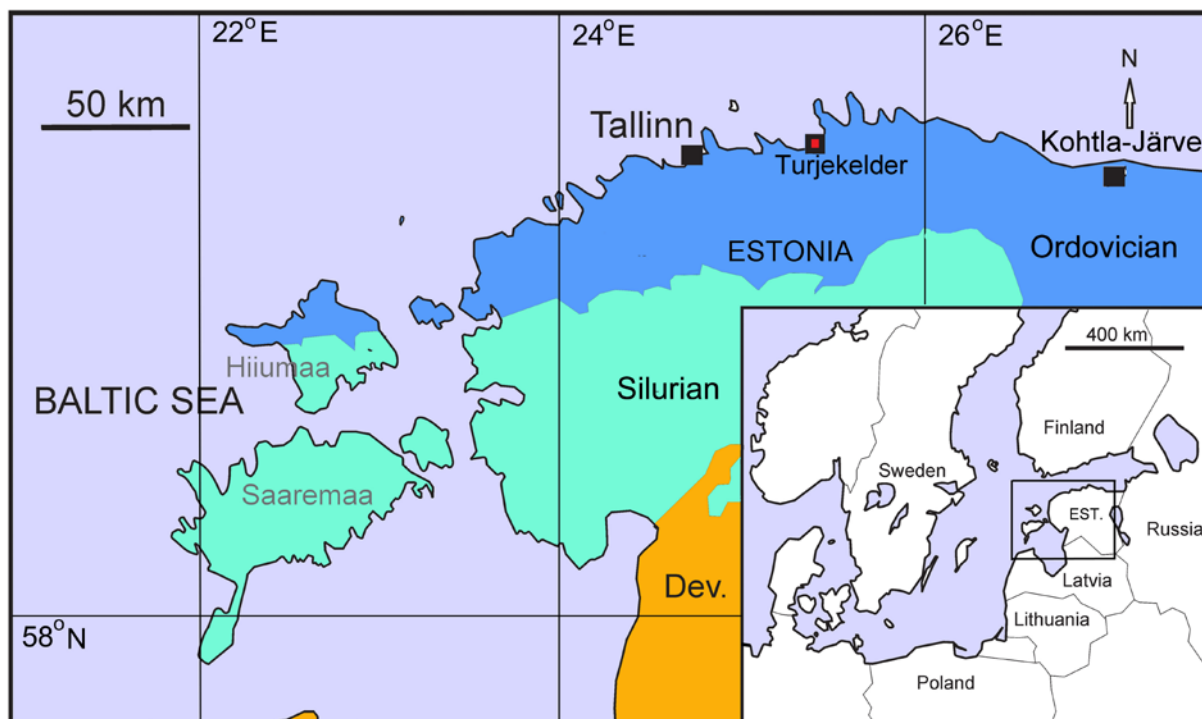
INTRODUCTION

Agglutinated tubes have a limited fossil record, despite being produced by several modern polychaete families. As such, fossilized agglutinated tubes provide valuable insights into the evolution of tube-building strategies in polychaete annelids (Vinn and Luque 2013). The oldest known agglutinated fossil tubes of *Onuphionella* Kirjanov, 1968 date back to the Cambrian (Signor and McMenamin 1988), although these fossils may not belong to polychaetes, but instead to various problematic Palaeozoic tube-producing worms (Zatoń *et al.* 2012), which may not be classified as annelids (Vinn and Mutvei 2009). The earliest well-documented agglutinated tubes

with possible polychaete affinities are from the late Palaeozoic and Mesozoic (Ettensohn 1981; Zatoń *et al.* 2012; Vinn and Luque 2013). On the other hand, none of them has proven polychaete affinities since the fossilized soft body of the tube maker has never been found. These fossils also could have been produced by different benthic organisms capable of producing polychaete-like tubes. The diversity and evolutionary history of worms with agglutinated tubes has remained poorly understood.

