

A *Cloudina*-like fossil with evidence of asexual reproduction from the lowest Cambrian, South China

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Abstract – The earliest fossil record of animal biomineralization occurs in the latest Ediacaran Period (c. 550 Ma). *Cloudina* and *Sinotubulites* are two important tubular taxa among these earliest skeletal fossils. The evolutionary fate of *Cloudina*-type fossils across the Ediacaran–Cambrian transition, however, remains poorly understood. Here we report a multi-layered tubular microfossil *Feiyanella manica* gen. et sp. nov. from a phosphorite interval of the lowest Cambrian Kuanchuanpu Formation, southern Shaanxi Province, South China. This newly discovered fossil is a conical tube with a ‘funnel-in-funnel’ construction, showing profound morphological similarities to *Cloudina* and *Conotubus*. On the other hand, the outer few layers, and particularly the outermost layer, of *Feiyanella* tubes are regularly to irregularly corrugated, a feature strikingly similar to the variably folded/wrinkled tube walls of *Sinotubulites*. The *Feiyanella* tubes additionally exhibit two orders of dichotomous branching, similar to branching structures reported occasionally in *Cloudina* and possibly indicative of asexual reproduction. Owing to broad similarities in tube morphology, tube wall construction and features presumably indicative of asexual reproduction, *Cloudina*, *Conotubus*, *Sinotubulites* and the here described *Feiyanella* may thus constitute a monophyletic group traversing the Ediacaran–Cambrian boundary. The tube construction and palaeoecological strategy of *Feiyanella* putatively indicate evolutionary continuity in morphology and palaeoecology of benthic metazoan communities across the Ediacaran–Cambrian transition.

Keywords: *Cloudina*, *Sinotubulites*, asexual reproduction, early Cambrian, Kuanchuanpu Formation.

1. Introduction

Although molecular clock studies estimate the origin and earliest diversification of animals within the Cryogenian Period, evidence from the fossil record reveals that crown members of nearly all animal phyla appear in a relatively rapid diversification event in early Cambrian time (the ‘Cambrian explosion’). This evolutionary radiation follows after a global mass extinction of the Ediacaran fauna (Erwin *et al.* 2011), a benthic community dominated by sessile, substrate-sticking organisms (Seilacher, 1999; Fedonkin *et al.* 2007; Yuan *et al.* 2011). In addition, geological and geochemical data suggest that the Ediacaran–Cambrian transition was not only a transition in biological diversity and ecosystem structure, but was also associated with drastic environmental change. These changes in environment and biology were likely highly intertwined; for instance, the rise of oxygen (e.g. Fike *et al.* 2006; Canfield *et al.* 2008; Komiya *et al.* 2008; Canfield & Farquhar, 2009; Li *et al.* 2010) has been sug-

gested to have had profound effects on the evolution and diversification of metazoans (Sperling *et al.* 2013). Further, the innovation of novel ecological strategies, such as ecosystem engineering and predation, in Ediacaran communities nearing the Cambrian boundary may have served to set the stage for the impending Cambrian radiation (e.g. Schiffbauer *et al.* 2016). Thus, the Ediacaran–Cambrian boundary represents a revolutionary transition, wherein the combined effects of environmental, biological and ecological change impart a large influence on phylogenetic patterns for the next c. 540 million years of evolutionary history.

With several reports of the survival of a few taxa from the Ediacaran fauna into the early and middle Cambrian period (e.g. Jensen, Gehling & Droser, 1998; Hagadorn & Waggoner, 2000; Shu *et al.* 2006; Van Iten *et al.* 2006), palaeontologists have sought to better understand the nature of biotic replacement at the Ediacaran–Cambrian transition (Laflamme *et al.* 2013; Darroch *et al.* 2015), and moreover, to explore the possible extinction hold-overs and their place within this evolutionary story. One such group of possible hold-overs comprises the terminal Ediacaran

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tubular biomineralizing assemblage (part of the ‘wormworld fauna’, Schiffbauer *et al.* 2016), exemplified by such organisms as *Cloudina*, *Sinotubulites* and *Namacalathus* (e.g. Germs, 1972; Signor, Mount & Onken, 1987; Grant, 1990; Grotzinger, Watters & Knoll, 2000; Hofmann & Mointjoy, 2001; Cortijo *et al.* 2010; Zhuravlev *et al.* 2012; Cortijo *et al.* 2015). Although the presence of these and broadly comparable genera in Cambrian rocks is rare (e.g. Yochelson & Stump, 1977; McIlroy, Green & Brasier, 2001; Rogov *et al.* 2015), they may be evolutionarily tied to tubular forms present in small shelly fossil assemblages of the lowest Cambrian, such as the anabaritids.

The lower Cambrian Kuanchuanpu fauna (Fortunian Stage, c. 535 Ma) in South China has become increasingly significant in understanding the evolutionary history of animals in the Ediacaran–Cambrian transition. Apart from small shelly fossils, including various molluscs and protoconodonts (Bengtson *et al.* 1990; Qian, 1999), the Kuanchuanpu Formation has yielded several extraordinary discoveries including putative arthropod embryos (Steiner *et al.* 2004b), scalidophorans (Liu *et al.* 2014b; Zhang *et al.* 2015) and markedly diverse types of cnidarians (Han *et al.* 2010, 2013; Dong *et al.* 2013; Han *et al.* 2016a) with biomineralized exoskeletons. Particularly, the scalidophorans, molluscs and protoconodonts have established phylogenetic connections with the emerging complex Cambrian marine ecosystem, for example, the diversity of arthropods as represented by the Chengjiang fauna (Vannier *et al.* 2007, 2009). Perhaps more importantly, the abundant millimetre-scale tubular fossils in the Kuanchuanpu fauna at least superficially resemble the terminal Ediacaran tubular ecosystem (Fedonkin *et al.* 2007; Yang *et al.* 2016).

Here we describe a three-dimensionally preserved tubular microfossil—*Feiyanella manica* gen. et sp. nov.—from the lower Cambrian Kuanchuanpu Formation, Shaanxi Province, South China. It exhibits similar funnel-in-funnel tube construction to the late Ediacaran tubular fossil *Cloudina* (Hua *et al.* 2005), and also shows broadly comparable dichotomous branching features posited to indicate asexual reproduction. Further, it shows a similar wrinkled/folded tube wall exterior comparable to that of *Sinotubulites* (Chen *et al.* 2008; Cai *et al.* 2015). This newly described organism may therefore provide an important palaeobiological and palaeoecological link between tubular fossils in the latest Ediacaran Period and earliest Cambrian Period.

