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# Possible polychaete tubeworms from the Late Emsian (Early Devonian) of the Parana Basin, Brazil

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**Plastically deformed and silicified worm tubes from the Late Emsian (Early Devonian) of the Parana Basin are described herein as a new species and genus of annelid worms *Annulitubus mutveii* gen. et sp. nov. The tubes are straight and ornamented by smooth rings. Their microstructure is homogenous, which most likely is a diagenetic alteration. The characteristic early diagenetic compression of the tubes may point out to their original elastic organic tube wall. We cannot state it with full confidence but the most likely tube producers were tube-dwelling polychaete annelids, which were otherwise uncommon in the Paleozoic times.**

## Introduction

Worm tube-like fossils are known since the Ediacaran (Vinn and Zatoń 2012a; Cortijo et al. 2015a, b) and are increasingly more common in the Paleozoic (Vinn and Mutvei 2009). However, in contrast to their modern counterparts, the Paleozoic tubeworm fauna was dominated by non-annelids (Vinn and Mutvei 2009). The problematic Paleozoic tubeworms are difficult to classify, mostly because their tubes lack diagnostic features that would permit reliable taxonomic interpretation. According to Luci et al. (2013), the taxonomy of polychaetes (serpulids) is based on characteristics provided by the chaetae, which are very rarely preserved in the fossil record. The most important tube builders of the Paleozoic were tentaculitoids, both encrusting and free-living forms (Vinn and Mutvei 2009). Tentaculitoids are an extinct group of worm-like animals with small conical calcitic shells that have usually been affiliated either with molluscs or lophophorates (Vinn and Zatoń 2012b). Other abundant Paleozoic worm tubes have apatitic compositions, such as *Sphenothallus* and the hyolithelminths (Vinn and Mutvei 2009; Muscente and Xiao 2015). There are also reports of possible annelid tubeworms from hydrothermal vent and hydrocarbon seep sediments of the Paleozoic, but their phylogenetic relationships to modern annelids remain uncertain (Little et al. 1997; Boyce et al. 2003; Peckmann et al. 2005). The oldest record of non-tubicolous polychaetes dates back to the Cambrian (Conway Morris and Peel 2008; Vinther et al. 2011; Ippolitov et al. 2014).

Polychaete tubes might be composed of different materials: calcareous (Serpulidae, some Cirratulidae, and Sabellidae), muddy (some Sabellidae), mucous (Alvinellidae, Eunicidae, Chaetopteridae, Maldanidae, Nereididae, Onuphidae, Siboglinidae, and some Sabellidae), and agglutinated (Ampharetidae, Owenidae, Petcinaridae, Sabellariidae, and Terebellidae) (Day 1967; Fauchald 1977; Berke and Woodin 2008; Merz 2015). Serpulids with the tubes composed of calcium carbonate have the highest fossilization potential. In some cases also the organic polychate tubes can be preserved due to silicification. Such a process has been described for modern organic polychaete tubes from hydrothermal vents by Georgieva et al. (2015). Fossilized organic worm tubes with diverse morphologies in vent sites can be traced back to the early Silurian (Little et al. 1998, 1999). Fossilized organic vestimentiferan tubes are also well known from the Oligocene seep carbonates in Washington state of the USA (Goedert et al. 2000). The walls of these tubes apparently underwent an early microcrystalline aragonite mineralization, which might be subsequently replaced by quartz (Goedert et al. 2000).

The tubes reported in this contribution were first classified to *Serpulites* (Clarke 1913) and were later redescribed as *Sphenothallus* Hall, 1847 (see Van Iten et al. 1992) that is usually affiliated with the cnidarians. Here we describe a new genus and species of allegedly organic tubes and interpret them as polychaete annelids. These tubes represent the earliest known tubicolous annelids from South America.

The aims of this report are: (i) to describe tubeworm fossils from the Devonian of the Parana Basin, Brazil, (ii) to analyse the tube microstructure and composition, and (iii) to discuss the possible zoological affinities of these tubeworms.

*Institutional abbreviations.*—UFRJ MN, paleoinvertebrate fossil collection of the Geology and Paleontology Department of the National Museum, Rio de Janeiro Federal University, Brazil; UTFPR, Laboratory of Geology, Pedology and Paleontology of Paraná Technological Federal University, campus Dois Vizinhos, Brazil.

*Other abbreviations.*—sd, standard deviation; wt, weight percent.

