

Research



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Devonian agglutinated polychaete tubes: all in all it's just another grain in the wall

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Biom mineralized and organic metazoan tubular skeletons are by far the most common in the fossil record. However, several groups of organisms are also able to agglutinate particles to construct more rigid structures. Here we present a novel type of agglutinated tube from the austral and endemic palaeobiota of the Malvinokaffric realm (Devonian, Brazil). This fossil is characterized by an agglutinated tube made of silt-sized particles forming an unusual flanged morphology that is not known from the fossil record. Besides being able to select specific particles, these organisms probably lived partially buried and were detritus/suspension feeders. Comparisons across different modern groups show that these fossils are strongly similar to tubes made by polychaetes, specifically from the family Maldanidae. If this interpretation is correct, then an early divergence of the Sedentaria clade may have occurred before the Devonian.

1. Introduction

Metazoan tubular fossils of problematic affinities are a common feature of many fossil assemblages from the late Ediacaran period (*ca* 550 Ma) onwards (e.g. [1–3]). These fossils comprise a wide array of morphologies and skeleton compositions (e.g. calcite, aragonite, organic, apatite) [4–7]. Among these, one important but often overlooked group include the agglutinated tubes. Differently from biomineralized or purely organic constructions, agglutinated tubes are built by detrital particles, often glued together by an organic cement secreted by the living organism [8,9]. However, interpreting their biological affinities is often difficult due to the lack of diagnostic characters.

In modern marine settings, several different groups of organisms are capable of producing agglutinated tubes, including annelids [10], cnidarians [11], phoronids [12], nematodes [13], crustaceans [14], rotifers [15] and foraminifers [16]. Despite this diversity, annelids are considered the main producers of large agglutinated tubes, a situation that can also be true for the fossil record [17]. Thus, if properly addressed, the fossil record holds great potential to reveal further information about the relatively poorly known geological history of Annelida [18,19].