2. Stratigraphic setting, fossil material and methods

The specimens described here were recovered from Bed 31 of the lower Cambrian Kuanchuanpu Formation (Fortunian Stage, Terreneuvian Series) at the Shizhonggou section of Ningqiang County, and Bed 2 at the Zhangjiagou section, Xixiang, Shaanxi Province, South China. The Ningqiang and Xixiang areas were palaeogeographically located on the northwestern mar-

gin of the Yangtze Platform during Ediacaran and Cambrian times. The fossil-bearing beds belong to the classic *Anabarites trisulcatus* – *Protohertzina anabarica* small shelly fossil biozone, indicating a stratigraphic equivalent of the Nemakit–Daldynian interval in Siberia (Steiner *et al.* 2004a).

Insoluble phosphatized fossils were liberated from the phosphatic limestone using 10% acetic acid digestion. A *Hyalithellus* sp. specimen (ELIXX35-465) and a well-preserved specimen of *Feiyanella manica* gen. et sp. nov. (ELISN141-14) were imaged by scanning electron microscopy (SEM) (Fig. 1), and ELISN141-14 was three-dimensionally analysed using Synchrotron radiation X-ray tomographic microscopy (SRXTM) at SPring-8 in Hyogo, Japan (Figs 2–4). The 3D reconstructions of X-ray data were processed using VG Studio 2.2 Max, allowing us to document interior anatomic details of the tube structure. All specimens are deposited at the Early Life Institute (ELI), Northwest University, Xi’an, China.

3. Systematic palaeontology

Incertae sedis

Genus *Feiyanella* new genus

Type species. *Feiyanella manica* new species, by monotypy

Diagnosis. Minute, multi-layered sub-cylindrical fossil tube consisting of a number of nested funnel-shaped layers. Outermost layer strongly wrinkled/folded, inner layers ornamented with weaker transverse annulations. Tube exhibits two orders of dichotomous branching, forming three generations of tubes. Parent tube layers are fully nested in the preserved length, whereas daughter and granddaughter tube layers are partially stacked/overlapped.

Feiyanella manica gen. et sp. nov.

Figures 1–5

Etymology. Feiyan (Feiyan Zhao), an ancient Chinese beauty famous for her slender build, similar to the slight gross appearance of the tube; manica, Latin, referring to the wrinkled outermost layer of the tube that resembles a folded shirt sleeve.

Holotype. ELISN141-14.

Type locality and horizon. The Shizhonggou section in Ningqiang County, Shaanxi Province, South China. Lower Cambrian Kuanchuanpu Formation (Fortunian Stage).

4. Description

The holotype specimen of *Feiyanella manica* gen. et sp. nov. (ELISN141-14) is three-dimensionally preserved through authigenic phosphatization. The fossil is incomplete (Fig. 1a), with both apical and apertural

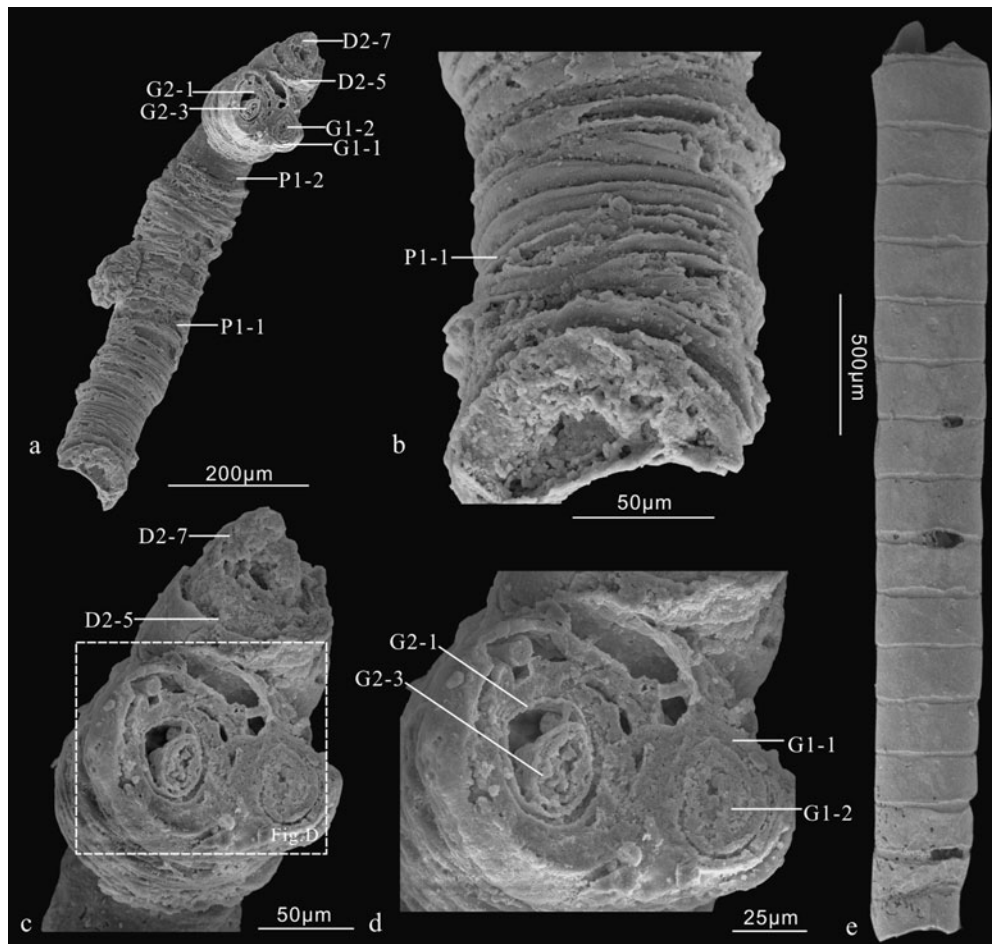


Figure 1. Secondary electron photomicrographs of *Feiyanella manica* gen. et sp. nov. (a–d) and *Hyolithellus* sp. (e). Fossils were recovered from the basal Cambrian Kuanchuanpu Formation at the Shizhonggou (a–d; Ningqiang County) and the Zhangjiagou (e; Xixiang County) sections. (a) Holotype specimen (ELISN141-14). Exterior view of the tube. (b) and (c) are enlarged views of the apical and apertural part, respectively. (d) is close up of (c). The tube is generally conical in shape, with the apical end (lower left) slightly tapering and the apertural end flaring (upper right) (a). The outermost layer of the tube is ornamented with transverse corrugations (b). Two daughter tubes (D1 and D2) and two granddaughter tubes (G1 and G2) can be seen in apertural fracture (c–d). (e) *Hyolithellus* sp. (ELIXX35-465). Abbreviations: P – parent tube; D – daughter tube; G – granddaughter tube. One parent tube (P1), two daughter tubes (D1 and D2) and three granddaughter tubes (G1, G2, and G3) are identified. Numberings suffixed P1, D1, D2, G1, G2 and G3 represent layers of walls in the parent, daughter and granddaughter tubes, respectively.