## Geological background

The Paraná Basin is a large intracratonic basin on the South-American platform located in southernmost Brazil and north/

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northwestern Uruguay, with its portions extending into Paraguay and Argentina (see SOM 1, in Supplementary Online Material available at http://app.pan.pl/SOM/app61-Vinn_etal_SOM.pdf). The basin has an area of about 1 700 000 km$^2$, a NE–SW elongated shape, and is approximately 1750 km long and 900 km wide (Petri and Fúlfaro 1983).

The sedimentary infill of the basin from Ordovician to Cretaceous was controlled by tectonic-eustatic cycles (i.e., rise and fall of the base level) linked to the late Palaeozoic orogenic events caused by subduction and terrain accretion along the southwestern margin of the Gondwana continent (Zalán et al. 1990; Milani et al. 2007). The process of the sedimentary infilling was largely arrested by the onset of the Mesozoic rifting of the South Atlantic (e.g., Zalán et al. 1990, Milani et al. 2007). The prevalence of tectono-eustatic cycles (Milani et al. 2007) has generated a stratigraphic record that is marked by numerous interruptions brought about by erosion and non-deposition. Milani et al. (1994, 1998) argued that the infill of the basin consisted of six second-order depositional sequences, ranging in age from the Late Ordovician to the Late Cretaceous. The stratigraphic interval studied herein occurs at the second sequence of Milani et al. (1994), the so-called Paraná Sequence, ranging from the Late Silurian to the Late Devonian. This sequence is represented by the Furnas and Ponta Grossa formations.

Several outcrops of the Ponta Grossa Formation are located in the mid-east region of the Paraná State. The Ponta Grossa Formation is represented by siliciclastic rocks that formed in a shallow epicontinental sea, located at 50–60º paleolatitude, with a predominantly temperate climate. The Ponta Grossa Formation is characterized by shoreface, transitional offshore and offshore deposits. It is mainly formed by grey and locally dark, bituminous and silty shales, with minor fine-grained sandstone beds. Weathering and its physico-chemical effects are commonly associated with fossil destruction or poor preservation (Lange and Petri 1967). The Ponta Grossa Formation is divided into three members: Jaguariaíva, Tibagi, and São Domingos (Lange and Petri 1967). Echinoderms (crinoids, blastoids), arthropods (trilobites), scolecodonts, molluscs (bivalves, gastropods), brachiopods (lingulides), tentaculitids, and *Palaeophycus* traces occur in Ponta Grossa Formation.

Sampling of Ponta Grossa sediments was done at the Rio Caniú outcrop, which is 18 km from Palmeira, PR 151 (Rodovia Deputado João Chede), Paraná State. The coordinates are 25°18’51” S; 50°05’32” W (see SOM 1). According to Scheffler and Fernandes (2007) and Bosetti et al. (2012), the outcrop microfossil assemblage indicates Late Emsian age of the sediments. The other fossil groups that co-occur at the Rio Caniú outcrop are listed in SOM 2.

## Material and methods

More than fifty tube fragments in fine-grained matrix were collected. The tubes were photographed with a scale bar using a Canon T3i digital camera, with a macro lens.

Scanning electron microscopy imaging and analyses of the samples were performed on a variable pressure Zeiss EVO MA15 SEM equipped with Oxford X-MAX energy dispersive detector system and Aztec Energy software for element analysis. The samples were studied as freshly broken surfaces perpendicular to the tube wall in coated samples prepared by depositing 5 nm thick Pt conductive layer using Leica EM SCD 500 high-resolution sputter.

X-ray diffraction (XRD) patterns were measured with a Bruker D8 Advance diffractometer with Johannson-type primary monochromator filtered CuKα radiation in the 2θ range 3–70°, with step size 0.02° 2θ and counting time 0.5 s per step using a LynxEye linear detector. The X-ray tube was operated at 40 kV and 40 mA. Host sediment samples and minute pieces of a tube were powdered by hand using an agate mortar. The host sediment was prepared for measurement as powdered unoriented preparation in a steel sample holder; the tube powder was suspended in ethanol and an XRD preparation was made dropping dense suspension of the sample on a low background silicon mono-crystal sample holder. Mineral composition was modelled using Rietveld algorithm based on code Siroquant 3.0 (Taylor 1991).

## Systematic palaeontology

### Phylum Annelida Lamarck, 1809

### Class Polychaeta? Grube, 1850

### Genus *Annulitubus* nov.

*Etymology*: From Latin *annulus*, ring, and *tubus*, tube.

*Type species*: *Annulitubus mutveii* sp. et gen. nov., monotypic; see below.

*Diagnosis*.—As for the type species.

*Stratigraphic and geographic range*.—Ponta Grossa Formation, Upper Emsian, Lower Devonian of Paraná Basin, Brazil.

