

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

Michał Zatoń<sup>1\*</sup> and David P. G. Bond<sup>2</sup>

<sup>1</sup>Faculty of Earth Sciences, University of Silesia, Będzińska 60, 41-200 Sosnowiec, Poland

<sup>2</sup>Department of Geography, Environment and Earth Sciences, University of Hull, Hull HU6  
7RX, United Kingdom

\*Corresponding author. E-mail: [mzaton@wnoz.us.edu.pl](mailto:mzaton@wnoz.us.edu.pl) (M. Zatoń).

## **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.

**Key words:** Polychaetes, worm tubes, particle selection, taphonomy, Frasnian

## 1. Introduction

In the modern world, worm animals that form protective tubes through agglutination of foreign particles gathered from the sea-bottom 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., Bush 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 Early Cambrian (Signor and McMenamin, 1988). They are largely represented by single finds in Palaeozoic (e.g., Howell, 1962; Etensohn, 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; Žitt 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; Etensohn, 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 the 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 *Crinincaminus* 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 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).

### **Figure 1 near here**

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 “*semichatovae* transgression” (Sandberg et al., 1997, 2002, 2003) and the base of transgressive-regressive cycle II<sub>d</sub> 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.

**Figure 2 near here**

### **3. Material and methods**

The sample presented in this paper derives from the uppermost Frasnian *linguiformis* Zone and was taken from a 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 part) of the tube of the largest and best-preserved specimen (GIUS 4-3660), corresponding to different ontogenetic stage, using the 1cm<sup>2</sup> 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 assess whether the tubes were constructed using components gathered in-situ, the host deposit was also analysed for its fossil content using the both binocular and ESEM microscopes. To obtain quantitative data of components present in the host deposit, a 1cm<sup>2</sup> grid was used when counting. Additionally, thin sections for microscopic observations were prepared from the tube-bearing deposit.

The specimens are housed at the Department of Palaeontology & Stratigraphy, Faculty of Earth Sciences, University of Silesia, Sosnowiec.

## **4. Results**

### *4.1. Small tubes*

The small tubes are flattened, and preserved as external surfaces on the lower surface of the limestone slab. The specimens are preserved close to, and parallel with each other. Both tubes are straight and have similar sizes: specimen GIUS 4-3659a (Fig. 3A) has length of 5 mm and width of 2.5 mm, and the specimen GIUS 4-3659b (Fig. 3B) has length of 6.7 mm and width of 2 mm. Their composition is similar, consisting of distinctly conical shells characteristic of tentaculitids and interpreted as such (Fig. 3D-E). The tentaculitids show nearly perpendicular alignment to the growth axis of the tube. The host deposit surrounding the tubes represents a packstone containing ostracodes, tentaculitid shells, as well as branching elements which may represent putative bryozoan fragments (Fig. 3C, F-G). Individual fossil components have worn surfaces. EDS analyses indicate that the fossils preserved in both tubes and the surrounding limestone are composed of calcite with some addition of silica (Si). However, some of the tentaculitid shells building the tubes have exteriors enriched in iron oxides and Si with characteristic, bright colour under BSE (Fig. 3D-E). It is possible that these shells were originally pyritised and later underwent oxidation. Thin section petrology reveals common pyrite crystals that are disseminated within the sediment and fill the interiors of some of the fossils (Fig. 3F-G).