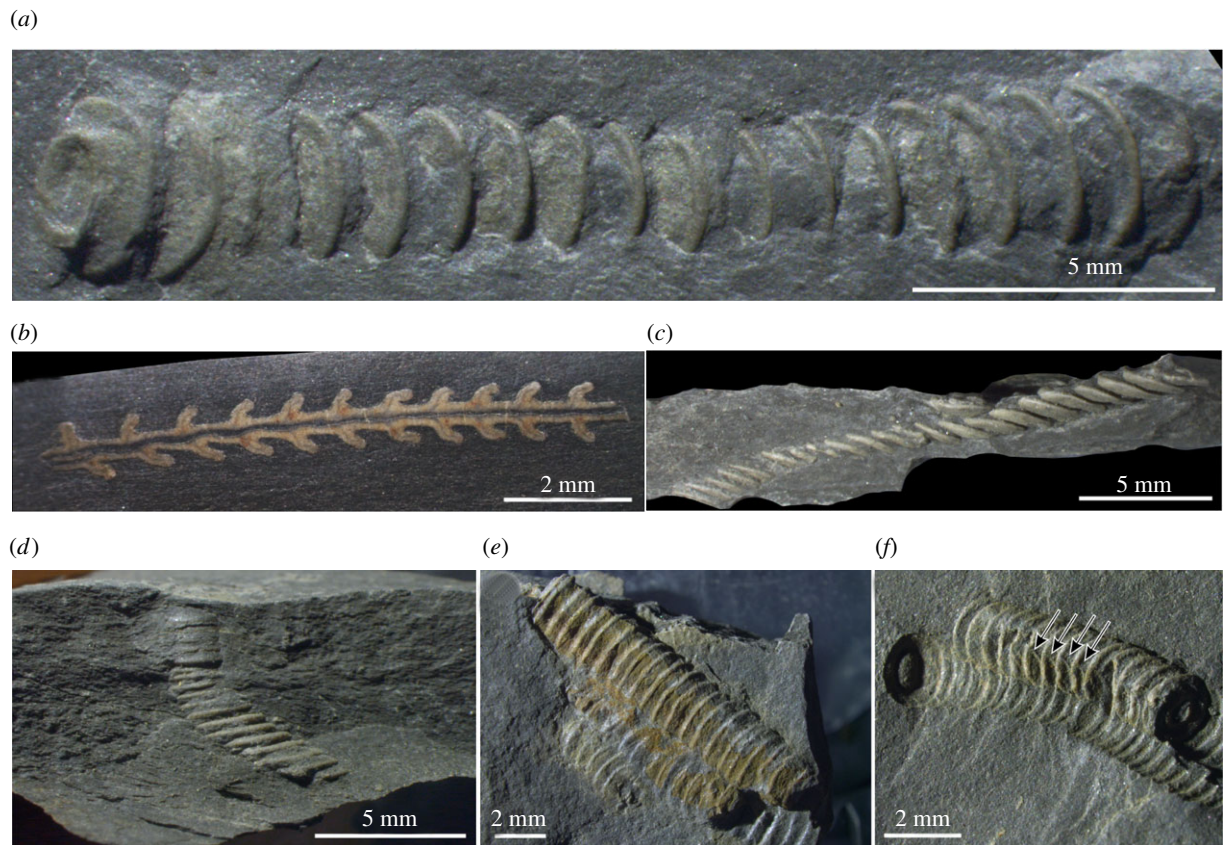


Figure 1. Morphology and life position of *Annulitubus mutvei*. (a) Bedding plane view of hand samples. (b) Polished section through a longitudinal cut of a tube showing the flanged morphology. (c,d) Specimens in life position, vertically/diagonally oriented within the sediment. (e,f) Individuals with interlocked flanges. (Online version in colour.)

Although the fossil record of agglutinated tubes extends back to the Early Cambrian [20], they are relatively rare throughout the remaining Phanerozoic. This is often related to their delicate nature [21–23], which would facilitated disaggregation and fragmentation upon transport. Thus, these fossils are mostly restricted to deposits with exceptional preservation. Here we present a new and unusual occurrence of agglutinated tubular fossils from the Devonian (Givetian) of Brazil. Contrary to previous cases, these fossils are abundant in the strata in which they are found. Additionally, these fossils show strong morphological similarities with modern polychaete flanged tubes; yet their mode of tube construction have no counterpart in the fossil record.

2. Results

(a) Occurrence, morphology and ecology

The tubes occur in the São Domingos Member of the Ponta Grossa Formation. This unit was deposited in storm-influenced shallow marine settings, varying from lower shoreface to offshore environments with expressions of *Cruziana* ichnofacies [24,25]. These fossils are common in Lower Givetian strata (post-Kaçák event), although they are preserved in Eifelian strata, mostly in sections B and C of Sedorko *et al.* [24]. The specimens studied are abundant and occur associated with some elements of the Malvinokaffric biota such as brachiopods and trilobites [26,27]. Details regarding its stratigraphic distribution are available in the electronic supplementary material.

The tubes are centimetric in length (0.6–35 mm), with widths varying between 1.7 and 3.9 mm. The diameter seems to be constant throughout the length. The most singular morphological feature of these tubes is the presence of ‘rings’ throughout most of the length (figures 1 and 2). However, microtomographic and polished section analyses show that this is only an apparent annulation due to the presence of flanges (or collars) along the tube (figures 1b and 2). Each flange has a paraboloid morphology that is more evident in vertically oriented specimens or in micro-CT reconstructions (figure 2). The distance between each flange is also mostly constant (approx. 1.3 mm). The internal surface of the tube does not show any particular morphological feature and appears to have been relatively smooth originally (electronic supplementary material, figure S2).

Although most of the specimens studied here are characterized by flanged tubes, one sample showed some individuals with transitional morphologies, from smooth to collared zones (electronic supplementary material, figure S3). Interestingly, these smooth portions are strikingly similar to the previous described species *Annulitubus mutvei* Vinn *et al.* [28], strongly suggesting that they represent the same taxon at different moments of tube construction; therefore, they are here identified as such, and an emended diagnosis is provided in the electronic supplementary material.

All the tubes studied here displayed evidences of strong plastic deformation (figures 1b and 2). Fragmented remains are also common in assemblages with tubes disposed parallelly to the bedding plane. In these samples, very small fragments can also be observed (figure 2). On the other hand, vertically oriented individuals were also noticed (figure 1c,d; electronic