### *Annulitubus mutveii* sp. nov.

Figs. 1, 2.

*Etymology*: After Harry Mutvei, in honour to his studies on skeletal structures of various organisms.

*Type material*: Holotype: MN 9571-Ia, tube fragment (Fig. 1B). Paratypes: MN 9571-Ib–g (Fig. 1A).

*Type locality*: Rio Caniú outcrop, Palmeira City, Brazil.

*Type horizon*: Ponta Grossa Formation, Upper Emsian, Lower Devonian.

*Material*.—More than fifty tube fragments, belonging to the same sample (MN 9571-I) from the type locality.

*Diagnosis*.—Straight tubes with an almost constant diameter. External surface is smooth or covered with shallow rings 0.5 mm distant from one another. The interspaces of rings are flat. Tube lumen is smooth.

*Description*.—Tubes are straight to very slightly curved. Tube fragments are up to 2.5 cm long and are not attached to substrate. Tube diameter is almost constant throughout the studied fragments. Tubes are 2.9–5.8 mm wide (N = 18, mean = 4.3 mm, sd = 0.76 mm). Tube fragments are compressed and have an elliptical cross section. They have relatively thin walls and constant thickness (0.1–0.15 mm thick). Tube surface is usually smooth, but some tubes have variously developed perpendicular ornamentation in a form of complete rings. There are seven to ten rings per 5 mm. Two adjacent rings are always separated from each another with an interspace. These rings are somewhat irregularly spaced, usually longer than typical rings. The interspaces between the rings are flat and smooth. The boundary between the interspaces and rings is not sharp. There are no growth-lines between the rings. Tube lumen is smooth without any ornamentation.

*Remarks*.—These tubeworm fossils from the Devonian of Brazil have usually been attributed to *Sphenothallus sica* (Salter, 1856). This tradition follows Clarke (1913) who identified them as *Serpulites sica* from the Ponta Grossa Shales of the Devonian of Brazil. *S. sica* is similar to the described species in having long tubes. However, the described species differs from *S. sica* by the lack of branching and longitudinal thickenings of the tube. It also has transverse rings that are not known in *S. sica*. All *Sphenothallus* tubes have a phosphatic composition that is inconsistent with the composition of the described tubes. The described tubes differ from the other known Paleozoic "worm" tubes, such as cornulitids (Vinn and Mutvei 2009: 288, fig. 1) and microconchids (Wilson et al. 2011: 787, fig. 2) by their almost constant diameter and external ornamentation.

*Stratigraphic and geographic range*.—Type locality and horizon only.

## Results

**Preservation and morphology**.—Tube fragments occur in clusters and are packed closely together. They are of similar size and most fragments have the same orientation (Fig. 1A). The compression of tube fragments varies even within a single fragment. Most of the fragments show somewhat "plastic" deformations (Fig. 1A). Microscopically, the tube surface is not smooth and contains numerous small caverns (Fig. 2B). Tube surface does not reveal any signs of encrustation or bioerosion, only some cracks of possible telodiagenetic origin (Fig. 2B). Among the concordant deformed tubes, one small circular tube was encountered, preserved perpendicular to the bedding plane (Fig. 2D). This portion is thought to represent the attachment structure of tubiculous animal, as represented by the reconstruction (Fig. 3). This small circular tube has similar composition and external morphology to co-occurring larger tube fragments, and presumably does not belong to another type of tube.

**Microstructure and mineral composition**.—Tube microstructure is homogenously composed of small quartz crystals, mostly 2–5 μm in diameter; some crystals can reach 10 μm in diameter (Fig. 2C). Mineral composition of the host sediment is dominated by kaolinite and K-mica, and illitic mixed-layer clay mineral that altogether compose about 70 wt% of crystalline phases. Quartz constitutes ca. 25 wt% of the mineral phases in host rock and also some small admixtures (< 5 wt%) of K-feldspar, boehmite and anatase were identified (SOM 3). The analysed tube fragments are composed of quartz (SOM 3). Small amounts (< 10 wt%) of K-mica and kaolinite identified in this sample are most probably due to the host rock contamination.