**Figure 3 near here**

#### *4.2. Large tube*

The tube preserved on the upper surface of the slab (GIUS 4-3660) is much larger than those described above. It is flattened, slightly curved and distinctly tapering toward its posterior part (or presumed base, see Fig. 4). The preserved tube's length is 55 mm, while its width is 6 mm at the preserved base and 8.5 mm at the anterior part (or presumed aperture). The state of preservation of the tube suggests that it may originally have been slightly longer, at least at its narrower base. The overall external preservation is good enough to recognise the building components. The fossils used for the tube construction consist of ostracode carapaces, echinoderm ossicles, tentaculitid shells and those which may represent putative bryozoan fragments (Figs 4-5). The preservation of the exterior of fossils building the tube is poor, so specific determination is difficult. The most numerous components are ostracodes, followed by echinoderm ossicles and tentaculitids. Those interpreted as putative bryozoans are the rarest and consist of single fragments only. Particular components are more or less dominant in different parts of the tube. For example, in the posterior (basal) part of the tube, echinoderm ossicles were the dominant component used for tube construction, followed by ostracodes and tentaculitids (Fig. 4). In the middle and anterior parts of the tube, ostracode carapaces became the dominant building components, whilst the contribution of other components is minor (Fig. 4). The fossil particles have badly preserved, worn surfaces, probably as a result of weathering (Fig. 5). The EDS analysis showed that the fossils are composed of calcite with some addition of Si.

**Figure 4 near here**

The agglutinated fossil components are oriented with their longest axis perpendicular to the growth axis of the tube, and usually are densely packed. Apart of complete carapaces of ostracodes, isolated valves were also used (Figs 4-5). In total, fossil components range in size from 214 to 1680  $\mu\text{m}$ . The size ranges of particular fossil groups used in the construction of the tube are given in Table 1. With respect to size, the components used for tube construction have a non-normal distribution (Shapiro-Wilk  $W = 0.9152$ ,  $p < 0.05$ ); however, there is a clear dominance of particles ranging between 600 and 800  $\mu\text{m}$  (Fig. 6).

**Table 1 near here**

**Figure 5 near here**

The surrounding sediments contain all three main components that have been used to construct the tube; however, the dominant taxa, at least on the visible surface, are tentaculitids (Fig. 7).

## **5. Discussion**

### *5.1. Biological affinity*

All previously described fossil agglutinated worm tubes are assigned to Polychaeta, and usually to the order Terebellida on the basis of characteristic tube morphology and composition, as well as the palaeoecological context (free-living or encrusting) (e.g., Howell, 1962; Ettensohn, 1981; Barnard, 1956; Finger et al., 2008; Vinn and Luque, 2013; Lazăr and Grădinaru, 2014; Keupp et al., 2014). Of course, in the absence of preserved soft tissues of the producer, this assignment of the tubes is uncertain. It is possible that at least some tubes, especially those found in older Palaeozoic deposits, may have been produced convergently by

completely different animals (such uncertainty was highlighted by Signor and McMenamin [1988] when describing agglutinated tubes composed of mica flakes from the Lower Cambrian of USA). However, taking the morphology, characteristic composition and behavioural traits during the tube formation into account, it is very possible that many, if not all, of the fossil agglutinated worm tubes described in the literature may have indeed been constructed by polychaetes closely related to modern Terebellida and Sabellida. It must be noted here, that the oldest representative of Canalipalpata, a polychaete clade to which the tube-building polychaetes belong (Parry et al., 2014), comes from the Middle Devonian (an exceptionally well-preserved spionid, see Cameron, 1967). Interestingly, it has also been suggested that the modern reef-like masses of agglutinated tubes constructed by sabellariid polychaetes may provide an analogue for the Lower Palaeozoic *Skolithos* “piperock” (Ekdale and Lewis, 1993). Therefore, the fossil record of agglutinated tube-building polychaetes may in fact extend deep in time.

### **Figure 6 near here**

The cylindrical tube of the larger specimen, slowly tapering toward its base, is reminiscent of other agglutinated tubes of the Palaeozoic (Howell, 1962; Ettensohn, 1981) and Jurassic (e.g., Barnard, 1956; Keupp et al. 2014). Ettensohn (1981) tentatively classified his *Crinanicaminus* tube to the family Amphictenidae (= Pectinariidae, see Hutchings and Peart, 2002). However, this assignment is probably incorrect, since pectinariid tubes exhibit a very characteristic conical shape, rapidly tapering to their posterior end (see Kato, 1976; Finger et al., 2008; Vinn and Luque, 2013). Thus, the Carboniferous tube of Ettensohn (1981), apart from its building material, is similar (e.g. in shape) to the tube *Ekllexibella*