Furthermore, although worms that produce agglutinated tubes are important components of modern marine ecosystems, their role in ancient ecosystems is not well understood (Fournier *et al.* 2010). The presence of agglutinated tubes composed of skeletal





Text-fig. 1. Location of Turjekelder locality with Furongian sandstones yielding *Cryptosiphon oboloides* sp. nov.

particles across different continental blocks and palaeolatitudes suggests that this type of structure was already broadly distributed by the Early Ordovician (Muir *et al.* 2019). This widespread distribution indicates some diversification of annelids, at least in their ecological roles, as part of the Great Ordovician Biodiversification Event (Muir *et al.* 2019).

The aim of the present paper is to: 1) describe the first specimen of an agglutinated worm tube from the Furongian (upper Cambrian) of Baltica; and 2) discuss the evolution, palaeoecology, and palaeobiogeography of this agglutinated tubeworm.

GEOLOGICAL BACKGROUND AND LOCALITY

During the Furongian and Early Ordovician, Baltica (with the area of Estonia) was positioned in the Southern Hemisphere within the temperate climatic zone (Mens and Pirrus 1997). In Estonia, Furongian strata are predominantly composed of sandstones, whose fossil content is dominated by lingulids and acrotretids, i.e., lingulate brachiopods. The Tsitre Formation, in which the discussed specimens were found, was first introduced by Popov and

Khazanovich (1985), with the stratotype located in the Turjekelder section (N 59.509556, E 25.496161; Text-fig. 1). The Tsitre Formation extends as a narrow belt from Tallinn to Kohtla-Järve (Mens and Pirrus 1997). Its thickness in outcrop sections is slightly more than 3 m. In drill core sections, the thickness is unclear due to a low core yield, but it is likely less than 10 m. The formation is primarily composed of light grey, weakly cemented, fine-grained quartzose sandstones, interspersed with a few thin layers of variegated, predominantly brownish-grey clayey rocks. These interbeds are often associated with bedding planes featuring convex-up lingulate shells (Mens and Pirrus 1997).

MATERIAL AND METHODS

Ivar Puura found the single agglutinated tube described herein when collecting lingulate brachiopods. The specimen was digitally photographed in an uncoated state with a CANON EOS R6 camera by Mare Isakar and Ivo Paalits. The measurements were digitally obtained from calibrated photographs. The specimen is deposited at the Natural History Museum, University of Tartu (collection acronym TUG).

SYSTEMATIC PALAEONTOLOGY (O. VINN)

Phylum Annelida? Lamarck, 1809
 Class Polychaeta? Grube, 1850
 Order and family unknown
 Genus *Cryptosiphon* Prantl, 1948
Cryptosiphon oboloides sp. nov.
 (Text-fig. 2A–E)

TYPE MATERIAL: Complete tube, holotype TUG 1209-100 from Turjekelder, Tsitre Formation, Furon-gian of Estonia.

DIAGNOSIS: Agglutinated tube composed of pieces of lingulate shells that fit well together. Shell fragments oriented with their longer axis parallel to the tube's main axis.

ETYMOLOGY: After the material of the tube: wall fragments of obolid brachiopods.

DESCRIPTION: The cylindrical tube is mostly (about 90%) composed of large angular, variably shaped and coloured fragments of phosphatic lingulate shells. The tube is 12 mm long and 4.2 mm wide. The pieces of lingulate shells are placed to form an overall pattern. Almost all shell fragments touch one another but do not overlap. The shell fragments in the tube wall are poorly sorted. The size of shell fragments varies from 0.7 to 4.1 mm ($N = 15$, mean = 2.1 mm, SD = 0.99 mm). The tube also contains some quartz sand grains, somewhat angular in shape (about 0.7 mm in diameter). The sand grains are much smaller than the brachiopod detritus. All agglutinated shell fragments are oriented with their longer axis parallel to the tube's main axis. The tube does not contain mica flakes. The tube wall is composed of a single layer of shell fragments. The tube lumen is filled with medium-grained yellow sandstone.