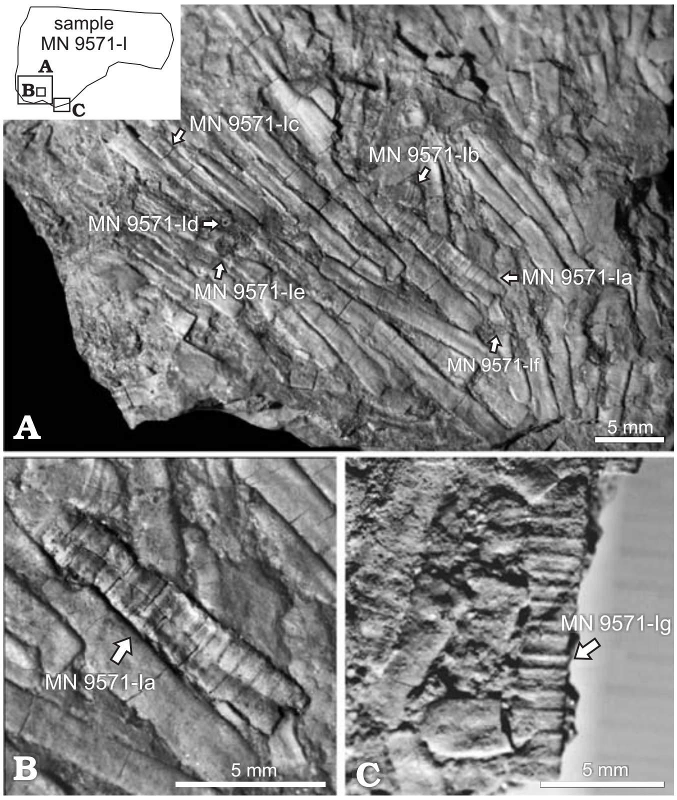

Fig. 1. Sample (MN 9571-I) from Rio Caniú outcrop, Brazil; Ponta Grossa Formation, Upper Emsian, Lower Devonian. **A**. Fragment showing numerous tubes; holotype of *Annulitubus mutveii* gen. et sp. nov. (MN 9571-Ia) and paratypes (MN 9571-Ib–e). Note that all tube fragments are straight and have similar orientation, some show smooth surfaces, with very subtle striae, in others it is possible to see shallow rings. **B**. Enlarged holotype (MN 9571-Ia), note the smooth rings. **C**. Fragment showing paratype (MN 9571-Ig).

## Discussion

**Taphonomy and preservation**.—As living organisms these worms probably formed clusters of high density populations. In the analysed sample the tubes appear to have been transported and fragmented by water currents that led to somewhat oriented deposition of tube fragments. Therefore, these tube fragments are not preserved in situ as indicated by the almost complete absence of proximal attachment parts. It is likely that they represent a parautochthonous assemblage as they are not severely fragmented and abraded. The tubes were probably originally circular in cross section and are deformed due to the sediment compression. Some tubes reveal some "plastic" deformations which suggest their original flexibility. This flexibility can be explained by their originally high content of organics and relatively thin walls. The low number of preserved fragments of smaller tubes (e.g., juveniles) could indicate their sorting in transport. The tube fragments probably originate from a nearby area of mass occurrence of the

