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DISCUSSION

Discussion of 'First finds of problematic Ediacaran fossil *Gaojiashania* in Siberia and its origin'

Keywords: *Gaojiashania*, *Shaanxilithes*, Gaojiashan, Ediacaran.

Y. Cai & H. Hua comment: Zhuravlev, Gámez Vintaned & Ivantsov (2009) reported the problematic Ediacaran fossil *Gaojiashania annulucosta* in Siberia and they considered that this is the first find of *Gaojiashania* outside China, since *Gaojiashania* had previously only been reported from the Gaojiashan Member of the middle Dengying Formation in the Ningqiang area, southern Shaanxi Province, South China. However, we believe that the so-called Siberian *Gaojiashania* was mis-identified, and what was described as *Gaojiashania annulucosta* by Zhuravlev, Gámez Vintaned & Ivantsov (2009) is more appropriately ascribed to *Shaanxilithes ningqiangensis*, another problematic Ediacaran fossil that has also been known from the Gaojiashan Member in Shaanxi Province of South China (Chen, Chen & Lao, 1975; Xing *et al.* 1984), as well as the stratigraphically equivalent Taozichong Formation in Guizhou Province (Hua, Chen & Zhang, 2004) and the Jiucheng Member (Dengying Formation) in Yunnan Province of South China (Zhu & Zhang, 2005), the Zhoujieshan Formation in Qinghai Province (Shen *et al.* 2007), and the Zhengmuguan Formation in Ningxia Hui Autonomous Region of North China (Shen *et al.* 2007).

Here we illustrate diagnostic features of *Gaojiashania* and *Shaanxilithes* from their type localities (the Gaojiashan section and Lijiagou section, respectively) in southern Shaanxi in order to clarify their identification.

1. *Gaojiashania*

The genus *Gaojiashania* Yang, Zhang & Lin, 1986 (not Yin, Zhang & Lin, as cited in Zhuravlev, Gámez Vintaned & Ivantsov, 2009) was established in Lin *et al.* (1986; see also Zhang, 1986). According to Lin *et al.*'s (1986) and Zhang's (1986) initial description, the type species *Gaojiashania cyclus* (Fig. 1a–f) is a tubular body fossil and is characterized by densely articulated body rings. The rings can be disarticulated and preserved as isolated pieces (see pl. 1, fig. 15 of Lin *et al.* 1986). The fossils can be straight (Fig. 1a) or sinuous (Fig. 1d). The tubes of *Gaojiashania* are typically 50–60 mm in length (although most specimens are incompletely preserved, and the longest specimen we have observed is > 200 mm in length) and 7–9 mm in diameter, and the rings (Fig. 1e, f) are 1–2 mm in thickness (Lin *et al.* 1986; Zhang, 1986). *Gaojiashania cyclus* occurs in fine-grained sediments, primarily siltstone/calcisiltite and mudstone/calcilutite beds. It is typically pyritized and preserved approximately parallel to bedding surface.

Gaojiashania annulucosta Zhang, Li & Dong (Zhang *et al.* 1992; Li *et al.* 1992) was identified from thin-sections of limestones in the Gaojiashan Member. According to the initial description, the tubes are slightly curved and preserved parallel to bedding plane, with a length of 4.5–6.2 cm, diameter 8–12 mm. The body rings, with a thickness of 0.8 mm, can be clearly identified in thin-sections and average spacing between body rings is approximately 2 mm. The size variations in the diameter of body rings are due to obliquely cut thin-sections. The tubes are calcified and filled with microsparitic calcites, and the surrounding matrices are lime muds.

After examining the type specimens of *G. cyclus* and *G. annulucosta*, we believe that their basic morphology and size are similar. The only difference is their taphonomy: *G. cyclus* is pyritized and preserved in siltstone and mudstone, whereas *G. annulucosta* is calcified and preserved in limestone. We think that these two species are taphonomic variants and should be ascribed to one species, that is, the type species, *Gaojiashania cyclus* Yang, Zhang & Lin, 1986 (*in* Lin *et al.* 1986; Zhang, 1986).