ends not intact (Fig. 1b–d). The preserved portion of the tube is roughly conical and gently curved (Fig. 1a). The apertural end flares with three slightly divergent, concentric sub-units (Fig. 1a, c, d). The tube is multi-layered and nested, composed of a number of stacked layers with varying overlap (Figs 1–5). The outermost layer of the tube is corrugated with closely spaced transverse ridges, showing stronger folds or wrinkles (Figs 1a, b, 2a–d, 3a–c). Only weaker transverse annulations can be seen in inner layers (Fig. 4b–l). SRXTM analysis reveals that three units of tube layers with unambiguously different lengths and diameters can be identified in the holotype specimen. Although these three sets of tubes are of quite different sizes, they all show the funnel-in-funnel tube construction. They are here interpreted as representing three generations – namely the parent, the daughter and the granddaughter tubes, respectively – which are described separately below.

4.a. Parent tube

The parent tube is sub-cylindrical in gross morphology, with the apertural end slightly flaring. It consists, from exterior to interior, of four nested funnel-shaped layers (the outermost four layers of the tube of *Feiyanella*, marked with P1-1, P1-2, P1-3, P1-4 in all figures). The preserved length of the parent tube is c. 1379 μm (= the length of the longest third layer; P1-3). The four layers of funnels, ranging from 193 to 304 μm in diameter, are fully stacked and overlapped, reminiscent of the ‘tube-in-tube’ construction of late Ediacaran tubular fossil *Sinotubulites* (Cai *et al.* 2015). The first layer (P1-1) is strongly wrinkled and/or folded, forming stronger, closely spaced, irregular, transverse corrugations on the exterior surface of the tube (Fig. 1a, b), strongly distinct from those on the inner layers. Transverse corrugations often bear a few secondary transverse irregular folds (Fig. 1b), which

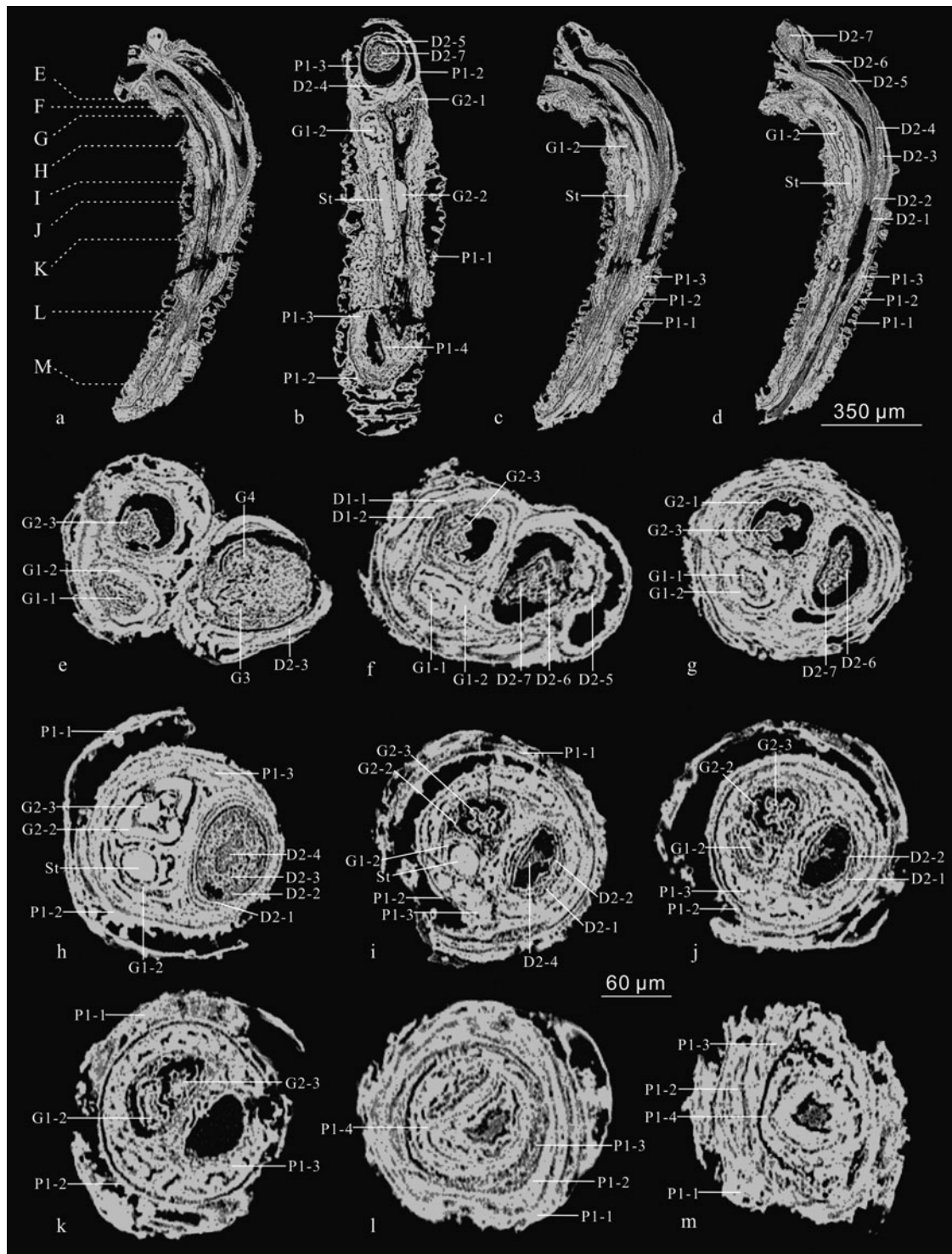


Figure 2. SRXTM virtual sections of the holotype specimen (ELISN141-14) of *Feiyanella manica* gen. et sp. nov. (a–d) Vertical bisecting sections of the entire specimen; (e–m) transverse sections. Positions of the sections are indicated in (a). Abbreviations: St – soft tissue. For all other abbreviations, see Figure 1. Scale bars: 350 μm for (a–d) and 60 μm for (e–m).