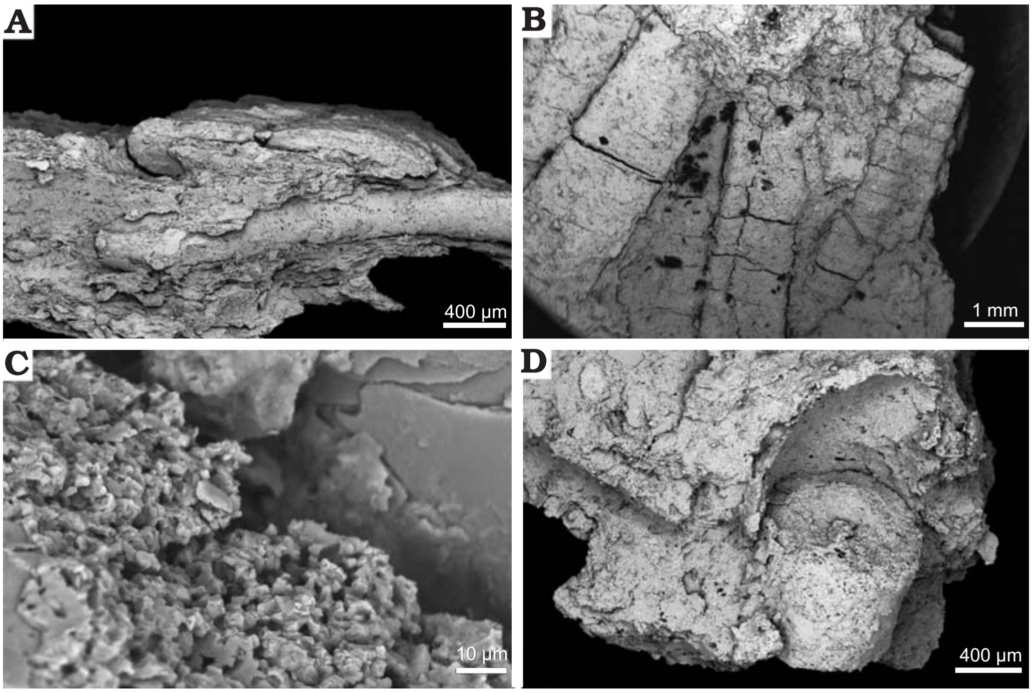

Fig. 2. Tubes of *Annulitubus mutvei* gen et sp. nov. (MN 9571-I) from Rio Caniú out crop, Brazil; Ponta Grossa Formation, Upper Emsian, Lower Devonian. **A**. Two tubes in lateral view showing plastic deformation. **B**. Tubes showing cracks of possible diagenetic origin, upper view. **C**. Middle to left of the image is the tube's surface showing caverns. **D**. Small circular tube fragment, showing no lateral thickenings.

living tubeworms. The worms may have grown gregariously but they probably were not attached to each other. So far it is impossible to determine whether these worms grew within soft sediment, as many Recent polychaetes do, or were attached to hard substrates. It is known that the Devonian strata of the Apucarana Sub-basin are mostly composed of silty shale, and that coquinas are almost absent there. The lack of hard substrates with holdfasts or encrusting juvenile worm tubes supports the possibility that these tubeworms may have been partially infaunal and grew within the sediment. The only fossils commonly occurring in these rocks, which could serve as attachment substrate are shells of lingulide brachiopods. Indeed some intensely bored lingulide valves are known from the studied region (though not from the same locality as the tubes). The numbers and distribution pattern of the borings (numerous borings in various shells with no preference of a specific region) indicate that most likely they were produced by epibionts. The identity of this epibiont remains unknown and there is no direct evidence that the tubiculous animal was indeed the producer of such borings.

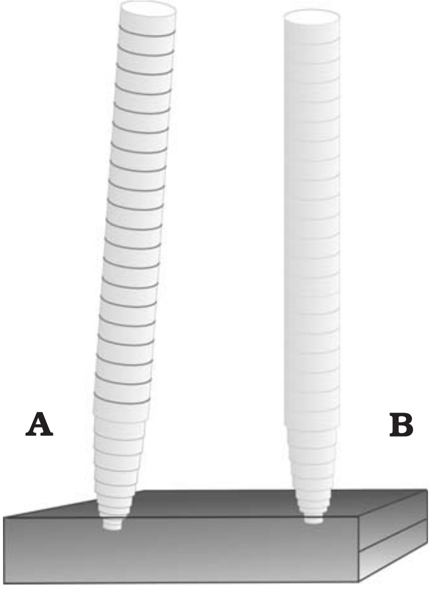

Fig. 3. Reconstruction of the tubes in life position. Specimens with shallow rings (**A**) and with very thin striation on their surface (**B**).

**Mineral composition and microstructure**.—Biomineralized worms, both Recent and fossil, have aragonitic, calcitic, or mixed aragonitic-calcitic skeletons. Skeletons with such compositions are known in serpulids (Vinn et al. 2008). Apatitic tubes occur in the tubeworm-like cnidarian *Sphenothallus* (Van Iten et al. 1992). The tubes studied here are silicified. Silicification is a common fossilization process that enables preservation of biological structures at very different scales from single cell structures to macro-objects like trees. Silica precipitation replicating organisms can be initiated from silica-saturated pore-fluids by changing (lowering) pH or temperature (cooling) if the circulating waters are of hydrothermal origin (e.g., Raymond 2002). It is worth to note that silicification of organic worm tubes has been observed at hydrothermal vents (see Georgieva et al. 2015). It is also possible that during diagenesis, ion-migration of silica may result in its concentration in some beds and depletion in others, which dissolves and redistributes biogenic amorphous silica (Maliva et al. 1989). Typically calcitic organisms are silicified because the calcite and silica ($SiO_2$) show contrasting precipitation-dissolution behaviour at pH 9 (Clayton 1986). At reaching $pH > 9$, solubility of silica increases exponentially with pH while calcite is precipitated. In contrast, when pore water pH is lowered ($pH < 8–9$), calcite starts to dissolve and silica precipitation is favoured. Though silicification of biogenic phosphate (e.g., lingulates) has been described in deeply buried sediments due to pressure dissolution of apatite and replacement by silica