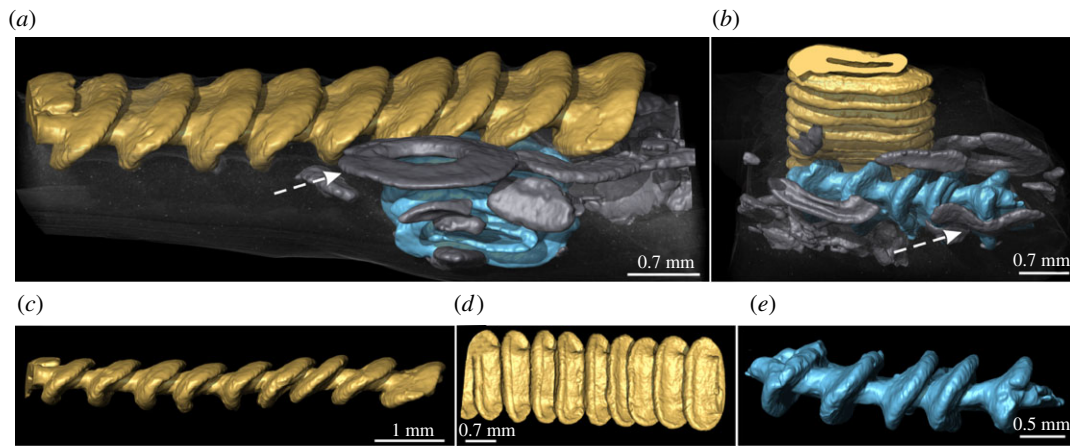


Figure 2. Micro-CT three-dimensional reconstructions. (a,b) Concentration of tubes highlighting the compressed flanges and the presence of tube fragments (arrows), some showing plastic deformation. (c,e) Individualized tubes in lateral (c,e) and 'ventral' (d) view. (Online version in colour.)

supplementary material, figures S4–S6), suggesting the *in situ* preservation of these organisms, which probably had at least a partial, infaunal mode of life. Remarkably, one of these *in situ* samples shows the vertically oriented portion marking the tube passing to a horizontal orientation with respect to the bedding plane (electronic supplementary material, figure S6).

One polished vertically oriented tube showed both opened extremities (electronic supplementary material, figure S5), although this characteristic should be confirmed with additional samples. Notably, some transported individuals show interlocked tubes, with the flanges inside the interspaces of each other (figure 1e,f). This highly unusual conformation is unlikely to result from transport.

(b) Agglutinated nature of the tubes

Although under naked eye and stereomicroscopes investigation the tubes show a whitish solid appearance, scanning electron microscopy (SEM), microCT and petrographic analyses demonstrated that the tubes are composed of angular, silt-size grained clastic particles (figure 3; electronic supplementary material, figures S7 and S8). Rare detrital micas were also perceived within the walls of the tubes (electronic supplementary material, figure S8). Moreover, there is a clear trend of increasing clast size from the internal to the external regions of the wall, from fine-grained silt to coarse-grained silt, respectively.

Energy dispersive spectroscopy (EDS) and synchrotron-based micro X-ray fluorescence (SR- μ XRF) results reveal the dominant siliceous composition of the tubes and confirm their agglutinated nature (figure 4). EDS maps also show the common occurrence of Na-enriched clasts, which Raman spectroscopy demonstrated to correspond to the Na-plagioclase albite (electronic supplementary material, figure S9). The more abundant and silicon-rich grains were confirmed to correspond to quartz (electronic supplementary material, figure S9). Although the host rock also contains quartz and albite, it shows the presence of several other types of detrital clasts. Indeed, the elemental maps corroborates this mineralogical difference: most of the elements are concentrated in the host rock, the exception being silicon and sodium. Interestingly, the strontium map (figure 4v) seems to highlight the increase in granulometry, being more discernible in the larger clastic grains (probably feldspar) at the external edge of the tube walls. Sulfur also shows high intensities in small spots inside the tubes,

which can be related to the presence of occasional pyrite octahedral crystals. These pyrite crystals may be associated with the high-density grains observed in microCT slices and occasional opaque minerals seen in thin sections (electronic supplementary material, figures S7c,d and S8, and movie S1).

3. Discussion

(a) Palaeobiology of *Annulitubus mutvei*

Our results yielded that *A. mutvei* was a gregarious, sedentary, tube-dwelling invertebrate (figure 5). These organisms probably lived partially buried in the substrate, as evidenced by the vertically oriented specimens (figure 1c,d). Although flanged tubes are dominant in our samples, some specimens showing changes from smooth to flanged morphologies indicate that these organisms had some plasticity during skeletogenesis, probably following their ontogeny or lifestyle conditions. Interlocked tubes in transported individuals suggest an original gregarious habit, with some organisms growing closely associated with each other (figure 1e,f). Changes from a vertically to a horizontally oriented tube in one specimen (electronic supplementary material, figure S6) suggests that either the producer was able to construct the tube in different orientations, or that the upper portion of this specimen represents a fallen region of the tube, which extended above the sediment/water interface. Giving this sedentary and semi-infaunal lifestyle, these organisms probably had detritus/suspension feeding strategies. In the same outcrop, *Skolithos* is a common trace fossil in fine-grained sandstones, some of them possibly produced by similar organisms. Indeed, at the stratigraphic level that these fossils occur there are abundant plant fragments that could have been a potential food source.