Gaojiashania has always been interpreted as a body fossil since its publication. The interpretation is supported by the observation that some of the body rings of *Gaojiashania* can be disarticulated (Fig. 1e, f). Such disarticulation is inconsistent with a trace fossil preservation.

2. *Shaanxilithes ningqiangensis*

Chen, Chen & Lao (1975) first described cf. *Sabellidites* sp. from the Gaojiashan Member in southern Shaanxi and they interpreted it as a body fossil. Similar fossils from the same stratigraphic horizon at the Lijiagou section were later described as *Shaanxilithes ningqiangensis* (Fig. 1g–l) Xing, Yue & Zhang, 1984 (*in* Xing *et al.* 1984). In Chen, Chen & Lao's (1975) description, cf. *Sabellidites* sp. is a slender ribbon-shaped and annulated fossil, with a length from 20 to 30 mm, width from 1 to 3 mm (up to 4–5 mm), and 60–90 annulations spaced at ~ 0.34 mm intervals (see Fig. 1i). Although Xing *et al.* (1984) described *Shaanxilithes ningqiangensis* in the chapter on trace fossils, they interpreted it as an impression (thus not necessarily a trace fossil) of an annulated ribbon-shaped organism. According to Xing *et al.*'s (1984) description, *Shaanxilithes ningqiangensis* is a ribbon-shaped impression with a constant width (1–6 mm or more) and is characterized by a series of closely spaced transverse annulations. The observed length ranges from 25 to 60 mm. Since no completely preserved specimens have yet been reported, the full morphology of *Shaanxilithes ningqiangensis* is uncertain. Subsequently, *Shaanxilithes ningqiangensis* has also been described from the Taozichong Formation in Guizhou Province, South China (Hua, Chen & Zhang, 2004; Fig. 1k, l) and the Zhoujieshan Formation in Qinghai Province and the Zhengmuguan Formation in Ningxia Hui Autonomous Area of North China (Shen *et al.* 2007).

3. Morphological and taphonomic comparisons between *Gaojiashania* and *Shaanxilithes*

Based on our observation of the type materials and new materials collected from the type localities, the key differences between *Gaojiashania cyclus* (or *G. annulucosta*) and *Shaanxilithes ningqiangensis* are their different size,