*buttenheimensis* described from the Lower Jurassic by Keupp et al. (2014) which is assigned to the Terebellidae. The oldest known tube that looks similar to Recent *Pectinaria*, is from the much younger Santonian (Cretaceous) deposits of Colombia (Vinn and Luque, 2013). However, unlike the Palaeozoic agglutinated tubes presented by Howell (1962) and Ettensohn (1981), and Jurassic tubes described by Keupp et al. (2014), the Upper Devonian specimen from Nevada is distinctly curved. In being so, the Devonian tube is not only somewhat similar to the Terebellidae (see Vinn and Luque, 2013, p. 109), but also to some species of the family Pectinariidae (see e.g., Bush and Loveland, 1975, fig. 3; Fournier et al., 2010). Thus, having morphological features of both families, the larger tube described here may only tentatively be classified within the order Terebellida.

The two smaller tubes may also be classified to the order Terebellida. However, it is not certain whether they represent the same taxon as the larger tube-making animal but record earlier stages of ontogeny, or are the product of a completely different species. Interestingly, in the tubes of the smaller specimens, only tentaculitid shells have been noted, indicating greater selectivity with respect to the collected components than the larger specimen.

Although all three tubes are clearly different from others described in the literature, we refrain from formally naming them (ichno)taxonomically due to the scarcity of the material. With respect to external appearance (cylindrical and curved tube) and even its size, the Upper Devonian larger tube is similar to those described as *Onuphionella* by Signor and McMenamin (1988). However, the latter tubes are built by mica flakes and are Early Cambrian in age. Thus, the distinct differences in building material and stratigraphic occurrence make the tube rather unrelated taxonomically.

**Figure 7 near here**

## 5.2. Tube-building

Modern polychaetes that build their tubes through agglutination of foreign objects use a variety of different particles such as are available in their surrounding environment. However, particle selection may be very specific depending on the polychaete species. Tube-building sabellids such as *Owenia fusiformis* (see Noffke et al., 2009) for example, are size-selective but use different kinds of particles (quartz grains, shell material, echinoid fragments and foraminifera). Similarly the terebellid *Lanice conchilega* uses a variety of particles including sand grains, mollusc shells, echinoid fragments, foraminifera tests and ostracod carapaces (e.g., Callaway, 2006; Van Hoey et al., 2008). Some species of pectinariids, such as *Pectinaria gouldi* and *P. koreni*, on the other hand, are more selective and use sand grains only (e.g., Bush and Loveland, 1975; Finger et al., 2008; Fournier et al., 2010).

The large agglutinated tube from the Upper Devonian of Nevada discussed here evidently shows size-selection of the collected particles. The dominant particles fit a narrow size-range between 600 and 800  $\mu\text{m}$  (Fig 6). The composition of the particles, on the other hand, is variable, comprising ostracode carapaces, echinoderm ossicles, tentaculitid shells and possibly even rare bryozoan fragments. All of these occur in the host sediment, in which they are the largest grains present. This may indicate that during its life the worm animal selected the largest and most suitable (of a certain size) particles for tube-building, no matter what their origin was. In fact, there is a clear dominance of ostracode carapaces (Fig. 4), and even though tentaculitid shells are very common in the host deposit (Fig. 7), they were rarely selected for tube-building (see the graphs in Fig. 4). The animal's preference for ostracode carapaces is evident in that not only articulated specimens, but also single valves were used (Fig. 5A, D), indicating that not only particle size but also its shape mattered. It is also interesting that the preference toward ostracode carapaces was not the case throughout the