The tubes were composed of fine detrital grains (fine- to coarse-grained silt) with a high cohesivity of the agglutinated material, since it is possible to find very small fragments with rounded edges, as well as strong evidence of plastic deformation (figure 2a,b). This suggests that the tubes probably had an organic 'glue' keeping the agglutinated structure relatively resistant. The presence of occasional pyrite grains inside the tube wall may reflect the anaerobic decomposition of this original organic matter, although we did not find evidence of remaining kerogenous material. The almost absence of other types of particles, except for quartz and albite, suggests that this organism was able to select the type and

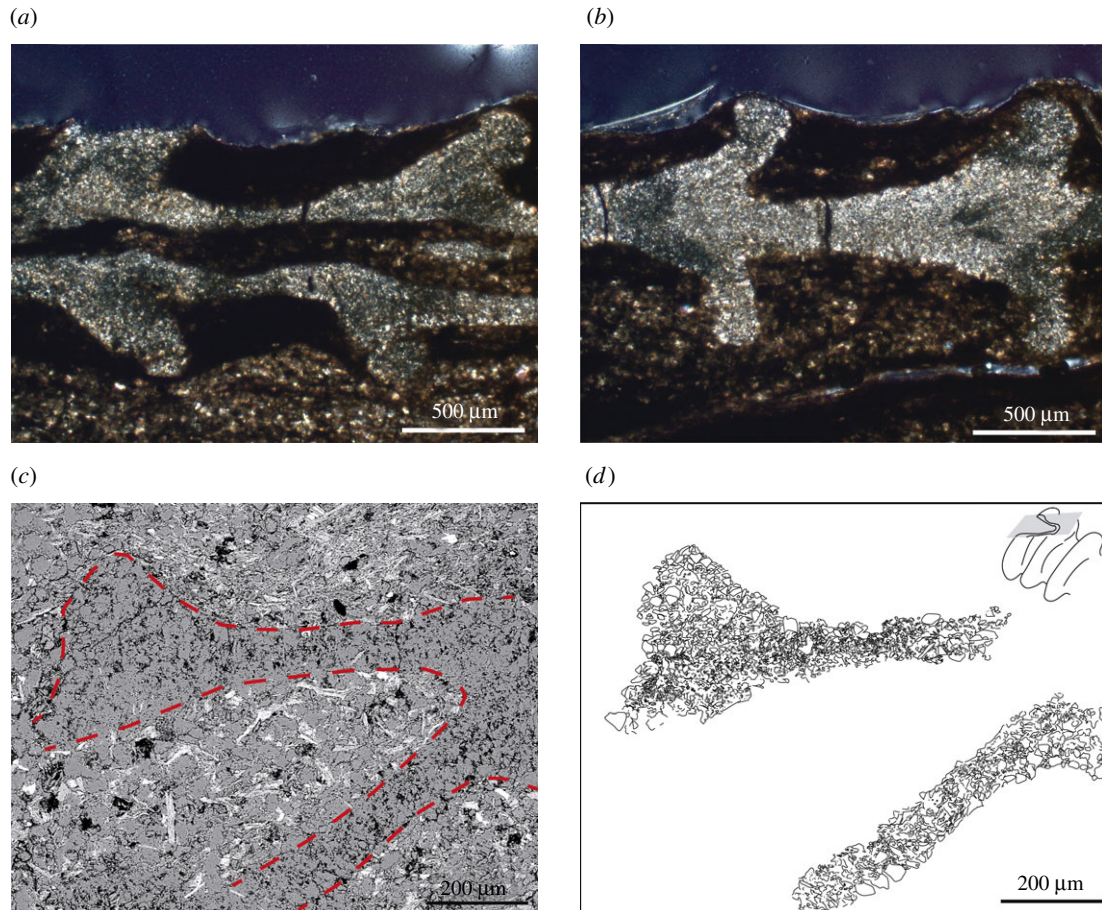


Figure 3. Thin section and SEM micrographs of the tubes. (a,b) Tubes in longitudinal cuts (thin sections) showing the granular texture due to the agglutinated nature of the walls and the increase in clast size from the internal to the external regions of the wall. Crossed Nicols. (c) SEM micrograph of a polished thin section highlighting the region with the fossil. (d) Schematic drawing showing the observed individual clasts in (c), highlighting the increase in granulometry towards the outermost region of the wall. (Online version in colour.)

size of the detrital particle for tube construction. Moreover, these organisms were able to select the size of particles according to the stage of tube construction, leaving the coarser material to the outermost part of the walls.

