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Discussion

Comment on “Trace fossil evidence for Ediacaran bilaterian animals with complex behaviors” by Chen et al. [Precambrian Res. 224 (2013) 690–701]

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ABSTRACT

Trace fossils from the Shibantan Member of the Denying Formation (551–541 Ma) of South China, interpreted by Chen and colleagues as evidence of undermat feeding, epibenthic locomotion and temporary dwelling of a small worm-like animal (Metazoa, Bilateria), show four features incompatible with that interpretation: (1) bulbous ends, (2) interruptions, (3) variable width, (4) narrow ends and (5) beaded levees. These features are better explained as due to formation of a sorocarp base, looping upward, shape changing, cell aggregation and slime nodules, respectively, of the slug (grex or pseudoplasmodium) phase of a cellular slime mold comparable with living *Dictyostelium discoideum* (Amoebozoa, Mycetozoa). Another three features are found in worm as well as slime mold trails: (6) transverse markings, (7) central ridge and (8) small size. Similar observations can be made, and mycetozoa affinities considered for comparable trace fossils from the 550 Ma Ediacaran Member of South Australia, 558 Ma Ust Pinega Formation of Russia, 585–600 Ma Tacuari Formation of Uruguay, 1100 Ma Chorhat Sandstone of India and 2000–1800 Ma Stirling Range Sandstone of Western Australia. Slime molds are terrestrial eucaryotic protists, and may have a fossil record extending back as far as the likely 1900 Ma age of aquatic metazoans.

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1. Introduction

Chen et al. (2013) report trace fossils in the Shibantan Member of the Denying Formation (551–541 Ma) near Wuhe, South China, and interpret them as traces of worm like animals (Metazoa, Bilateria) distinct from other body and trace fossils of animals. A variety of features of the Shibantan fossils supports an alternative hypothesis that they are traces of the migratory slug (grex or pseudoplasmodium) phase of cellular slime molds, like that of living *Dictyostelium discoideum* (Fig. 1). Cellular slime molds (Mycetozoa) live most of their lives as dispersed amoeboid cells in soil, but come together to form a multicellular slug, which migrates, then stops and expands to form a sessile stalked sorocarp (Bonner, 2009).

2. Mycetozoa or metazoan features?

2.1. Bulbous ends

The Shibantan trace fossils have bulbous ends and nodes with high relief and diameter up to twice the width of the rest of the burrow or trail (Chen et al., 2013, Figs. 3A–C, 5A–D, 6C and D).

This would not happen if a burrow of a worm-like creature turned upwards or downwards into sediment or microbial mats: worm burrows are relatively constant in diameter regardless of direction of travel or orientation (Seilacher, 2007). Mycetozoa slugs are not constrained by musculature and characteristically thicken when putting up vertical stalks to sporulate (Fig. 1C). The spores disperse, leaving the trail, stalk and base behind (Bonner, 2009).

2.2. Interruptions

The Shibantan trails show interruptions, as if the creature left the surface then came down again at a different width (Chen et al., 2013, Fig. 5C and D). Slime mold slugs commonly expand basally to raise themselves from the substrate and then loop back at narrower diameter to the substrate (Bonner, 2009). In contrast, animals have trails of equal width in all parts (Seilacher, 2007). Few cases of comparable animal looping behavior are known, such as inchworms (larvae of geometrid moths).

2.3. Variable width

Shibantan trails and molds of horizontal tunnels vary in width, with bulges and constrictions, (Chen et al., 2013, Fig. 3A–C, 5B, 6C and D). These observations are difficult to reconcile with wormlike animal widths constrained by musculature. Slime mold slugs are

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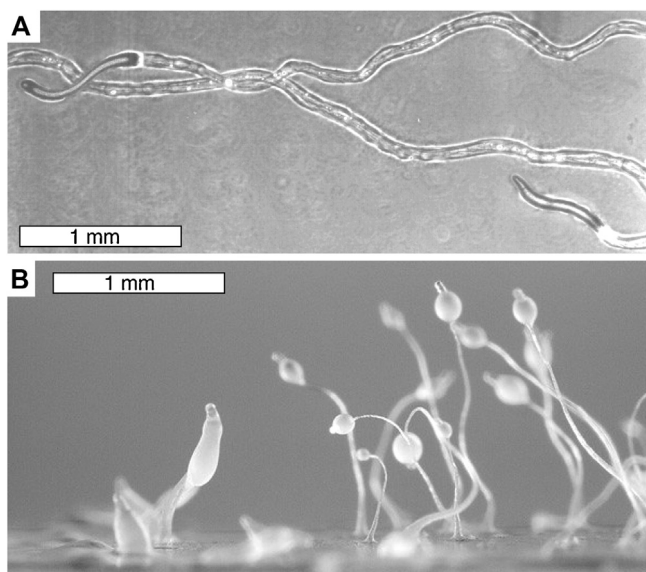