animal's full ontogeny because the narrower, posterior part of the tube is dominated by echinoderm ossicles, and ostracodes were only minor components (Fig. 4). In the middle part of the tube, there is a clear shift toward the selection of ostracode carapaces which were used right to the end of the preserved tube (Fig. 4). This pattern may suggest that either there was a natural preference for echinoderm particles at the beginning of tube formation, or during that period of building the echinoderm particles were more abundant in the surrounding environment and thus easier to collect for tube builder. The smaller agglutinated tubes preserved on the other side of the sample, however, are built entirely of tentaculitid shells. As the tubes are small-sized, it is uncertain whether such a behaviour in selecting material only took place at the beginning of the tube formation, as in the case of the larger tube discussed above, or these worm animals preferred only tentaculitid shells, or instead whether tentaculitid shells were simply the most abundant components in the host sediment during tube formation. However, both in the larger tube and smaller tubes reported, there seems to be specificity of particle selection with respect to their size and shape, even though the surrounding deposit contained particles of different kinds.

The selectivity towards specific particles which are abundant in surrounding environment is well-known from other fossil agglutinated tubes. For example, the Carboniferous worm forming the *Crininicaminus* tube lived in a 'crinoid garden' and thus selected echinoderm ossicles (Ettensohn, 1981) which were abundant and easily accessible for the worm animal. The Jurassic (Barnard, 1956; Keupp et al., 2014) and Miocene (Finger et al., 2008) agglutinated tubes selected only foraminifera tests as these were the only particles of the appropriate size in the sediment. The other tube described by Keupp et al. (2014) as *Eklexibella johanni*, selected only nuculid bivalve shells of varying sizes. The encrusting agglutinated tubes from the Middle Jurassic of Romania (Lazăr & Grădinaru, 2014) and Poland (Zatoń et al., 2012) were formed using ooids of certain sizes. Some other worms,

however, were not so selective in the agglutination of their tubes. For example, the Ordovician *Cryptosiphon* used different particles ranging from brachiopod and mollusc shells, ostracod carapaces and even trilobite exoskeletons (see Howel, 1962; Keupp et al., 2014). Some encrusting terebellid worm tubes from the Upper Cretaceous (Žitt and Vodrážka, 2013), selected various phosphatic particles which were also abundant and thus easy to collect. The Upper Cretaceous *Pectinaria*-like tube not only selected sand grains, but also shelly detritus and fish debris (Vinn and Luque, 2013).

The alignment of the particles in the larger Upper Devonian tube from Devils Gate, well-seen in the ostracod carapaces (Figs 4, 5D), is not random but has a clear pattern, in which particular carapaces are added close to each other with their longer axes perpendicular to the main growth axis of the tube. Similarly the smaller tubes added tentaculitid shells nearly perpendicular to the tube growth axis (Fig. 3A-B, D-E). Such behaviour during tube formation is well-known in many other fossil examples. It is present in some Lower Jurassic, free-living terebellids (Barnard, 1956; Keupp et al., 2014) and Miocene pectinariid-like tubes (Finger et al., 2008) in which elongated foraminifera tests were tightly aligned perpendicular to the main axis of the worm tubes. In some Middle Jurassic (Lazăr and Grădinaru, 2014) and Upper Cretaceous (Žitt and Vodrážka, 2013) encrusting terebellids, the selected ooids and phosphatic faecal pellets, respectively, were aligned in a similar manner. However, such alignment is not a rule, as in the case of encrusting agglutinated tubes (terebellids?) from the Middle Jurassic of Poland (Zatoń et al., 2012), the ooids seem to be aligned parallel to the tube's main axis. Such differences clearly indicate different behaviour of the worm animals during tube building.

### *5.3. Palaeoecology and taphonomy*

As evidenced from their state of preservation (solitary specimens embedded in host deposit), the Upper Devonian agglutinated tubes discussed here were constructed by non-encrusting worms. Such agglutinated worm tubes are today produced by sedentary, deposit-feeding polychaetes burrowing headfirst into the sediment, such as *Pectinaria* (Busch and Loveland, 1975; Finger et al., 2008; Fournier et al., 2010; Vinn and Luque, 2013), or deposit- and suspension-feeding species the tubes of which protrude above the sediment surface, such as the terebellid *Lanice* (Callaway, 2006) or the sabellid *Owenia* (Noffke et al., 2009).