(b) Biological affinities

Although agglutinated tubes in the fossil record are usually attributed to annelids, there are many other groups that should be taken into consideration when interpreting such fossils; even more given that these fossils usually occur as isolated specimens. Here, the abundance of specimens, allied to their good preservation, particle selectivity, distinct morphology and evidence of life habits, help to better constrain their biological affinities within Annelida.

The tubes of *Annulitubus mutveii* strongly differ from modern agglutinated tubes of several major groups. For instance, ceriantharian tubes often show branching, and, more importantly, do not show particle selection or specific particle arrangement within their tubes [11]. This is likely to be due to their peculiar mode of tube formation that uses ptychocyst tubules; these either rarely trap sediments (Cerianthidae) or work as driftnets, trapping higher amounts of sediment (Arachnactidae and Botrucnidiferidae) [29]. Similarly, phoronids also do not show particle selectivity, and the detrital material comprises a single external layer of agglutinated particles that are not glued together by organic material [12,30]. Phoronids that live in the substrate also present a small opening at the

posterior end of the tube that is not observed in our fossils [30]. Nematodes and rotifers are known to produce agglutinated tubes, but these have much smaller dimensions (approx. 50–100 µm in width; e.g. [13,31]) than the tubes observed here.

Crustaceans (mainly Amphipoda and Tanaidaceae; e.g. *Haploops* sp.) are well-known tube builders, and they can also show a high degree of particle selectivity [14]. Nevertheless, the tubes of crustaceans are usually not as long as those observed in annelids; although some species can still show comparable dimensions to those reported from the fossil record (e.g. *Tanais cavolini* and *Ampelisca abdita* [32,33]). At least for amphipods, molecular evidence suggests that this group emerged during the Permian Period and only diversified during the Late Mesozoic [34]. The fossil record of tanaidaceans is mostly restricted to Mesozoic and Cenozoic occurrences, although some species of the suborder Anthracocaridomorpha are found in Carboniferous and Permian rocks [35].

Modern and fossil unbranched tubular foraminifers are usually attributed to the genus *Bathysiphon*. These organisms also can show particle selectivity, and some specimens may even reach up to 10 cm in length [36,37]. However, in contrast to our fossils, bathysiphonids usually show a more slender nature, have thicker walls that contrast with their narrow lumens, and usually have longitudinal constrictions [36,37].

Finally, and possibly most importantly, none of the above-mentioned groups show flanged tubular morphologies, besides annelids. Indeed, many extant polychaete families