form complex exterior corrugations and make this layer appear to be much thicker than any other layers (Figs 2a–d, 3b, c). The notably stronger corrugation on the outermost layer of *Feiyanella* is a diagnostic feature characterizing this taxon. The second, third and fourth parent layers (P1-2–P1-4) share a similar morphology with the first layer. However, layers P1-2–P1-4 are ornamented with weaker transverse annulations

(Fig. 4b–d), quite different from those in layer P1-1. The second parent layer is *c.* 120 and *c.* 259 μm in minimum and maximum diameters, respectively. The third parent layer (P1-3) is the longest one (1379 μm) in the preserved specimen (Fig. 4c). The fourth parent layer is obviously shorter (631 μm) and smaller (77 and 108 μm in minimum and maximum diameters) than the other three parent funnels (Fig. 4d).

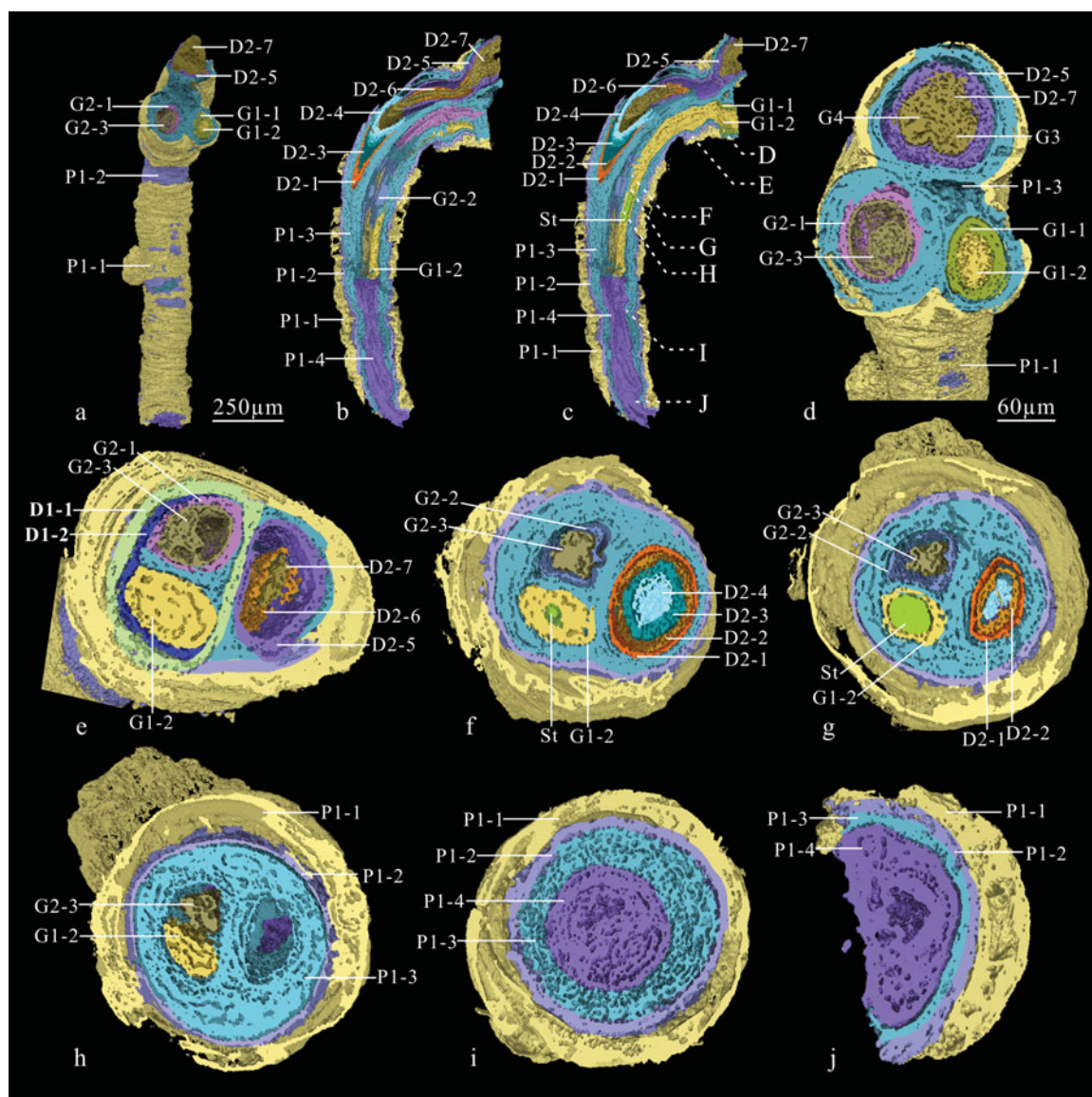


Figure 3. (Colour online) SRXTM reconstructions of the holotype specimen (ELISN141-14) of *Feiyanella manica* gen. et sp. nov. (a) External view of entire specimen; (b–c) vertical bisection of the specimen; (d–j) transverse sections. Positions of the sections are indicated in (c). Abbreviations: see Figure 1. Scale bars: 250 μm for (a–c) and 60 μm bar (d–j).

4.b. Daughter tube

Two daughter tubes (denoted as D1 and D2 in all figures) are discernible at the apertural end of the tube of *Feiyanella* (Figs 1c, 2, 3, 4), which extend from the apertural opening of the fourth parent funnel (Fig. 4d). The two daughter tubes stand side-by-side, and the outermost funnel of each daughter tube appears nearly cemented together (Fig. 2e). The daughter tubes consist of a number of nested, funnel-shaped layers, sharing similarities in tube wall morphology and nesting patterns with the parent tube. The two daughter tubes are not equal in size. The larger one (D1) consists of two tube wall layers (Fig. 2f) and is irregular in cross-section (Fig. 2e–g). The two layers (D1-1 and D1-2) are only situated in the apertural part of *Feiyanella*. Its width increases greatly towards the apertural end (Fig. 4a–d). The smaller daughter tube (D2) is composed of seven tube wall layers (D2-1–D2-7 in

Figs 2d–j, 3b–c, 4d–f). In contrast, ornamentations on the daughter funnels are noticeably diminished, with closely spaced transverse annulations but without complicated corrugations (e.g. funnel D2-1), as compared to the parent funnels.