As the agglutinated worm tubes reported are preserved horizontally to the bedding plane, it is difficult to unequivocally interpret their mode of life. The shape of the large tube (distinct boundaries, tapering and slightly curved) is very similar to that seen in pectinariids. Thus, it is possible that the worm also was oriented head-down within the sediment during its life for feeding and particle collecting. The narrower (posterior) part of its tube would have protruded above the sediment surface. As the tubes of the species which grow head-up (such as *Lanice* or *Owenia*) are thin, long and have rough and uneven boundaries due to the presence of various sized grains, they are less likely analogues for the Devonian tube. Burrowing head-first, the worm animal ingested suitable, small-sized, organic-rich particles and using long tentacles it was able to collect suitable, larger objects of its preferred size and type for tube-building.

The protective tubes of agglutinating polychaetes are built by foreign particles glued together with the aid of biomineral cement secreted by specialized organs (e.g., Fournier et al., 2010). Such tubes certainly have less strength than solid, calcitic tubes of other sedentary polychaetes such as serpulids. Indeed, the tubes of modern *Pectinaria* are fragile (see Katto, 1976) and thus the rarity of solitary agglutinated worm tubes in the fossil record suggests that such tubes needed rather rapid burial to enable preservation (Ettensohn, 1981). The Upper Devonian sedimentary rocks of the Devils Gate section were deposited in an off-shore, basin

slope setting as evidenced by common occurrences of limestone breccias, conglomerates, turbidites and slumped horizons with soft sediment deformation (Sandberg et al., 1989; Morrow, 2000; Morrow and Sandberg, 2003; Sandberg et al., 2003; Bond and Wignall, 2005).

The preservation of agglutinated worm tubes in such a setting was likely enhanced by rapid gravity flows of sediment. Although the same species of Recent pectinariids and terebellids may inhabit a wide range of habitats, ranging from shallow, littoral zones up to the deep, abyssal depths (e.g., Carey, 1987; Finger et al., 2008; Van Hoey et al., 2008), we interpret that the agglutinated worm tubes reported were buried *in situ* or very close to their natural, deeper-water habitat. This interpretation is supported by the presence of abundant tentaculitids, a group of pelagic zooplankton (Bond, 2006; Berkyová et al., 2007) indicative of deposition in a hemipelagic environment. Although the ostracodes in the Frasnian and Famennian portions of the Devils Gate section are commonly redeposited from shallower habitat (Casier and Lethiers, 1998), the overall preservation of the larger tube, which shows no signs of disaggregation of its forming components suggests that the tubes were not transported within a gravity flow. The common disseminated pyrite crystals suggest reducing conditions within the sediment during the burial of the tubes, which might have further enhanced their preservation.

## 6. Conclusions

Agglutinated worm tubes, probably belonging to polychaetes of the order Terebellida, are reported for the first time from the Upper Devonian of Nevada, USA. Two smaller tubes are composed entirely of tentaculitid shells. One large specimen is built from a variety of particles of a certain size, dominated by ostracode carapaces plus echinoderm ossicles, and rarer tentaculitid shells and possibly even bryozoan fragments. While the builders of the

smaller tubes may have preferred only tentaculitid shells, the animal forming the larger tube seems to have specifically selected ostracode carapaces and isolated valves, even though the surrounding deposit is rich in tentaculitid shells. Such specificity toward the certain particle size and type is well known in many Recent agglutinating polychaetes of terebellid and pectinariid groups. Here we report this behaviour in one of the oldest agglutinated worm tubes in the fossil record. The agglutinating worms might have burrowed the sediment subsurface headfirst, like modern pectinariid species. It is likely that the tubes were buried beneath a gravity flow deposit, which are common in the Devils Gate section. Thus, the agglutinated worm tubes were probably buried *in situ* or very close to their natural, deeper-water habitat.