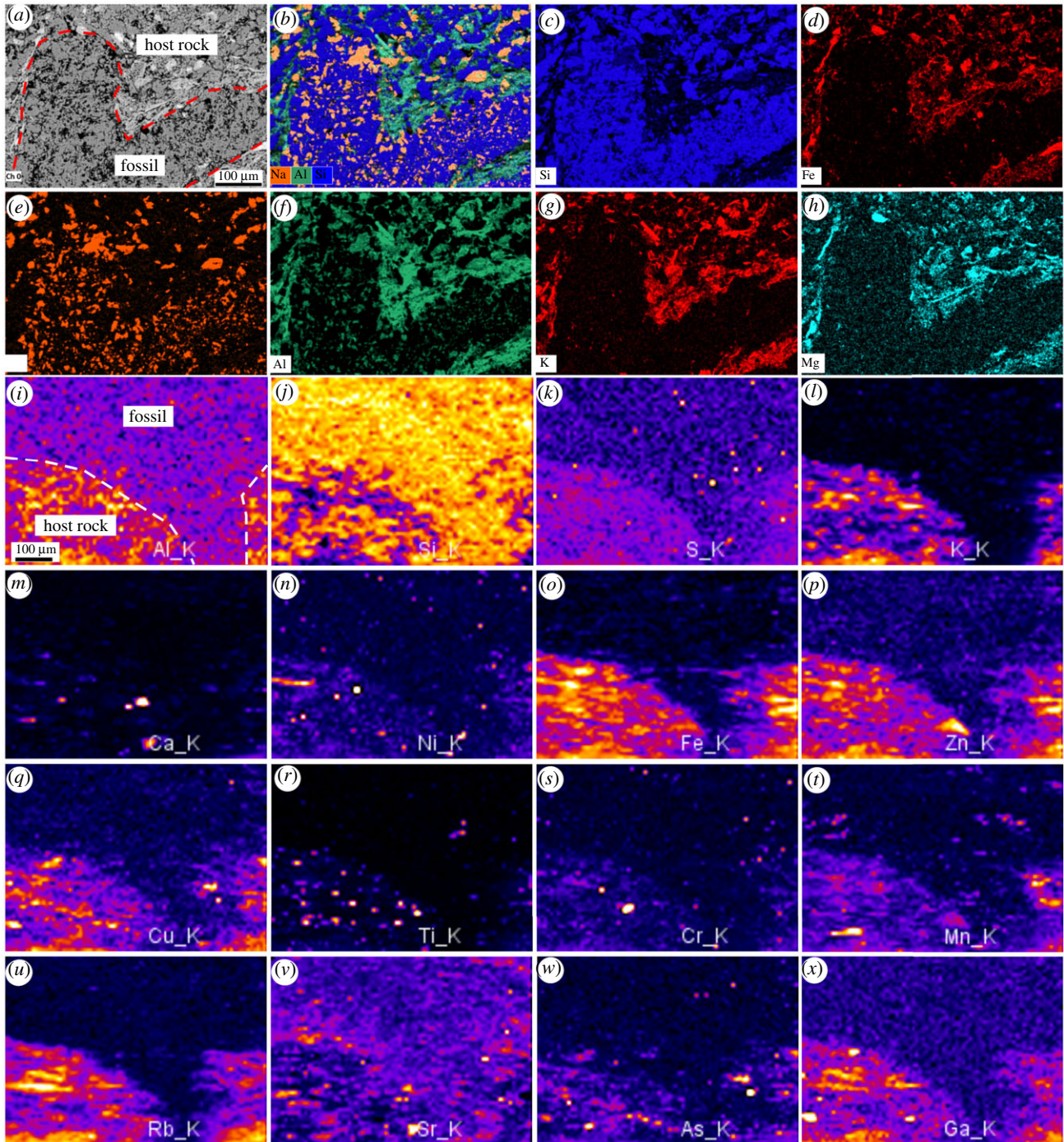


Figure 4. Elemental composition of the tubes. (a–h) SEM/EDS results. Electron image (a), mix elemental map (b), and maps of specific elements (c–h). (i–x) SR-μXRF maps of the fossil, showing the higher concentration of almost all mapped elements in the host rock, while the fossil shows a siliceous composition. Sulfur is concentrated in small points inside the fossils. The average XRF pattern can be found in the electronic supplementary material, figure S10. (Online version in colour.)

are capable of building tubular constructions with agglutinated material (some with high capacity of particle selectivity), including Sabellariidae [38], Pectinariidae [39], Oweniidae [10], Terebellidae [40], Maldanidae [41], Sabellidae [42], Capitellidae [43], Cirratulidae [43], Spionidae [44], Ampharetidae [45], Eunicidae [46], Fabricidae [47], Onuphidae [48], Nereididae [49], Trichobranchidae [50] and possibly even Phyllodocidae [51]. However, most of these groups produce agglutinated tubes that are simple cylindrical forms, without complex morphologies.

Although species with flanged tubes are common in Siboglinidae, Serpulidae and Chaetopteridae [52], they do not produce agglutinated tubes. Indeed, some chaetopterids are able to form tubes with externally aggregated detrital particles, but these species do not show flanged morphologies

[53–55]. Interestingly, some species of these three families can show longitudinal variation in morphology [56,57] (electronic supplementary material, figure S11), from unornamented to collared regions, similar to those observed in *A. mutvei* (electronic supplementary material, figure S3). However, the only group that shows both an agglutinated wall and flanged tubes is the family Maldanidae. Some works [58] have shown that some species (e.g. *Maldane sarsi*) can produce parabolic mud discs throughout the tube, strikingly similar to the morphology of *A. mutvei*. Some Maldanidae species (i.e. *Nicomache lumbricalis*) can even show an increase in particle size from the inner to the outer portions of the wall [41]. Despite the fact that this is also the case for the sabellariids *Sabellaria alveolata* and *Phragmatopoma caudata* (electronic supplementary material, figure S12), their tube morphologies