(Horowitz 1967), at moderate burial depths the apatite is stable down to pH 6–7 (Dill 2001) and its diagenetic replacement by silica is unlikely. If the tubes were originally calcareous then their structure would have been broken into many little pieces, if ever compressed under the load of overlying sediment, and should not show the deformations observed in the studied tubes. Also, all calcareous fossils associated with the tubes are preserved as molds, which means that the calcite was dissolved during diagenesis. Therefore, it is likely that the tubes were originally not calcareous or phosphatic, but organic, which could explain the properties of the tubes described herein. Alternatively, the composition of tubes dominated by silica could hint at agglutinated worms. However, the microstructure of the tubes does not resemble agglutinated worm tubes that are usually composed of detrital quartz sand/silt grains (Signor and McMenamin 1988). Studied tubes are composed of homogenous microcrystalline quartz aggregate indicating direct precipitation/recrystallization of silica at numerous nucleation sites. Therefore, it seems that the studied tubes were not agglutinated. Similar homogeneous microstructure occurs in several biomineralized tubeworms, but the composition of these structures is different. However, it must be pointed out that the observed microstructure of the studied tubes likely does not reflect the original microstructure of these worm tubes.

**Zoological affinities**.—Exoskeletons of various invertebrates can have a tubicolous shape. Most common are the tubeworms belonging to annelids. In the Paleozoic there are several groups with tube-like skeletons. In contrast to modern oceans, possible lophophorates, such as cornulitids, microconchids, and tentaculitids, formed an important portion of the animals with tubicolous exoskeletons (e.g., Zatoń and Krawczyński 2011; Zatoń et al. 2014). They form an extinct group of tentaculitoid tubeworms (Vinn and Mutvei 2009). They had conical calcitic skeletons that were usually attached to a hard substrate. The studied worm tubes differ from tentaculitoids by not being conical in adult part, though they may have been tapering distally. Thus, it is unlikely that they belong to the tentaculitoids. The other common Palaeozoic tubeworm-like fossils belong to cnidarians. The most important Paleozoic tubicolous cnidarian is *Sphenothallus*, which has apatitic tubes with lateral thickenings (Van Iten et al. 1992). The studied tubes do not show lateral thickenings and were probably originally not apatitic. Therefore, it is unlikely that the worm tubes described here belong to *Sphenothallus*. In the modern oceans numerous annelids are tube builders. Most annelid tubes are not biomineralized (i.e., alvinellids, chaetopterids, eunicids, maldanids, nereidids, onuphids, sabellids, siboglinids; Day 1967; Fauchald 1977; Berke and Woodin 2008; Merz 2015) and it is possible that the described tubes were also originally organic. The general shape of the tubes, their almost constant diameter throughout the studied fragments, is consistent with various annelid tubes. Annelids are an ancient group and it is possible that tube-building annelids were present in the middle Palaeozoic (Little et al. 1997; Boyce et al. 2003; Peckmann et al. 2005). The consistency of the described tube morphology compared to those known in several polychaetes could indicate an annelid affinity. Organic annelid tubes with rings are present in frenulates. Some chaetopterid tubes are also annulated, and have constant diameters along their length (Fauchald 1977).

## Conclusions

Late Emsian silicified tubes were found at the Rio Caniú outcrop, Paraná State, Brazil. These tubes are here attributed to *Annulitubus mutveii* gen. et sp. nov. They are straight, smooth and sometimes show shallow rings. Tube fragments occur packed together and are of similar size. All tube fragments are concordant to the bedding plane and show plastic deformation. One probable distal portion was found, perpendicular to the bedding plane; it is rounded and smaller than the majority of the tubes. Original flexibility, suggested by the plastic deformation of the tubes, can be explained by their original high content of organics and relatively thin walls. Therefore, it is possible that the tubes were produced by polychaete annelids which are known to build similar organic tubes.

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## References

Berke, S.K. and Woodin, S.A. 2008. Tube decoration may not be cryptic for *Diopatracuprea* (Polychaeta: Onuphidae). *Biology Bulletin* 214: 50–56.

Bosetti, E.P. Grahn, Y., Horodyski, R.S., and Mauller, M. P. 2012. The first recorded decline of the Malvinokaffric Devonian fauna in the Paraná Basin (southern Brazil) and its cause; taphonomic and fossil evidences. *Journal of South American Earth Sciences* 37: 228–241.

Boyce, A.J., Little, C.T.S., and Russel, M.J. 2003. A new fossil vent biota in the Ballynoe barite deposit, Silvermines, Ireland: evidence for intracratonic sea-floor hydrothermal activity about 352 Ma. *Economic Geology* 98: 649–656.