### **Acknowledgements**

Fieldwork in Nevada, USA in 2015 was supported by the MAESTRO grant 2013/08/A/ST10/00717 (to Grzegorz Racki). DB wishes to acknowledge the field guidance of the late Jared Morrow, who guided him to many Late Devonian sections in the Great Basin in 2001. DB also acknowledges financial support from the Natural Environment Research Council (NERC) in the form of Advanced Research Fellowship NE/J01799X/1, which supported fieldwork in 2015 and his time on this project. Two journal referees are greatly acknowledged for their constructive comments, useful remarks and corrections.

### **References**

Barnard, T. 1956. An unusual worm tube from the Lower Lias. *Journal of Paleontology* 30, 1273–1274.

- Berkyová, S., Frýda, J., Lukeš, P. 2007. Unsuccessful predation on Middle Paleozoic plankton: shell injury and anomalies in Devonian dacryoconarid tentaculites. *Acta Palaeontologica Polonica* 52, 407–412.
- Bond, D., 2006. The fate of the homoctenids (Tentaculitoidea) during the Frasnian-Famennian mass extinction (Late Devonian). *Geobiology* 4, 167–177.
- Bond, D., Wignall, P.B., 2005. Evidence for Late Devonian (Kellwasser) anoxic events in the Great Basin, western United States. In Over, D.J., Morrow, J.R., Wignall, P.B. (Eds), *Understanding Late Devonian and Permian-Triassic Biotic and Climatic Events: Towards an Integrated Approach. Developments in Palaeontology and Stratigraphy* 20. Elsevier, Amsterdam, 225–262.
- Busch, D.A., Loveland, R.E., 1975. Tube-worm-sediment relationships in populations of *Pectinaria gouldi* (Polychaeta: Pectinariidae) from Barnegat Bay, New Jersey, USA. *Marine Biology* 33, 255–264.
- Callaway, R., 2006. Tube worms promote community change. *Marine Ecology Progress Series* 308, 49–60.
- Cameron, B., 1967. Fossilization of an ancient (Devonian) soft-bodied worm. *Science* 155, 1246–1248.
- Carey, D.A., 1987. Sedimentological effects and palaeoecological implications of the tube-building polychaete *Lanice conchilega* Pallas. *Sedimentology* 34, 49–66.
- Casier, J.-G. & Lethiers, F., 1998. Les ostracodes du Frasnien terminal (Zone á linguiformis des Conodontes) de la coupe du col de Devils Gate (Nevada, USA). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 68, 77–95.
- Ekdale, A.A., Lewis, D.W., 1993. Sabellariid reefs in Ruby Bay, New Zealand: a modern analogue of *Skolithos* “piperock” that is not produced by burrowing activity. *Palaios* 8, 614–620.

- Ettensohn, F.R., 1981. *Crininicaminus haneyensis*, a new agglutinated worm tube from the Chesterian of east-central Kentucky. *Journal of Paleontology* 55, 479–482.
- Finger, K.L., Flenniken, M.M., Lipps, J.H., 2008. Foraminifera used in the construction of Miocene polychaete worm tubes, Monterey Formation, California, USA. *Journal of Foraminiferal Research* 38, 277–291.
- Fournier, J., Etienne, S., Le Cam, J.-B., 2010. Inter- and intraspecific variability in the chemical composition of the mineral phase of cements from several tube-building polychaetes. *Geobios* 43, 191–200.
- Howell, B.F., 1962. Worms. In Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology, Part W, Miscellanea*. Geological Society of America and University of Kansas Press, W144–W177.
- Hutchings, P., Peart, R., 2002. A review of the genera of Pectinariidae (Polychaeta) together with a description of the Australian fauna. *Records of the Australian Museum* 54, 99–127.
- Johnson, J.G., Klapper, G., Sandberg, C.A., 1985. Devonian eustatic fluctuations in Euramerica. *Geological Society of America Bulletin* 96, 567–587.
- Katto, J., 1976. Additional problematica from southwest Japan. *Contribution from the Department of Geology* 68, 17–24.
- Keupp, H., Gründel, J., Wiese, R., 2014. New agglutinated polychaete worm-tubes from the Lower Jurassic (Late Pliensbachian) of southern Germany. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 273, 241–251.
- Lazăr, I., Grădinaru, M., 2014. Paleoenvironmental context and paleoecological significance of unique agglutinated polychaete worm tube-ferruginous microstromatolite assemblages from the Middle Jurassic of the southern Carpathians (Romania). *Facies* 60, 515–540.