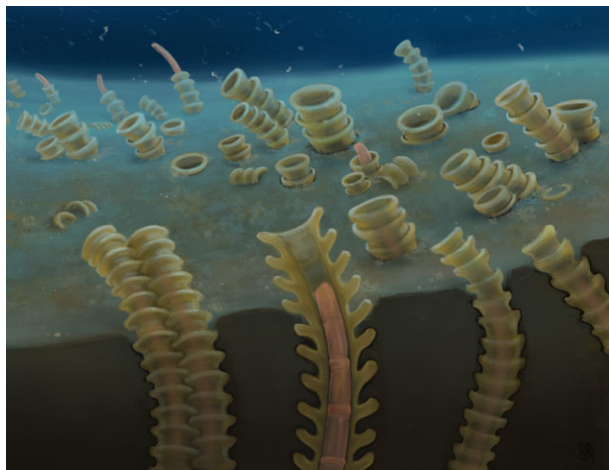


Figure 5. Artistic representations of the living tube-dwelling *Annullitubus mutvei*. (Online version in colour.)

are very different from our fossils. Several recent maldanids are tubicolous deposit feeders living head-down in the sediment ([59] and references therein), a life habit that could have been the case for *A. mutvei* considering its vertical orientation in the substrate and the abundant vegetal remains observed in association with the fossils.

Taking together, the comparisons with modern groups strongly suggest an annelid affinity to *A. mutvei*, with possible relationships to the family Maldanidae. If this interpretation is correct, then this is the first case of tubes attributed to Maldanidae and one of the oldest cases of the clade Sedentaria in the fossil record. Together with the occurrence of a possible Spionidae in Middle Devonian deposits of the Marcellus Formation [60], these results show that the groups within the Sedentaria clade may have already diverged before this time. Unfortunately, there is still no molecular clock data for annelid relationships [61]. Nevertheless, both molecular and palaeontological studies show a Cambrian to Ordovician crown-group diversification of Annelida [19,62], implying that, at least, our interpretation is not in disagreement with both molecular and fossil data for polychaetes in general.

(c) The fossil record of agglutinated tubes with polychaete affinities

The fossil record of agglutinated tubes has been as patchy as it has been controversial. Some of the first agglutinated tubes appeared at the Ediacaran–Cambrian transition (e.g. *Platysolenites*) [63], or even earlier [64], but they are largely regarded as foraminifers. The basal Cambrian already show the presence of other tubes made of agglutinated detritus, such as *Volborthella* and *Onuphionella* [20,65]. While the latter was suggested to have putative polychaete affinities [20], the former have even more enigmatic biological relationships and was even considered a separate phylum [65], mostly due to its peculiar conical morphology constructed by internal laminations of agglutinated grains.

From the Cambrian onwards, only a small number of agglutinated tubular taxa have been reported and interpreted to have possible polychaete affinities. For instance, Muir *et al.* [23] described *Echinokleptus anileis* and other agglutinated tubes from the Early Ordovician of north Wales (UK), south China, Morocco and France. Muir *et al.* [66] also described *Onuphionella corusca* from the Upper Ordovician of the First Bani Group (Morocco). Unnamed agglutinated tubes were

found in the Upper Devonian of the Great Basin by Zatoń & Bond [17]. Ettensohn [21] reported a tube constructed by pelmatozoan ossicles (*Crininicaminus haneyensis*) from the Early Carboniferous of Kentucky (USA).

During the Mesozoic many examples of the agglutinated tube *Terebella* occur worldwide (e.g. [67–69]), although their simple morphology and the fact that they are usually observed in thin sections indicate that *Terebella* probably represents a form taxon. Keupp *et al.* [70] described *Eklexibella buttenheimensis* and *E. johanni* from the Lower Jurassic of Germany, and Vinn & Luque [71] reported one agglutinated tube with remarkable similarities to those observed in modern Pectinariidae annelids. Throughout the Cenozoic, just few cases of agglutinated tubes are known as well, mainly including tubes with Pectinariidae affinities [22,72,73].

Considering this context, besides the fossils with Pectinariidae similarities that occur in Mesozoic and Cenozoic sediments, our work shows that *A. mutvei* can be regarded as one of the oldest agglutinated tubes that can be more confidently assigned to annelids, and possibly even to the family Maldanidae.