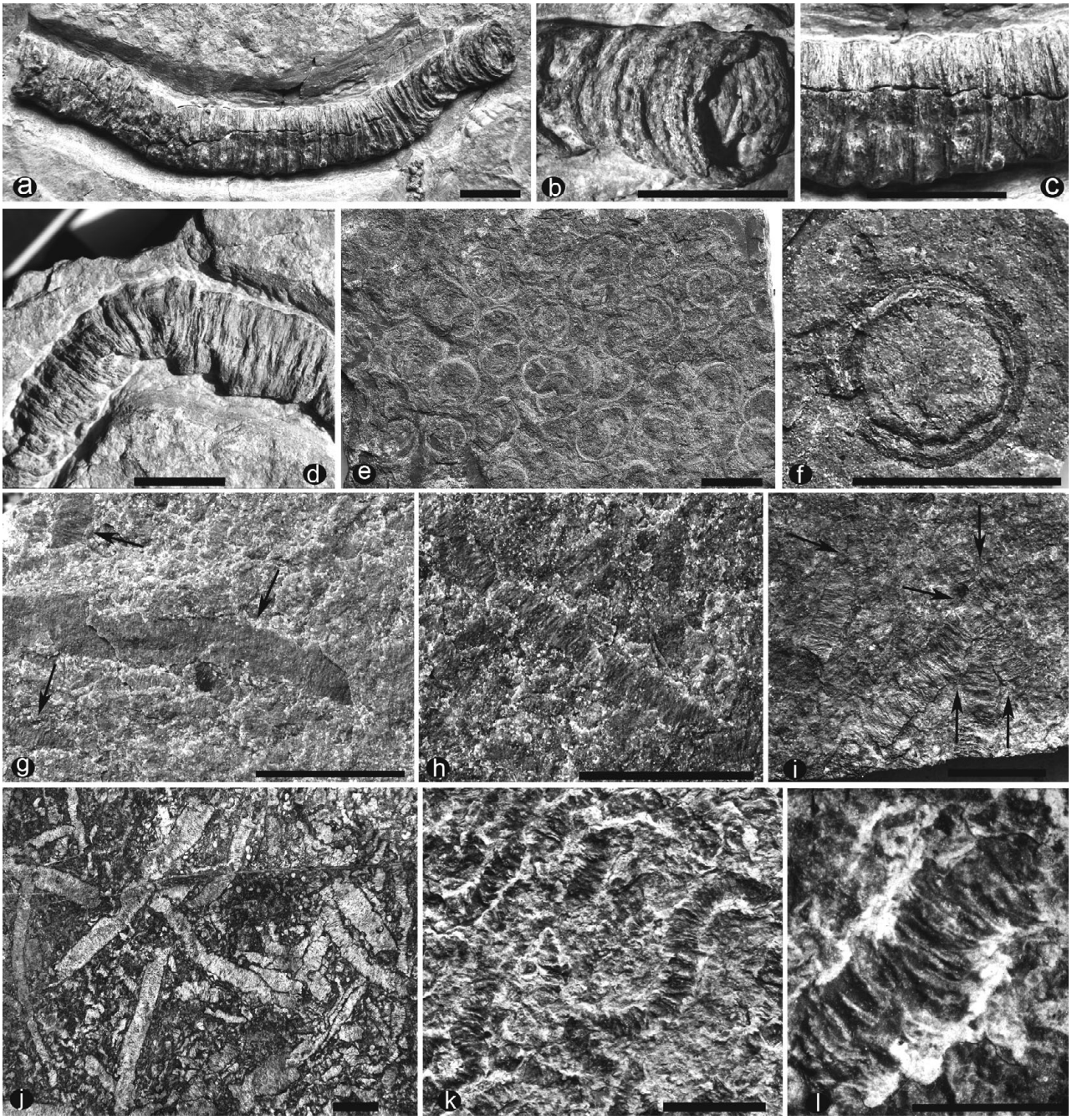

Figure 1. *Gaojiashania cyclus* and *Shaanxilithes ningqiangensis* from the Gaojiashan Member at the type localities (a–j) and Taozichong Formation in Guizhou (k–l). (a) Three-dimensionally pyritized and well-preserved *Gaojiashania cyclus*; (b) close-up of 'aperture' part in (a); (c) close-up of (a) showing thickened body rings; (d) *G. cyclus* showing sinuous tube (possibly due to post-mortem bending and twisting); (e) disarticulated body rings of *G. cyclus* preserved on the bedding surface of siltstone/mudstone beds in the Gaojiashan Member; (f) isolated and pyritized body ring of *G.* sp. (g, h) *Shaanxilithes ningqiangensis* from the Gaojiashan Member (Dengying Formation) at the Lijiagou section (type section; Xing *et al.* 1984), southern Shaanxi Province, South China. Note three *S. ningqiangensis* specimens (arrows in g), with different sizes, are preserved in slightly different layers (g). (i, j) *S. ningqiangensis* from the Gaojiashan Member (Dengying Formation) at the Gaojiashan section (~ 20 km southeast of the type section, Lijiagou section), southern Shaanxi Province, South China. Note that the ribbon compressions overlap but do not cross-cut (arrows in i). Also note the mass accumulation (specimens are preserved in slightly different layers) and varying degrees of fragmentation (j). (k) *S. ningqiangensis* from the Ediacaran Taozichong Formation, Guizhou Province, South China. Note sinuous ribbons. (l) Close-up of *S. ningqiangensis* showing closely spaced annulations. All scale bars represent 1 cm, except in (l) 5 mm. A colour version of this figure is available at http://www.cambridge.org/journals/geo.

thickness and density of transverse structures (rings and annulations), and how the transverse structures are disposed. Quantitative measurements (Chen, Chen & Lao, 1975; Shen *et al.* 2007) show that *Shaanxilithes ningqiangensis* possesses 2–3 annuli per millimetre (Fig. 1h, l). However, the thickness of a body ring of *Gaojiashania cyclus* often exceeds 1 mm (Fig. 1f) and their spacing can be up to 3 mm. Furthermore, *Shaanxilithes ningqiangensis* is more sinuous (typically more than 2 bends; Fig. 1k) than *Gaojiashania cyclus* or *G. annulucosta* fossils (typically 1–2 bends;