Clarke, J.M. 1913. Fósseis devonianos do Paraná. *Monographia do Serviço Geológico e Mineralógico do Brazil* 1: 1−353.

Clayton, C.J. 1986. The chemical environment of flint formation in Upper Cretaceous chalk. *In*: G.D.G. Sieveking and M.B. Hart (eds.), *The Scientific Study of Flint and Chert*, 43–54. Cambridge University Press, Cambridge.

Conway Morris, S. and Peel, J.S. 2008. The earliest annelids: lower Cambrian polychaetes from the Sirius Passet Lagerstätte, Peary Land, North Greenland. *Acta Palaeontologica Polonica* 53: 137–148.

Cortijo, I., Cai, Y., Hua, H., Schiffbauer, J.D., and Xiao, S. 2015a. Life history and autecology of an Ediacaran index fossil: Development and dispersal of *Cloudina*. *Gondwana Research* 28: 419–424.

Cortijo, I., Martí Mus, M., Jensen, S., and Palacios, T. 2015b. Late Ediacaran skeletal body fossil assemblage from the Navalpinoanticline, central Spain. *Precambrian Research* 267: 186–195.

Day, J.H. 1967. A monograph on the Polychaeta of Southern Africa. *British Museum (Natural History)* 656: 1–878.

Dill, H.G. 2001. The geology of aluminium phosphates and sulphates of the alunite group minerals: a review. *Earth-Science Reviews* 53: 35–93.

Fauchald, K. 1977. The polychaete worms. Definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County, Science Series* 28: 1–188

Georgieva, M.N., Little, C.T.S., Ball, A.D., and Glover, A.G. 2015. Mineralization of *Alvinella* polychaete tubes at hydrothermal vents. *Geobiology* 13: 152–169.

Goedert, J.L., Peckmann, J., and Reitner, J. 2000. Worm tubes in an allochthonous cold-seep carbonate from Lower Oligocene rocks of Western Washington. *Journal of Paleontology* 74: 992–999.

Grube, A.E. 1850. Die Familien der Anneliden. *Archiv für Naturgeschichte, Berlin* 16: 249–364.

Hall, J. 1847. *Palaeontology of New York. Volume 1. Containing Descriptions of the Organic Remains of the Lower Division of the New York System*. 339 pp. C. Van Benthuysen, Albany.

Horowitz, D. 1967. Diagenetic replacement and solution of biogenic phosphate by silica. *Journal of Sedimentary Petrology* 37: 1238–1240.

Ippolitov, A.P., Vinn, O., Kupriyanova, E.K., and Jäger M. 2014. Written in stone: history of serpulid polychaetes through time. *Memoirs of Museum Victoria* 71: 123–159.

Lamarck, J.-B. 1809. Memoires sur les fossiles des environs de Paris. *Annales du Museum d'Histoire Naturelle* 1: 299–312.

Lange, F.W. and Petri, S. 1967. The Devonian of the Paraná Basin. *Boletim Paranaense de Geociências* 21−22: 5–55.

Little, C.T.S., Herrington, R.J., Maslennikov, V.V., and Zaykov, V.V. 1998. The fossil record of hydrothermal vent communities. *Geological Society of London, Special Publications* 148: 259–270.

Little, C.T.S., Herrington, R.J., Maslennikov, V.V., Morris, N.J., and Zaykov, V.V. 1997. Silurian hydrothermal vent community from the southern Urals, Russia. *Nature* 385: 146–148.

Little, C.T.S., Maslennikov, V.V., Morris, N.J., and Gubanov, A.P. 1999. Two Palaeozoic hydrothermal vent communities from the southern Ural mountains, Russia. *Palaeontology* 42: 1043–1078.

Luci, L., Garberoglio, R.M., and Lazo, D.G. 2013. Serpulids and other calcareous tube-dwelling encrusting polychaetes from the Early Cretaceous Agrio Formation (Neuquén Basin, Argentina). *Geobios* 46: 213–224.

Maliva, R.G., Knoll, A.H., and Siever, R. 1989. Secular change in chert distribution: A reflection of evolving biological participation in the silica cycle. *Palaios* 4: 519–532.

Merz, R.A. 2015. Textures and traction: how tube-dwelling polychaetes get a leg up. *Invertebrate Biology* 134: 61–77.

Milani, E.J., França, A.B., and Schneider, R.L. 1994. Bacia do Paraná. *Boletim Geociências da Petrobrás, Rio de Janeiro* 8: 69–82.