4. Conclusion

Although the fossil record of agglutinated tubes extends back to the latest Neoproterozoic, their biological affinities remain controversial and likely reflect many different groups of organisms. Here we showed that the Devonian *Annullitubus mutvei* was an agglutinated tubular metazoan with annelid affinities. These organisms constructed their flanged tubes by selecting and agglutinating silt-sized particles. Their unusual morphology allied to their agglutinated nature not only have modern counterparts within Annelida, but even suggest affinities to the family Maldanidae. This is the first time that a Palaeozoic agglutinated tube can be more confidently assigned to annelids, and it may even shed some light on the divergence timing within the Sedentaria clade.

5. Methods

(a) Samples

The samples were recovered from mudstones of the São Domingos Member of Ponta Grossa Formation at the coordinates: –24.709011360335367, –50.55652623416173. The material is housed at the Museu de História Geológica do Rio Grande do Sul (MHGEO-UNISINOS) under the codes ULVG-12881-12891. These sections are composed of dark mudstones and fine-grained sandstones and siltstones (see more details in electronic supplementary material).

(b) X-ray microtomography

This analysis was performed at the PLATINA platform of the IC2MP (University of Poitiers) with the RX-Solutions EasyTom XL Duo device. We used a nanofocus X-ray source (Hamamatsu L10711 with a LaB6 cathode) coupled with a flat panel imager (Varian PaxScan 2520 DX). The sample was scanned in a vertical stack mode (1440 projections in two turns) with a spatial resolution of 3.5 µm. Parameters of the acquisition are 100 kV (tube voltage), 25 µA (target current; middle spot size mode with target limiter), 2.8 frames per second, averaging of 13 frames per projections and an anti-ring procedure with random shifts of the imager. At the end of each acquisition, some additional

reference projections have been recorded to correct possible spot drift. The reconstruction was done with XAct software (RX-Solutions) with a filtered back projection algorithm based on the Feldkamp method for cone beam geometry with Tukey filter and attenuation of the beam hardening artefacts through linearization with a polynomial function. Segmentation (semi-automatically done with manual corrections), three-dimensional rendering and movies were produced using AVIZO v. 2019.2 (Thermo Fisher™-FEI).

(c) SEM/EDS

We analysed carbon coated polished thin sections using a JEOL JSM IT500 scanning electron microscope, equipped with secondary electron, backscatter electron detectors and coupled with a Bruker Lynxeye Energy Dispersive X-ray Spectrometer (EDX) at the IC2MP laboratory of the Université de Poitiers. Analyses were conducted in high-vacuum mode and with a current tension of 15 Kv.

(d) Raman

The spectra were recorded with a Labram HR 800 UV confocal scanning spectrometer (HORIBA Jobin Yvon), equipped with an internal 632 nm laser (He-Ne) and an external 532 nm laser. The confocal hole aperture was 200 µm and spectral resolution of 1.7 cm⁻¹ (with 532 nm excitation wavelength) and 1.2 cm⁻¹ (with 632 nm excitation wavelength). The spectrometer was calibrated using Si wafer. We used the software LabSPEC v. 5 for spectra acquisition.

(e) SR-µXRF

This analysis was carried out at the microXAS beamline (proposal 20190823) of the Swiss Light Source (SLS), in Villigen (Switzerland). The micro-XRF spectra were measured using a

Silicon Drift detector placed at 90° with the incident beam. The X-ray beam was focused down to 1 × 1 µm² using KB mirrors, using photons with energy of 17.2 keV, selected with a Double-Crystal Monochromator with Si(111) cut.

Ethics. This work has not involved any living subjects and conforms to the ethics guidelines of the National Mining Agency (ANA, Brazil).

Data accessibility. Data are available in this manuscript and its supplementary information [74]. X-Ray microtomography data (virtual slices) and three-dimensional model animation (mpg format) are available in the Zenodo Data Repository: <https://doi.org/10.5281/zenodo.5015076>.

Authors' contributions. B.B.-K.: conceptualization, data curation, formal analysis, investigation, methodology, writing-original draft, writing-review and editing; R.S.H.: conceptualization, project administration, supervision, writing-review and editing; L.d.M., A.M. and D.S.: investigation, writing-review and editing; I.L. and D.F.S.: Investigation; J.F. and A.E.A.: writing-review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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