REMARKS: The new species is assigned to the genus *Cryptosiphon* Prantl, 1948 because the brachiopod shell fragments in its tube are oriented parallel to the tube's main axis, similarly as the brachiopod valves in the type species *Cryptosiphon terebelloides* Prantl, 1948 from the upper Darriwilian (Llanvirn) of the Czech Republic. The new species differs from *C. terebelloides* in having a tube composed of small lingulate shell fragments instead of complete rhynchonellate valves. The described tube also resembles somewhat *Onuphionella* Kirjanov, 1968 in its cylindrical shape and agglutinated tube wall; however, the latter is composed of mica flakes (Signor and McMenamin 1988)

instead of lingulate shell fragments. *Onuphionella* also differs in having an imbricated armour. The rarity of agglutinated worm tubes in lingulate shell coquinas may result from collecting bias, as these delicate structures may usually be destroyed during the extraction of samples from poorly lithified sediments.

DISCUSSION

Interpretation of the fossil

Similar non-imbricated tubes of *Echinokleptus* Muir, Botting, Lefebvre, Upton, and Zhang, 2019 and *Cryptosiphon* have been assigned to polychaetes, and we do not oppose such an interpretation as polychaetes were common in the early Palaeozoic. Moreover, polychaetes are the major builders of agglutinated tubes in modern seas. We also interpret the studied tube as the domicile of a polychaete worm or a similar worm-like organism. Many polychaete families include species capable of incorporating sediment into their tubes. These families include the Sabelliidae, Sabellidae, Oweniidae, Alvinellidae, Pectinariidae, Terebellidae, Trichobranchidae, Apistobranchidae, Longostomatidae, Chaetopteridae, Arenicolidae, Maldanidae, and Capitellidae (Wilson and Taylor 2001). However, many modern and fossil agglutinated polychaete tubes are composed of smaller diameter grains in a thick wall of multiple grains as in *Sabellaria alveolata* (Linnæus, 1767) (Mancin *et al.* 2022) or slightly larger regularly sized sand fraction grains as in the Pectinariidae (Vinn and Luque 2013), though usually more regular or in a more imbricated manner than in *Cryptosiphon oboloides* sp. nov. The studied agglutinated tube strongly resembles the cases of modern caddisfly larvae (Text-fig. 2F), though we do not suggest any phylogenetic affinity to caddisflies here. Most certainly the morphological similarity is due to a convergent way of tube building, presumably by polychaetes. The earliest possible caddisfly larval cases have been described from the Cisuralian (lower Permian) marine deposits of Gondwana (Mouro *et al.* 2016). The case of a modern caddisfly larva is a tubular structure made of silk, produced by the larva's salivary glands near its mouth, and construction begins shortly after the egg hatches (Wiggins 2015). The structure often includes various reinforcements, with the choice of materials and design influenced by the larva's genetic traits. The materials used can include sand grains, larger rock fragments, bark, sticks, leaves, seeds, and mollusc shells, all carefully arranged and affixed to the



Text-fig. 2. *Cryptosiphon oboloides* sp. nov. from the Furongian Tsitre Formation of Turjekelder, northern Estonia (holotype, TUG 1209-100) in different lateral views (A–C) and showing tube endings (D, E). F – cases of modern caddisfly larvae (Photo by Waldemar Paetz).

outer surface of the silken tube (Wiggins 2015). We infer a similar building strategy for our agglutinated tube. It originally contained an organic inner lining with a sticky external surface on which the shell fragments and sand grains were glued. The relatively well-arranged grains in the tube wall suggest that the animal actively assisted in gluing the shell fragments, orienting, and finding the right place for them.

