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Insight into tube-building behaviour and palaeoecology of some agglutinating worms from the Upper Devonian of Nevada, USA

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ABSTRACT

Agglutinated worm tubes from the Upper Devonian of the Devils Gate section in Nevada, USA are reported for the first time, filling a major gap in their Palaeozoic fossil record. Two small (5 mm and 6.7 mm in length) tubes are composed entirely of tentaculitid shells, and one large tube (55 mm in length) is formed from particles including ostracode carapaces, echinoderm ossicles, tentaculitid shells and putative bryozoan fragments aligned perpendicularly to the tube's long axis. The tubes, in particular the large one have a cylindrical, curved and tapering tube morphology that is very similar to that of modern agglutinating polychaetes of the families Terebellidae and Pectinariidae. The large tube is dominated by objects that fall within a certain size-range, and although built from different types of particles, echinoderm ossicles are prevalent in the posterior part, whereas ostracode carapaces dominate in the middle and anterior parts of the tube. Tentaculitid shells are relatively rare in the large tube, despite being abundant in the surrounding host deposit. The faunal assemblage composing the tube suggests that the worm animal was rather specific in its selection of particles with a certain morphology. This is common behaviour amongst many modern agglutinating terebellid and pectinariid polychaetes. The preservation of such fragile tubes was enhanced by rapid burial, likely caused by gravity flow of sediment in a deep-slope setting.

1. Introduction

In the modern world, worm animals that form protective tubes through agglutination of foreign particles gathered from the seabottom belong primarily to Polychaeta (e.g., Finger et al., 2008; Vinn and Luque, 2013). Several families of polychaetes include species (see Wilson and Taylor, 2001) which are able to incorporate a variety of mineral and biogenic particles (e.g., Finger et al., 2008; Noffke et al., 2009; Vinn and Luque, 2013) which are glued together with the aid of a specific biomineralized and proteinaceous cement (e.g., Busch and Loveland, 1975; Zhao et al., 2005; Noffke et al., 2009; Fournier et al., 2010). However, such agglutinated tubes are much thinner and more fragile than calcareous tubes formed by serpulid, sabellid and cirratulid polychaetes (e.g., Vinn and Mutvei, 2009), and thus have a much lower fossilisation potential. Indeed, when compared to calcareous tube-bearing sedentary polychaetes, agglutinated worm tubes are much rarer in the fossil record, often represented only by single specimens from a particular time-interval.

Even though agglutinated worm tubes have low fossilisation potential, their fossil record extends as far back as the Early Cambrian (Signor and McMenamin, 1988). They are largely represented by single finds in Palaeozoic (e.g., Howell, 1962; Ettensohn, 1981), before becoming more abundant from the Mesozoic, as exemplified by numerous examples from the Jurassic and Cretaceous (e.g., Barnard, 1956; Wilson and Taylor, 2001; Zatoń et al., 2012; Vinn and Luque, 2013; Žítt and Vodrážka, 2013; Keupp et al., 2014; Lazăr and Grădinaru, 2014), as well as the Miocene (e.g., Katto, 1976; Finger et al., 2008). The vast majority of described fossil agglutinated worm tubes have been assigned to the polychaete order Terebellida (especially families Terebellidae and Pectinariidae, see e.g., Howell, 1962; Ettensohn, 1981; Finger et al., 2008; Vinn and Luque, 2013; Lazăr and Grădinaru, 2014; Keupp et al., 2014). This taxonomic approach is based on similarities with Recent representatives of the group in their general morphology and character of tube construction.

The oldest agglutinated worm tube which shares its tube construction style with modern terebellid polychaetes is the Ordovician *Cryptosiphon* (Prantl, 1948; see also Howell, 1962). The next oldest Palaeozoic agglutinated tube having a strong relationship with these polychaetes is *Crininicaminus* from the Lower Carboniferous (Chesterian) of Kentucky, USA (Ettensohn, 1981). Here we present the first finds of new agglutinated worm tubes from the Upper Devonian of Nevada, USA. These samples not only fill a major gap in the Palaeozoic fossil record of agglutinated worm tubes, but also provide insight into

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the behaviour and paleoecology of ancient representatives of tube-building animals with possible polychaete affinities.

2. Geological setting

The Great Basin Devonian outcrops of Nevada record deposition adjacent to a foreland basin. This formed the central part of a large continental carbonate shelf extending northward from Mexico to western Canada, along the western edge of Laurasia (Sandberg and Poole, 1977; Sandberg et al., 1989; Morrow, 2000), located at 5–10° N (Scotese and McKerrow, 1990). The highly accessible Devils Gate section is regarded as one of the most important Frasnian–Famennian (F–F) reference sections from the Great Basin (Sandberg et al., 1988, 2002), and the F–F boundary is well constrained by conodont dating. The base of the section is reached by following Highway 50 for 13 km west from Eureka (Fig. 1). Shortly before the road passes through "Devils Gate", a track (the old highway) branches off to the right. After following this track for 300 m, the section begins immediately to the north, in the hillside. Devils Gate records deposition in the Woodruff basin, which lay to the west of the proto-Antler forebulge (Sandberg et al., 2003) and is characterised by debris-flow carbonates, turbidites, siltstones, mudstones, and cherts (Sandberg et al., 2003). The full F–F sequence is a composite of three closely spaced sections requiring a traverse of 200 m, which total over 50 m of sediment (Fig. 2).