4.c. Granddaughter tube

Four granddaughter tubes are identified in *Feiyanella*: two (G1 and G2) originated from the larger daughter tube (D1) and the other two (G3 and G4) from the smaller daughter tube (D2). The granddaughter tubes G1 and G2 are situated at the upper half of the preserved parent tube (Fig. 3b, c), whereas G3 and G4 are at the apertural end (Figs 2e, 3d). Morphological details of G3 and G4 are very limited, as they can only be identified in cross-sections near the apertural end of the tube (Figs 2e, 3d). Granddaughter tubes G1

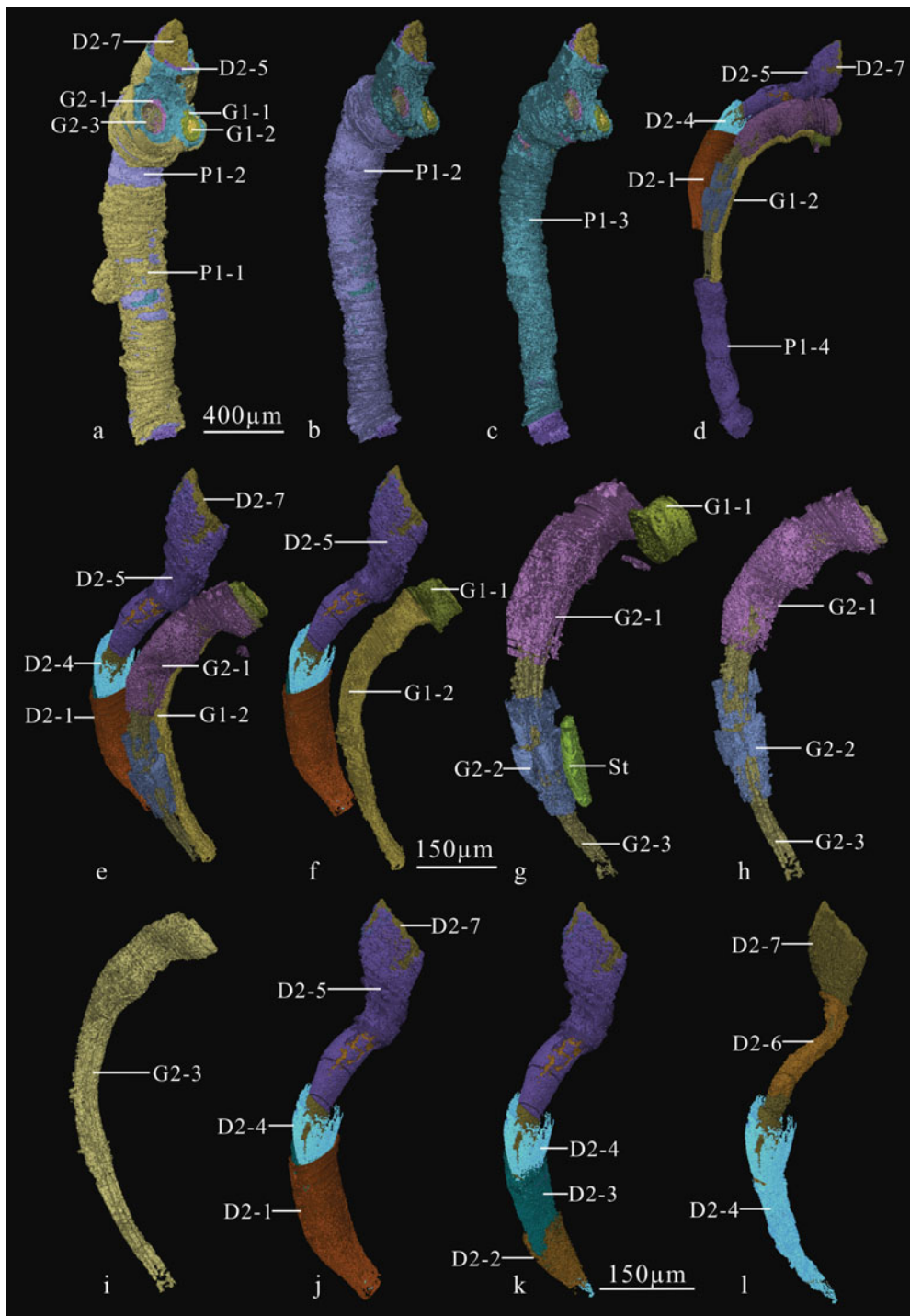


Figure 4. (Colour online) SRXTM reconstruction of the holotype specimen (ELISN141-14) of *Feiyanella manica* gen. et sp. nov. Different tube layers are in different colours. The outer layers are stepwise removed (from a–l) to expose the inner layers. Abbreviations: see Figure 1. Scale bars: 400 μm for (a–d) and 150 μm for (e–l).

and G2 are deeply nested into the daughter tube D1 (located at the middle to apertural portion of the parent tube; Fig. 2e–k). G1 and G2 are more or less equal in size (c. 39 μm). Notably, the splitting plane along the tube between the two granddaughter tubes G1 and G2 is orientated perpendicular to the splitting plane of the daughter tubes (Figs 2e, 5). G1 contains two layers of funnels (G1-1 and G1-2) and G2 has three layers (G2-1–G2-3) (Fig. 4d–i). The innermost layer of the grand-

daughter tube G2 (G2-3) displays four lobes separated by four longitudinal furrows in cross-section (Figs 2i, j, 3g). This tetradial symmetry only occurs at the apical end, and traverses approximately one-fourth of the granddaughter tube G2 (Fig. 4g–i). A spindle-shaped structure was preserved in the innermost funnel of the granddaughter tube G1 (denoted as St in Figs 2b, h, i, 3g, 4g). It is situated in the central portion of the granddaughter tube G1 and is oval (Fig. 2h, i)