- Morrow, J.R., 2000. Shelf-to-Basin Lithofacies and Conodont Paleoecology across Frasnian-Famennian (F-F, mid-Late Devonian) Boundary, Central Great Basin (Western U.S.A.). *Courier Forschungsinstitut Senckenberg* 219, 1–57.
- Morrow, J.R., Sandberg, C.A., 2003. Late Devonian sequence and event stratigraphy across the Frasnian-Famennian (F-F) boundary, Utah and Nevada. In Harries, P.J. (Ed.), *High-Resolution Approaches in Stratigraphic Paleontology*. Kluwer Academic Publishers. Dordrecht, 351–419.
- Noffke, A., Hertweck, G., Kröncke, I., Wehrmann, A., 2009. Particle size selection and tube structure of the polychaete *Owenia fusiformis*. *Estuarine, Coastal and Shelf Science* 81, 160–168.
- Parry, L., Tanner, A., Vinther, J., 2014. The origin of annelids. *Palaeontology* 57, 1091–1103.
- Prantl, F., 1948. Some terebelloid remains from the Ordovician of Bohemia. *České Společnosti Nauk, Trída Mathematico-Přírodovědecká, Věstník* 1948 (8), 1–8.
- Sandberg, C.A., Poole, F.G., 1977. Conodont biostratigraphy and depositional complexes of Upper Devonian cratonic-platform and continental-shelf rocks in the western United States. In Murphy, M.A. et al. (Eds), *Proceedings of the 1977 annual meeting of the Paleontological Society on Devonian of western North America*, Campus Museum Contributions no. 4, University of California, Riverside, 144–182.
- Sandberg, C.A., Ziegler, W., Dreesen, R., Butler, J.L., 1988. Part 3: Late Frasnian mass extinction: Conodont event stratigraphy, global changes, and possible causes. *Courier Forschungsinstitut Senckenberg* 102, 263–307.
- Sandberg, C.A., Poole, F.G., Johnson, J.G., 1989. Upper Devonian of Western United States. In: McMillan, N.J., Embry, A.F., Glass, D.J. (Eds), *Devonian of the World. Proceedings of the Second International Symposium on the Devonian System*, Calgary, Canada. Canadian Society of Petroleum Geologists, *Memoir* 14 (1), 183–220.

- Sandberg, C.A., Morrow, J.R., Warme, J.E., 1997. Late Devonian Alamo impact event, global Kellwasser events, and major eustatic events, eastern Great Basin, Nevada and Utah. *Brigham Young University Geology Studies* 42, 129–160.
- Sandberg, C.A., Morrow, J.R., Ziegler, W., 2002. Late Devonian sea-level changes, catastrophic events, and mass extinctions. In Koeberl, C., MacLeod, K.G. (Eds), *Catastrophic Events and Mass Extinctions: Impacts and Beyond*. Geological Society of America, Special Papers 356, 473–487.
- Sandberg, C.A., Morrow, J.R., Poole, F.G., Ziegler, W., 2003. Middle Devonian to Early Carboniferous event stratigraphy of Devils Gate and Northern Antelope Range sections, Nevada, U.S.A. *Courier Forschungsinstitut Senckenberg* 242, 187–207.
- Scotese, C.R., McKerrow, W.S., 1990. Revised world maps and introduction. *Memoirs of the Geological Society, London* 12, 1–21.
- Signor, P.W., McMenamin, M.A.S., 1988. The Early Cambrian worm tube *Onuphionella* from California and Nevada. *Journal of Paleontology* 62, 233–240.
- Wilson, M.A., Taylor, P.D., 2001. Palaeoecology of hard substrate faunas from the Cretaceous Qahlah Formation of the Oman mountains. *Palaeontology* 44, 21–41.
- Van Hoey, G., Guilini, K., Rabaut, M., Vincx, M., Degraer, S., 2008. Ecological implications of the presence of the tube-building polychaete *Lanice conchilega* on soft-bottom benthic ecosystem. *Marine Biology* 154, 1009–1019.
- Vinn, O., Mutvei, H., 2009. Calcareous tubeworms of the Phanerozoic. *Estonian Journal of Earth Sciences* 58, 286–296.
- Vinn, O., Luque, J., 2013. First record of a pectinariid-like (Polychaeta, Annelida) agglutinated worm tube from the Late Cretaceous of Colombia. *Cretaceous Research* 41, 107–110.