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Fig. 1d). More importantly, *Gaojiashania cyclus* body rings appear to be thickened and articulated by a very thin membrane, which can be degraded easily. In a sense, *Gaojiashania cyclus* is morphologically analogous to an accordion-like tube, with the thickened rings held together by a thin cylindrical membrane. When this membrane is degraded before pyritization, the rings can be preserved as disarticulated and isolated rings (Fig. 1e, f). Of course, the ribbons of *Shaanxilithes ningqiangensis* could originally have been cylindrical tubes as well (Shen *et al.* 2007), but these tubes are relatively thin and the annulations on the tubes are closely spaced and not strongly thickened. Additionally, *Gaojiashania cyclus* (or *G. annulucosta*) and *Shaanxilithes ningqiangensis* from the Gaojiashan Member are preserved differently, although it is unclear whether their different taphonomic styles reflect any differences in underlying biological attributes. Nonetheless, *Gaojiashania* fossils are typically pyritized in siltstones/mudstones or preserved as weakly skeletonized fossils in limestones. In contrast, *Shaanxilithes ningqiangensis* are typically preserved as flattened ribbons or more commonly as impressions. Finally, they have different biostratigraphic ranges: at the Gaojiashan section (Fig. 2) and other sections in the Ningqiang area where both *Shaanxilithes ningqiangensis* and *Gaojiashania cyclus* are present, the occurrence of *Shaanxilithes ningqiangensis* is invariably below that of *Gaojiashania cyclus*.

Among Chinese specimens in our collections, some Guizhou specimens (Fig. 1k–l) are of primary importance for morphological reconstruction because they have preserved the best three-dimensional resolution of the tube structures. Fossils from other localities were subjected to varying degrees of compression (e.g. Fig. 1g–j). The Siberian fossil specimens sometimes show isolated torus-like structures with clear central openings that are similar to *Gaojiashania*. However, the inner tube structure is unknown, although some of the specimens (Fig. 1g) may be funnel-shaped as suggested by Zhuravlev, Gámez Vintaned & Ivantsov (2009). It is remarkable that *Shaanxilithes* are preferentially preserved as fragmented pieces with different sizes, but the annulations are still connected; *Gaojiashania* are preferentially disarticulated rather than fragmented. We argue that this may indicate that these two taxa may have possessed distinctive tube structures, at least in terms of connective tissues which made the two taxa preserve in different taphonomic ways.

Some of the newly reported Siberian *Shaanxilithes* (Zhuravlev, Gámez Vintaned & Ivantsov, 2009, fig. 2a, c) are preserved with a relatively lower width/length ratio than Chinese specimens, most of which are often preserved as fragmented pieces. This may be due to different hydrodynamic conditions during deposition of the fossils, with the Chinese specimens preserved in higher energy environments and the Siberian specimens in lower energy environments. We also argue that the five genera and five species of ribbon-like fossils reported by Shen *et al.* (2007) from North China would be ascribed to one taxon, *Shaanxilithes*, and the different preservations of specimens are due to varying degrees of taphonomic resolution. This is supported by *Shaanxilithes* from the Gaojiashan section (southern Shaanxi, South China, Fig. 2) that are preserved as fragmented pieces with different sizes and different morphological resolutions on the same bedding plane (e.g. Fig. 1j). In Shen *et al.*'s (2007) descriptions, well-preserved specimens that were ascribed to *Shaanxilithes* cf. *ningqiangensis* share very similar tube structures to those of Siberian fossil specimens, particularly in terms of ornaments and ribbon sizes.