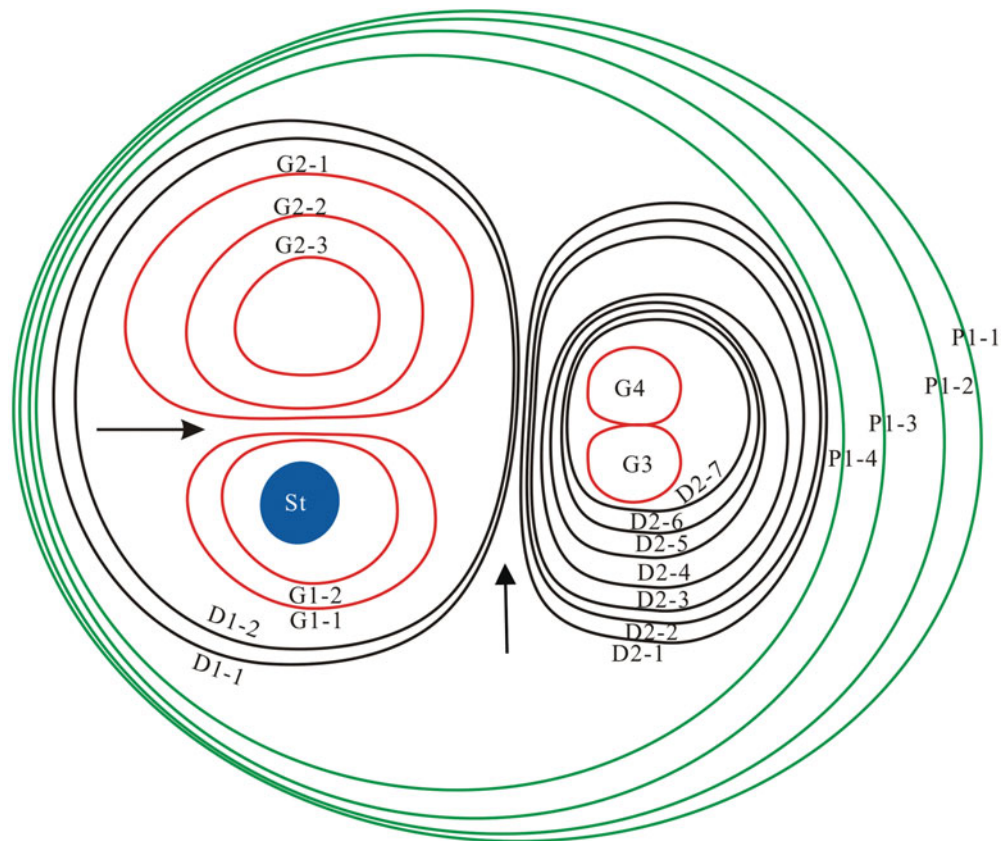


Figure 5. (Colour online) Schematic drawing of the cross-section of *Feiyanella manca* gen. et sp. nov. illustrating growth patterns between parent, daughter and granddaughter tubes. Note the orthogonal splitting planes between daughter (rightward arrow) and granddaughter (upward arrow) tubes. Abbreviations: see Figure 1.

in cross-section. The spindle exhibits a bright phase under SRXTM observation, *c.* 39 μm in diameter and 188 μm in length, occupying nearly one-third of the full length of granddaughter tube G1 (Fig. 4g).

5. Discussion

The incomplete preservation of the *Feiyanella* tube leaves uncertainties as to its full morphology and nesting patterns of the parent layers. Two overlapping patterns can be identified from the preserved portion, however: the outer parent tube layers (P1-1–P1-4) fully overlap (Fig. 4a–d), whereas all of the other inner tube layers only partially overlap (Fig. 4d-1). Two contrasting degrees of ornamentation are observed in *Feiyanella*: the outer parent tube layers (P1-1–P1-4) are visibly folded/wrinkled and form stronger transverse and/or slightly oblique corrugations (Fig. 4a–d), whereas all of the other inner tube layers are ornamented with weaker transverse annulations (Fig. 4d-1). The outermost layer of the tube in particular shows strongly folded/wrinkled corrugations (Figs 1a, b, 3a, 4a), making this layer appear much thicker (Figs 2a–d, 3b–c). With regard to nesting, although the four funnel-shaped parent layers (P1-1–P1-4) are completely nested in the preserved portion of the *Feiyanella* tube, it

is uncertain whether their full morphology is funnel-shaped and whether they are fully or partially stacked.

As an Örsten-type Lagerstätte, the Kuanchuanpu Formation biota is characterized by the selective preservation of refractory cuticular tissues of meiofauna (see review in Schiffbauer *et al.* 2014) and only fragments of larger organisms (i.e. putative grasping spines of *Protohertzina anabarica*; see Steiner *et al.* 2004a). However, *Feiyanella* was not likely a fragment of a more complex organism: for example, an appendage of an annelid or ecdysozoan (panarthropod cycloneuralian). Several lines of evidence are summarized here: (1) Both annelids and ecdysozoans have a cuticularized integument overlying the epidermis, particularly a tri-layered cuticle (epi-, exo- and endocuticles) in cycloneuralians (Bereiter-Hahn, Matoltsy & Richards, 1984; Peterson & Eernisse, 2001). The appendages of these animals, if fossilized, would not be preserved as loosely multi-layered, funnel-in-funnel structures. (2) The cuticle of a complex organism usually bears complex ornaments, such as sensory organs, chaetae, glands, scalds and net-like structures. These ornaments are absent in *Feiyanella*. (3) The branched, segmented appendages in arthropods differ from the unsegmented funnel of *Feiyanella*. (4) The parapodium of annelids, although varying among species, tapers apparently towards one end, in visible

contrast with the sub-cylindrical shape of *Feiyanella*. (5) Some species of cycloneurians (Liu *et al.* 2014b; Zhang *et al.* 2015) have been discovered from the Kuanchuanpu Formation. These fossils, together with a large number of specimens in our collection, collectively exhibit specific cuticle ornaments that are markedly different from *Feiyanella*. In addition, the integument of the cycloneurialian fossils is preserved as a single layer. In short, the characteristic multi-layered, funnel-in-funnel structure of *Feiyanella* is more appropriately interpreted as a dwelling tube of an organism, comparable to those known from the upper Ediacaran (e.g. Hua, Pratt & Zhang, 2003; Cai *et al.* 2011, 2014, 2015), rather than a body fragment of a larger complex organism.