The expanded Devils Gate F–F sequence belongs to the upper member of the Devils Gate Limestone Formation which ranges in age from the lower part of the Early *rhenana* conodont Zone to the Late *triangularis* Zone. The "s*emichatovae* transgression" (Sandberg et al., 1997, 2002, 2003) and the base of transgressive–regressive cycle IId of Johnson et al. (1985) is clearly recorded at the base of the section, where it is manifest as a transition from medium-grey, massive micrite to organic-rich, dark, finely laminated radiolarian chert, finely laminated siltstone, and finely laminated, calcareous shale (Bond and Wignall, 2005). Hemipelagic sedimentation during the Late *rhenana* to *triangularis* zones comprises cherts, silty shales, micritic limestones, and calcareous siltstones, with common slumping and soft sediment deformation (Fig. 2). The fine-grained sediments are interbedded with thick beds of clast supported limestone breccia and conglomerate (Bond and Wignall, 2005). During the upper part of the *linguiformis* Zone, there was a brief pause in allodapic deposition, allowing persistent hemipelagic (mudstones and shales) sedimentation with occasional slumping across the F–F boundary (Bond and Wignall, 2005). The basal Famennian is characterised by turbidites, interbedded with siltstones and shales. Finally, the Early and Middle *triangularis* zones are characterised by numerous thick conglomerates, which again are interbedded with siltstones.

3. Material and methods

The sample presented in this paper derives from the uppermost Frasnian *linguiformis* Zone and was taken from slumped deposits immediately below the F–F boundary (Fig. 2). The limestone sample contains three specimens: two smaller specimens (GIUS 4-3659a, b) are preserved on the upper surface of the slab, and one large specimen (GIUS 4-3660) is preserved on the lower surface. The specimens were investigated using both the binocular microscope and environmental scanning electron microscope (ESEM) Philips XL30 at the Faculty of Earth Sciences, University of Silesia in Sosnowiec, Poland. Specimens were inspected in order to identify and assess the preservation of tube-forming components, first using the binocular microscope, supplemented later by ESEM observations using the back-scattered imaging (BSE). Elemental composition of particular fossils building the tubes and scattered in the host rock was performed using the EDS detector coupled with the ESEM. To evaluate whether components were selected differently during the ontogeny of the tube-builder, they were counted in three sectors (proximal, middle and distal parts) of the tube of the largest and best-preserved specimen (GIUS 4-3660), corresponding to different ontogenetic stages, using the 1 cm^2 grid under the binocular microscope. The orientation of components with respect to the long axis of the tube was noted at the same time. To test whether the tube-builder selected particles on the basis of size, the components were measured with the aid of the ESEM-integrated electronic calliper. To

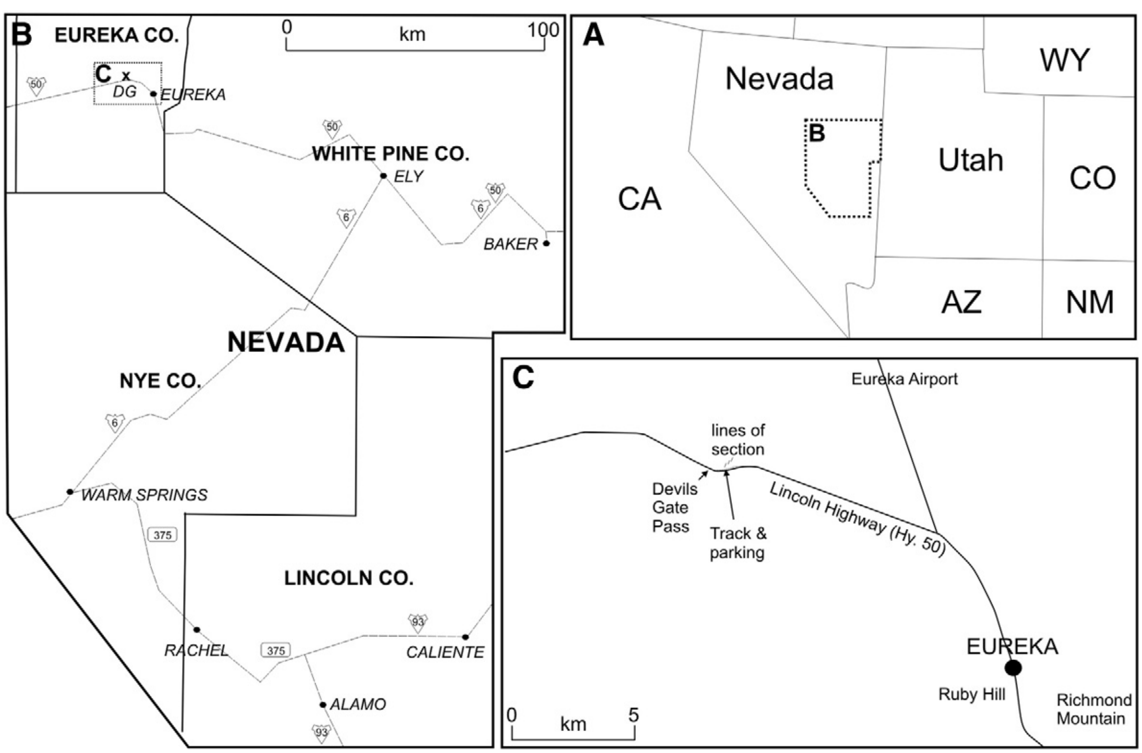

Fig. 1. Locality map of the Devils Gate section near Eureka in Nevada, USA. A. Nevada within western USA. B. the Great Basin area of central eastern Nevada. C. close up of the section location near Eureka.