- Zatoń, M., Kano, Y., Wilson, M.A., Filipiak, P., 2012. Unusual tubular fossils associated with microbial crusts from the Middle Jurassic of Poland: agglutinated polychaete worm tubes? *Palaios* 27, 550–559.
- Zhao, H., Sun, C., Stewart, R.J., Waite, J.H., 2005. Cement proteins of the tube-building polychaete *Phragmatopoma californica*. *The Journal of Biological Chemistry* 280, 42938–42944.
- Žítt, J., Vodrážka, R., 2013. *Terebella phosphatica* Leriche (Polychaeta) associated with phosphatic crusts and particles (Lower Turonian, Bohemian Cretaceous Basin, Czech Republic). *Cretaceous Research* 41, 111–126.

Table and figure captions:

**Table 1.** Size ranges of particles used for building of the large agglutinated tube.

**Figure 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.

**Figure 2.** The upper Frasnian and lowermost part of the Famennian of the Devils Gate section with a tube-bearing sample indicated by an arrow (based on Bond and Wignall, 2005). Sample numbers DVG8, DVG7 etc. show the position of samples and painted bed numbers from Sandberg et al. (1988).

**Figure 3.** Smaller agglutinated worm tubes from Nevada and the surrounding deposit. A-B. Agglutinated tubes, A. GIUS 4-3659a, B. GIUS 4-3659b. C. Surrounding host deposit rich in tentaculitids (black arrows) and putative bryozoan fragments (white arrows). D-E. ESEM photomicrograph showing some tentaculitid shells (coated by Fe oxides) forming the tube showed in A, aligned nearly perpendicularly to the tube's main axis. F-G. Thin section photomicrograph of the sample revealing a packstone containing ostracodes and tentaculitids. Black spots scattered in the matrix are euhedral crystals of pyrite (black arrows), while those filling the fossils mainly represent pyrite framboids (white arrows); te - tentaculitids, os - ostracodes.

**Figure 4.** Large agglutinated worm tube from Nevada and specific composition in different parts of the tube, formed by ostracodes (white arrows), echinoderm ossicles (grey arrows) and

tentaculitids (white arrows), GIUS 4-3660. The quantity of different particles forming the tube is shown on the histograms. Due to their rarity, the putative bryozoan fragments were omitted.

**Figure 5.** ESEM photomicrographs showing particular objects used for construction of the large tube. A. ostracode carapaces and isolated valves (white arrows), and tentaculitid shells (black arrows). B. Ostracode carapaces and valves (white arrows) and echinoderm ossicles (grey arrows). C. Packed tentaculitid shells (black arrows). D. Closely spaced ostracode carapaces (white arrows) and a putative bryozoan fragment (asterisk).

**Figure 6.** Size distribution of particles used for building of the large tube. *n* - number of measured particles.

**Figure 7.** Binocular microscope (A-B) and ESEM (C-D) photomicrographs of sediment surrounding the large tube, showing the presence of ostracode carapaces (white arrows), tentaculitid shells (black arrows) and putative bryozoan fragments (grey arrows).