Feiyanella is distinct from other early Cambrian tubular fossils, i.e. Hyolithelminths, *Byronia* and *Sphenothallus*. Hyolithelminths, a problematic group of mineralized tubular fossils characterized by more or less regular annulations or growth lines (Bengtson, *et al.* 1990; Li, 2004), exhibit a multi-laminated tube wall, and in some species, a cone-in-cone structure (see Kouchinsky *et al.* 2015, fig. 67). However, the micro-laminations of the tube wall are closely cemented together and each lamella (in some species) is composed of fine fibres (i.e. Bengtson *et al.* 1990; Vinn, 2006; Skovsted & Peel, 2011). *Hyolithellus* from the Kuanchuanpu Formation – a common element in the Kuanchuanpu Formation in the Xixiang and Ningqiang areas Steiner *et al.* (2004a) – is another tubular fossil sharing a similar morphology with *Feiyanella*. But the tubes of *Hyolithellus* are much larger in size (> 2 mm in length) than *Feiyanella* and the exterior smooth surface bears a number of wide-spaced circular grooves (Fig. 1e). In addition, ellipse-shaped pores occasionally occur in the grooves, which may be produced by soft tissue inside the tubes. *Hyolithellus* may have been a more complex organism (e.g. an annelid; Skovsted & Peel, 2011). The smooth tube, transverse grooves and ellipse-shaped pores indicate contrasting morphological and palaeobiological relationships with *Feiyanella*.

Byronia, a sessile tube-dwelling organism characterized by a lenticular cross-section and a deep split along the broader end (Bengtson *et al.* 1990), differs from *Feiyanella* in its wide-spaced transverse ridges and longitudinal ribs (see fig. 6 in Skovsted & Peel, 2011) that resemble the peridermal tube of olivoids (e.g. *Olivoides* and *Quadrapyrgites*; Liu *et al.* 2014a; Steiner *et al.* 2014) from the Kuanchuanpu Formation. Both *Byronia* and olivoids have been proposed to have close affinities with thecate medusozoans in the phylum Cnidaria (see Bengtson *et al.* 1990; Zhu *et al.* 2000; Dong *et al.* 2013; Han *et al.* 2016b).

Sphenothallus, a cone-shaped tube characterized by a more or less elliptical cross-section and a basal hold-fast and proposed as a thecate medusozoan (Van Iten, Cox & Mapes, 1992; Zhu *et al.* 2000; Li, 2004), differs from *Feiyanella* in its finely laminated and cemented

tube wall consisting of alternating apatite and organic laminae.

Instead, *Feiyanella* shares similarities in tube morphology and construction with some late Ediacaran tubular fossils, including *Cloudina* (Hua *et al.* 2005; Cortijo *et al.* 2010, 2015), *Conotubus* (Cai *et al.* 2011) and *Sinotubulites* (Chen *et al.* 2008; Cai *et al.* 2015). Each of these taxa shows a nested tube construction, cylindrical or oval-shaped cross-section and the absence of transverse internal structures such as septae or tabulae.

The perceived nesting pattern and the wrinkled tube-wall features of the parent layers (particularly P1-1) of *Feiyanella* are visibly similar to those of *Sinotubulites* (Cai *et al.* 2015). This may indicate that the parent layers of *Feiyanella* fully overlap, which would thus be comparable to the nesting patterns of *Sinotubulites*. On the other hand, the funnel-shaped tube layers of *Feiyanella* are strikingly similar to those of *Cloudina* (Hua, Pratt & Zhang, 2003; Hua *et al.* 2005; Cortijo *et al.* 2010) and *Conotubus* (Cai *et al.* 2011). Furthermore, the dichotomous branching of *Feiyanella*, which is most likely indicative of an asexual reproduction strategy, is also comparable to that of *Cloudina* (Hua *et al.* 2005; Cortijo *et al.* 2010, 2015).

While similar, *Feiyanella* also shows distinct differences from *Cloudina*, *Conotubus* and *Sinotubulites*. First, as compared to *Sinotubulites*, *Feiyanella* differs in tube layer morphology and overlapping patterns: *Feiyanella* is composed exclusively of funnel-shaped layers with partial overlap between adjacent layers (except for those of the parent funnels), whereas *Sinotubulites* is composed exclusively of cylinder-shaped layers with full overlap between two adjacent layers. The funnels of *Feiyanella* differ from the funnels of *Cloudina* and *Conotubus* in that the former lacks thickened rims on the apical and apertural ends of the funnels (Hua *et al.* 2005; Cortijo *et al.* 2010; Cai *et al.* 2011). In addition, *Feiyanella* differs from *Cloudina* in the manner of asexual reproduction. *Cloudina* is characterized by two manners of asexual reproduction strategies: dichotomous branching of daughter tubes in the same parent tube (see fig. 1L of Hua *et al.* 2005 and fig. 8 of Cortijo *et al.* 2010, 2015) and budding of a daughter tube between two adjacent funnels (see fig. 1P of Hua *et al.* 2005). *Feiyanella*, however, displays a pattern of multiple-ordered dichotomous branching of the younger generation of tubes within the older generation tubes.

Most broadly, *Feiyanella* shares similarities in the tube morphology, nesting patterns and presence of asexual reproduction strategies with *Cloudina*, and in the corrugation and nesting patterns of outer layers with *Sinotubulites*. Considering its similarities with *Cloudina* (Cai *et al.* 2014) and *Conotubus* (Cai *et al.* 2011), *Feiyanella* is thus interpreted as a sessile organism with periodic growth by secretion of new funnels within the older funnels (Grant, 1990), with the animal presumed to have lived within the innermost, most recently secreted funnel (Cortijo *et al.* 2010). The tube

of *Feiyanella* is hollow, indicating the soft tissue of the organism likely was able to move up and down within the tube, rather than being fixed within an isolated chamber. Although the full morphology of the tube is unknown, the apical end may have been closed, comparable to the basally closed apical end of *Cloudina* (Cortijo *et al.* 2015).