Milani, E.J. and Ramos, V.A. 1998. Orogenias Paleozóicas no Domínio Sul-Ocidental do Gondwana e os ciclos de subsidência da Bacia do Paraná. *Revista Brasileira de Geociências, São Paulo* 28: 473–484.

Milani, E.J., Melo, J.H.G., Souza, P.A., Fernandes, L.A., and França, A.B. 2007. Bacia do Paraná. *Boletim de Geociências da Petrobrás* 15: 265–287.

Muscente, A.D. and Shuhai, X. 2015. New occurrences of *Sphenothallus* in the lower Cambrian of South China: Implications for its affinities and taphonomic demineralization of shelly fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology* 437: 141–164.

Peckmann, J., Little, C.T.S., Gill, F., and Reitner, J. 2005. Worm tube fossils from the Hollard Mound hydrocarbon-seep deposit, Middle Devonian, Morocco: Palaeozoic seep-related vestimentiferans? *Palaeogeography, Palaeoclimatology, Palaeoecology* 227: 242–257.

Petri, S. and Fúlfaro, V.J. 1983. *Geologia do Brasil*. 631 pp. EDUSP, São Paulo.

Raymond, L.A. 2002. Cherts, evaporites, and other precipitated rocks. *In*: M.J. Kemp and R. Russian (eds.), *Petrology: The Study of Igneous, Sedimentary, and Metamorphic Rocks*, 436–447. McGraw-Hill, Boston.

Salter, J.W. 1856. Description of Palaeozoic Crustacea and Radiata from South Africa. *Transactions of the Geological Society of London, Series 2* 7: 215–224.

Scheffler, S.M. and Fernades, A.C.S. 2007.Crinoidea da Formação Ponta Grossa (Devoniano, Bacia do Paraná), Brasil. *Arquivos Do Museu Nacional* 65: 83–98.

Signor, P.W. and McMenamin, M.A.S. 1988. The early Cambrian worm tube *Onuphionella* from California and Nevada. *Journal of Paleontology* 62: 233–240.

Taylor, J.C. 1991. Computer programs for standardless quantitative analysis of minerals using the full powder diffraction profile. *Powder Diffraction* 6: 2–9.

Van Iten, H., Cox, R.S., and Mapes, R.H. 1992. New data on the morphology of *Sphenothallus* Hall: implications for its affinities. *Lethaia* 25: 135–144.

Vinn, O., Hove, H.A. ten, Mutvei, H., and Kirsimäe, K. 2008. Ultrastructure and mineral composition of serpulid tubes (Polychaeta, Annelida). *Zoological Journal of the Linnean Society* 154: 633–650.

Vinn, O. and Mutvei, H. 2009. Calcareous tubeworms of the Phanerozoic. *Estonian Journal of Earth Sciences* 58: 286–296.

Vinn, O. and Zatoń, M. 2012a. Inconsistencies in proposed annelid affinities of early biomineralized organism *Cloudina* (Ediacaran): structural and ontogenetic evidences. *Carnets de Géologie* CG2012_A03: 39−47.

Vinn, O. and Zatoń, M. 2012b. Phenetic phylogenetics of tentaculitoids—extinct problematic calcareous tube-forming organisms. *GFF* 134: 145–156.

Vinther, J., Eibye-Jacobsen, D., and Harper, D.A. 2011. An Early Cambrian stem polychaete with pygidial cirri. *Biology Letters* 7: 929–932.

Wilson, M.A., Vinn, O., and Yancey, T.E. 2011. A new microconchid tubeworm from the Lower Permian (Artinskian) of central Texas, USA. *Acta Palaeontologica Polonica* 56: 785–791.

Zalán, P.V., Wolff, S., Conceição, J.C., Marques, A., Astolfi, M.A., Vieira, I.S., Appi, V.T., and Zanotto, O.A. 1990. Bacia do Paraná. *In*: G.P. Raja Gabaglia and E.J. Milani (eds.), *Origem e Evolução das Bacias Sedimentares*, 135–168. Petrobras, Rio de Janeiro.

Zatoń, M. and Krawczyński, W. 2011. New Devonian microconchids (Tentaculita) from the Holy Cross Mountains, Poland. *Journal of Paleontology* 85: 757–769.

Zatoń, M., Zhuravlev, A.V., Rakociński, M., Filipiak, P., Borszcz, T., Krawczyński, W., Wilson, M.A., and Sokiran, E.V. 2014. Microconchid-dominated cobbles from the Upper Devonian of Russia: Opportunism and dominance in a restricted environment following the Frasnian–Famennian biotic crisis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 401: 142–153.

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