Considering these morphological differences between *Gaojiashania cyclus* and *Shaanxilithes ningqiangensis*, it is clear that the Siberian fossils reported by Zhuravlev,

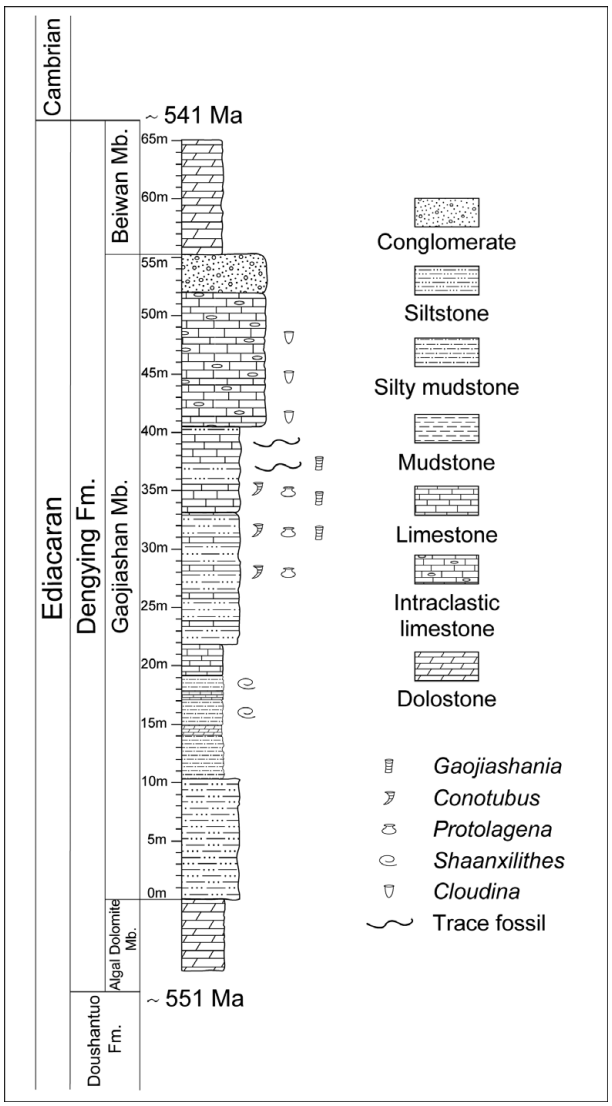

Figure 2. Biostratigraphic occurrences of *Gaojiashania*, *Shaanxilithes*, and other Ediacaran fossils in the Gaojiashan Member, middle Dengying Formation, at the Gaojiashan section, southern Shaanxi Province, South China.

Gámez Vintaned & Ivantsov (2009) are more similar to *Shaanxilithes ningqiangensis* in size and shape. Additionally, the preservational style of the Siberian fossils is particularly similar to *Shaanxilithes ningqiangensis* from Guizhou (Fig. 1k–l). Although *Shaanxilithes ningqiangensis* fossils from southern Shaanxi Province, Qinghai Province and the Ningxia Hui Autonomous Area are preserved in fine-grained siliciclastic sediments with varying carbonate contents, they do share the diagnostic features (compression or impression of thin ribbons with closely spaced annulations) and certain taphonomic features (dense accumulation on bedding surfaces, varying degree of fragmentation, ribbons overlapping but not penetrating each other). Importantly, *Shaanxilithes ningqiangensis* is not preserved as disarticulated rings like those of *Gaojiashania cyclus*.

We also argue that both *Gaojiashania* and *Shaanxilithes* are body fossils, not trace fossils. The disarticulated rings of *Gaojiashania* unambiguously suggest that it is a body fossil, since trace fossils cannot be disarticulated in this way. *Shaanxilithes* only show overlapping (Fig. 1i) but not cross-cutting relationships among ribbons, even in very dense populations preserved on bedding surfaces. The phylogenetic

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affinity of *Shaanxilithes* is still unknown, although they seem to represent some eukaryotic organisms with indeterministic growth (hence the very long ribbons). The Siberian find is an important extension of the geographic range of *Shaanxilithes ningqiangensis* and it therefore supports the biostratigraphic significance of *Shaanxilithes ningqiangensis* (Shen *et al.* 2007).