6. Zoological affinities and evolutionary implications

Together, *Cloudina*, *Conotubus*, *Sinotubulites* and *Feiyanella* may constitute a monophyletic group, as they are morphologically quite different from other Ediacaran and Cambrian tubular fossils (see summary in Cai *et al.* 2011; Cai, Hua & Zhang, 2013). The zoological placement of these *Cloudina*-type organisms, however, has been controversial. For example, *Cloudina* has been compared with both serpulid annelids (e.g. Glaessner, 1976; Hua *et al.* 2005) and cnidarians (e.g. Vinn & Zaton, 2012; Van Iten *et al.* 2014); the lack of preserved soft tissues in these fossils hinders convincing establishment of a palaeobiological interpretation.

While not reported in any other similar fossils, the spindle-shaped structure reported here in the innermost funnel of the granddaughter tube G1 may help provide a clue for phylogenetic placement of *Feiyanella* and, by extension, potentially other *Cloudina*-type organisms. This structure is three-dimensionally replicated by phosphate minerals, and its spindle-shaped morphology and massive size compared to the tube volume does not support an interpretation of an incompletely preserved funnel or other mineralized structure. Instead, we suggest that the spindle-shaped mass may be the phosphatized remains of the long-awaited tube dweller. Although it is difficult to depict the full morphology of the soft tissue inside the hollow tube, this spindle-shaped structure may represent the degraded organic remains of the organism that lived within these tubes. This interpretation is consistent with the morphological and palaeoecological reconstruction in *Conotubus* and *Cloudina* (Cai *et al.* 2011, 2014); they all possess hollow tubes which allowed for the tube dwellers to move up and down freely. This interpretation is also in accordance with the periodic growth of the tubes; the funnels were not simultaneously secreted by the soft issue, but instead were episodically secreted in the innermost layers.

A cnidarian planula interpretation for *Feiyanella* is largely compatible, and can be supported by several lines of evidence: (1) The asexual reproduction by longitudinal and transverse fissions of the soft body is more popular in extant cnidarians than in bilaterians. In addition, transverse fission has been reported from the sea-anemone-like cnidarians in the lower Cambrian Kuanchuanpu Formation in South China (Han *et al.* 2010). (2) The corrugated outermost layer of the tube broadly resembles the periderm of medusozoan polyps (Werner, 1973; Jarms, 1991). (3) The four-lobed mor-

phology seen in granddaughter tube G2 of *Feiyanella* shows symmetry comparable to another coeval fossil, *Carinachites spinatus* Qian, 1977 (Qian, 1977; Conway Morris & Chen, 1992) – a Cambrian medusozoan with a phosphatized skeleton showing triradial, tetradial and pentaradial symmetries (Conway Morris & Chen, 1992; Qian *et al.* 1997; Liu *et al.* 2011). (4) A colonial life habit proposed for *Feiyanella* is common in cnidarian hydropolyps (Hyman, 1940) (5) The funnel-in-funnel tube architecture of *Feiyanella* has also been observed in a few hydrotheca (e.g. *Sertularia quadrata*; plates 15 and 16 of Nutting, 1900). (6) The proposed closed apical end of *Feiyanella* is compatible with a cnidarian body plan, but inconvenient for defecating of a bilateral worm with a through gut.

The ontogeny of *Feiyanella* indicates a possible transition from cylindrical radial symmetry to tetradial symmetry. A similar transition from cylindrical radial symmetry to triradial symmetry was observed from a coeval fossil, *Anabarites*, which is also an early Cambrian tubular small shelly fossil suspected to be a cnidarian (Kouchinsky *et al.* 2009).

It is well known that Cambrian communities are quite different from those of the Ediacaran Period. Cambrian communities, exemplified by the Chengjiang and Burgess Shale biotas, are characterized by a complex food web with diverse types of feeding behaviours (Vannier *et al.* 2007; Hou, Siveter & Aldridge, 2008) and complex reproduction strategies (Duan *et al.* 2014; Caron & Vannier, 2015) similar to modern ocean ecosystems. Ediacaran communities, however, were instead comprised of slow creeping mat feeders and sessile benthic suspension feeders and/or osmotrophic feeders (e.g. Fedonkin *et al.* 2007; Laflamme, Xiao & Kowalewski, 2009; Rahman *et al.* 2015; Wood & Curtis, 2015). Although the early Cambrian small shelly fossil community – exemplified by the Kuanchuanpu Formation organisms – contains mat feeders (molluscs) (Qian & Bengtson, 1989) and microscopic predators (cycloneurians) (Liu *et al.* 2014b; Zhang *et al.* 2015), this ecosystem was characterized by a high richness and diversity of sessile organisms (i.e. predominantly cnidarians). Although a zoological placement remains unresolved, *Feiyanella* represents a Cambrian relict containing significant similarities in tube morphology, tube construction and reproduction strategy to some terminal Ediacaran tubular fossils (e.g. *Cloudina*, *Conotubus* and *Sinotubulites*). The early Cambrian small shelly fossil community revealed in the Kuanchuanpu Formation exhibits palaeobiological and palaeoecological features seemingly intermixed between both late Ediacaran and early Cambrian faunas. As such, it may support the notion that the late Ediacaran tubular biotas and their descendants represent important elements in a broader evolutionary prelude of the Cambrian explosion (Shu *et al.* 2014; Schiffbauer *et al.* 2016), rather than disappearing from the fossil record in an end-Ediacaran extinction (Smith *et al.* 2016).

7. Conclusions

The early Cambrian tubular fossil *Feiyanella manica* gen. et sp. nov. shares morphological similarities with the late Ediacaran tubular fossils *Cloudina*, *Conotubus* and *Sinotubulites*. Together, these tubular organisms may constitute a monophyletic group in the late Ediacaran through early Cambrian periods. The ‘funnel-in-funnel’ tube construction and the two-ordered dichotomous branching of *Feiyanella manica* gen. et sp. nov. are all comparable to those reported in *Cloudina*. The strongly corrugated outermost funnel and the gradational variations in the degrees of folding and/or wrinkling from exterior to interior tube layers of *Feiyanella manica* gen. et sp. nov. resembles those of *Sinotubulites*. *Feiyanella* thus embraces evolutionary continuity of typical late Ediacaran ‘funnel-in-funnel’ tube construction (exemplified by *Cloudina* and *Conotubus*), asexual reproduction by dichotomous branching of the tube (exemplified by *Cloudina*) and a gradational decrease in degrees of wrinkles and/or ornamentation from exterior to interior layers (exemplified by *Sinotubulites*). These continuities provide pivotal palaeobiological and palaeoecological insights into our understanding of the evolutionary history of the Ediacaran–Cambrian transition.

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