Palaeoecology

The dominant material on the sea floor was medium-grained quartz. However, the tube builder preferentially selected larger particles, as its tube is not composed of medium-grained material but of larger lingulate shell fragments. The host sediment contains also smaller phosphatic fragments of representatives

of the Order Hyolithelminthida Fischer, 1962, but those were not incorporated into the tube wall of *C. oboloides* sp. nov. The lingulate shell fragments are tile-like and differ from the grain-like quartz particles. The tile-like particles were probably actively selected by the worm to build a caddisfly case-like tube. It could also be possible that the tube-building organisms preferred phosphatic shell fragments to other particles of different compositions, but this cannot be shown based on the current data.

Some other ancient tube-builders were highly selective in their choice of biogenic particles (Muir *et al.* 2019). For instance, even early agglutinators such as the Cambrian *Volborthella* Schmidt, 1888 demonstrated selectivity in the types of grains used (Lipps and Sylvester 1968). *Volborthella* tubes are composed either of oriented heavy mineral grains or quartz (Lipps and Sylvester 1968). *Onuphionella*, which has a stratigraphic range from the latest Ediacaran to the Late Ordovician, was made entirely of mica flakes (e.g., Signor and McMenamin 1988; Muir *et al.* 2022). The Early Ordovician worm tubes of *Echinokleptus anileis* Muir, Botting, Lefebvre, Upton and Zhang, 2019 were selectively constructed of echinoderm fragments (Muir *et al.* 2019). Zatoń and Bond (2016) provided evidence of particle selectivity in a Devonian worm tube which was composed entirely of tentaculitid shells or formed from particles including ostracod carapaces, echinoderm ossicles, tentaculitid shells, and putative bryozoan fragments aligned perpendicularly to the tube's long axis. Another Devonian tubicolous fossil *Annulitubus mutveii* Vinn, Zabini, Sene-Silva, Kirsimae and Susan-Marcos, 2016 is characterised by an agglutinated tube made of silt-sized particles forming an unusual flanged morphology that is not otherwise known from the fossil record (Becker-Kerber *et al.* 2021). The Carboniferous agglutinated worm-tube *Crininicaminus* Etensohn 1981 was constructed entirely from pelmatozoan ossicles (Etensohn 1981). Additionally, Zatoń *et al.* (2012) described agglutinated tubes from the Jurassic of Poland that were made from ooids. *Cryptosiphon oboloides* sp. nov. is the earliest known worm species that used shell fragments to build its tube. Thus, the evolutionary innovation of using shell fragments to build agglutinated tubes appeared as early as the Furongian (late Cambrian) in marine invertebrates.

The original position of the tube in the sediment is unknown and in a shallow-water hydrodynamically active environment it likely did not preserve *in situ* anyway. There are two possibilities. The worm was sessile, like the modern agglutinating polychaetes,

or it was a mobile animal that carried around its agglutinated shell. If the tube-building organism was a polychaete, a sessile life mode is more likely based on modern analogues. In the case of a sessile life mode, the worm was either a detritivore or suspension feeder similar to modern tubicolous polychaetes. The function of the agglutinated tube was to protect soft-bodied worms against predators. Teeth of predatory conodont animals have been reported from the Tsitre Formation (Mens *et al.* 1993).

Palaeobiogeography

The only truly similar tubes to *Cryptosiphon oboloides* sp. nov. occur in the Middle Ordovician of Bohemia (Prantl 1948) which was part of the Armorican Terrane Assemblage close to Gondwana (Cocks and Torsvik 2021). *Cryptosiphon oboloides* sp. nov. predates this record. However, it is not currently clear whether worms capable of building agglutinated tubes from shell material had originated in Baltica or in some other region, later to be dispersed to the Armorican Terrane Assemblage and other regions in the Early to Middle Ordovician. Large agglutinated tubes of *Echinokleptus anileis* composed of skeletal particles, primarily articulated and disarticulated echinoderms, have been described from the Lower Ordovician Dol-cyn-Afon Formation in Wales (Muir *et al.* 2019). Similar tubes, though made from different materials, are found in the Lower Ordovician deposits in South China, and possibly in Morocco and France as well (Muir *et al.* 2019).

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