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A. Yu. Zhuravlev, J. A. Gámez Vintaned & A. Yu. Ivantsov reply: The nature of Ediacaran metazoan-type fossils in general is strongly disputed. Even Ediacaran multicellulars (vendozoans) differ significantly from any Phanerozoic animal in their ontogeny, type of symmetry and growth pattern, and character of lifestyle including movement, as well as in features of their burial compaction and preservation. The affinities of the pre-vendozoan Weng'an biota from the Doushantuo Formation of South China are even more controversial. Phosphorites of this formation yield putative fossil embryos and adult individuals of sponges and even cnidarians. The latter are tubular branching fossils (such as *Ramitubus*) that are commonly compared with Phanerozoic corals (Liu *et al.* 2008, pl. 1). However, they very much resemble in both their general appearance and size range most ubiquitous Cambrian cyanobacteria, for example, *Gordonophyton*, in phosphatized cases such as those described and figured by Luchinina (1988, pl. 22, figs 1–6, pl. 23, figs 1, 3). As a rule, a desire to identify among Ediacaran fossils the direct antecedents of Phanerozoic animals leads to shoehorning of unusual early organisms into the classical tree of life, and unfortunately, *Gaojiashania*-group fossils are no exception.

New data on *Gaojiashania*-group fossils provided here by Cai & Hua (this Discussion) and ourselves clearly show that these fossils are not comparable with either typical trace fossils of Phanerozoic type or with metazoan body fossils.

The somewhat confusing interpretation by Cai & Hua (this Discussion) of Siberian *Gaojiashania annulucosta* as a two-dimensional compressed carbonaceous ribbon leads them to deduce an affinity with *Shaanxilithes*. However, Siberian *G. annulucosta* is a three-dimensionally preserved fossil consisting of funnel-shaped segments with prominent relief and lacking carbon (e.g. Zhuravlev, Gámez Vintaned & Ivantsov, 2009, fig. 2g). Thus it matches the stated definition of *G. annulucosta* and not that of ribbon-like *Shaanxilithes* compressions (Xing *et al.* 1984; Weber, Steiner & Zhu, 2007). Nevertheless, some Chinese specimens that have been described as *Shaanxilithes* and its multiple synonyms do belong to *G. annulucosta*, and Cai & Hua (this Discussion) follow our synonymy exactly (Zhuravlev, Gámez Vintaned & Ivantsov, 2009, pp. 776, 778), despite the fact that they do not refer to it. We emphasize the assignment of Siberian *Gaojiashania* to the species *G. annulucosta* because it does not display disarticulation of segments as does the type species *G. cyclus* (Chen, Sun & Hua, 2002; Zhuravlev, Gámez Vintaned & Ivantsov, 2009, p. 778). Whether these two species are really congeneric is an open question for our Chinese colleagues, who have the type materials of all fossils under discussion available to them. (However, the authorship of *Gaojiashania* and its type species needs to be clarified in accordance with ICZN rules.) Neither dimensions and number of bends, which are highly variable even within a single sampling unit, nor mineralogy, which is not primary in any of these fossils, can be used to distinguish Siberian and Chinese specimens of *G. annulucosta*. Rather, all these features are a factor of sampling unit size and local taphonomic conditions, especially in the case of pyritization (Briggs, 2003; Gabbott *et al.* 2004).

The most interesting data of Cai & Hua (this Discussion), although not new, are their figures of undoubtedly disarticulated *G. cyclus* specimens. Of course, fragmentation, 'disarticulation' and even reworking of trace fossils are not unusual given specific taphonomic conditions including, among others, early diagenetic mineralization and/or particular constructional features and stratinomic conditions (e.g. Howard & Singh, 1985; Ekdale & Bromley, 1991; Savrda, 2007 and references therein). Nonetheless, the observations by Cai *et al.* (2010; Cai & Hua, this Discussion) confirm our interpretation of the stratigraphic distribution of the Ediacaran *Gaojiashania*-group assemblage, as well as our model of *Gaojiashania*-group fossils as segmented, elongate structures of indeterminate growth which characterize a 'slime mould behaviour model' representing a combination of trace fossils and fossilized fruiting bodies (Zhuravlev, Gámez Vintaned & Ivantsov, 2009, p. 779).

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