Fig. 1. Slug (grex or pseudoplasmodium) stage (A) and culmination stage (B) of the slime mold (Amoebozoa, Mycetozoa) *Dictyostelium discoideum*, showing trails in agar (A), and stalked sorocarps (B).

Panel A is cropped from one of Fisher (1997), used with permission of Paul R. Fisher. Panel B from Alexander Wild, used with permission.

more variable in shape as they move (Fig. 1A). The slime mold slug is generally a non-feeding phase of the life cycle (Bonner, 2009), but individual cells leave the slug if pockets of food are discovered (Kuzdzal-Fick et al., 2007). Although slime mold slugs lack musculature, they move through soft substrates such as microbial mats, loose soil, dung and agar gel (Fisher, 1997; Gilbert et al., 2007).

2.4. Narrow ends

Some Shibantan burrows taper in width to a narrow rounded end (Chen et al., 2013, Fig. 6C), as do some Shibantan trails (Chen et al., 2013, Fig. 5C and D). In neither case is there evidence that the trace is oblique back into the matrix, because wall or levee definition is consistent along the preserved length. Trails of animals launching upward into water could perhaps be made with more or less pressure to achieve this effect, but a burrowing animal leaving or entering the plane of the fossil could not have changed so much in size. These narrow ends may represent the tail of an aggregating slime mold slug formed on or within the substrate by coalescence of amoebae (Bonner, 2009). If the narrow end is the slug aggregation point and the bulbous end the sorocarp point, and the direction of travel away from convex collar marks, many of the Shibantan fossils show the whole transit of the slug over distances ranging from 28 cm to 12 cm and 9 cm (Chen et al., 2013, Fig. 3A, 6B, and 5C and D part and counterpart, respectively).

2.5. Beaded levees

Shibantan surface trails have characteristic beads a millimeter or less in diameter on either side (Chen et al., 2013, Fig. 5C–F), interpreted as sediment between scratch marks of an animal. This would require lateral setae or limbs, incompatible with the idea that the same creature made both trails and burrows, because the burrows show no sign of lateral appendages. As a slime mold however, the mounds can be regarded as collar impressions in the slime sheath, and as abandoned cells and slime nodules of cellulose, protein and polysaccharide (Breen et al., 1987; Blanton et al., 1999; Sternfeld and O'Mara, 2005).

2.6. Transverse marking

Shibantan trails and burrows also have transverse markings (Chen et al., 2013, Figs. 5A–D, 6A–F) comparable with spreiten of animal burrows and trails (Seilacher, 2007). Unlike spreiten however, these do not necessarily coincide with the lateral beads of their levees (Section 2.4). *Dictyostelium* moving across agar leaves comparable collar impressions (Breen et al., 1987; Fisher, 1997; Sternfeld and O'Mara, 2005). Interpreted as slime mold trails, the direction of movement would have been through convex collar impressions (Breen et al., 1987; Sternfeld and O'Mara, 2005), which is the opposite direction of worm burrows and trails away from concave backfills (Seilacher, 2007).

2.7. Central ridge

Shibantan trails and burrows commonly have a central ridge in natural molds (Chen et al., 2013, Figs. 5A and B, 6A and B). This could be taken as an indication of bilaterally opposed setae or appendages if interpreted as an animal trace (Seilacher, 2007). However, such a central thread could also be explained by the narrow tail and collapsed trailing slime sheaths observed behind *Dictyostelium* slugs (Smith and Williams, 1979; Breen et al., 1987).

2.8. Small size

The Shibantan trace fossils show a range of width (3–9 mm; Chen et al., 2013), comparable with growth series of small worms or other metazoans. This is larger than living *Dictyostelium discoideum* slugs, which reach 0.2 mm wide, but show great variance in width (0.03–0.2 mm) independent of development (Råfols et al., 2000).

3. Other Precambrian Mycetozoa?

The Shibantan fossils of Chen et al. (2013) are similar in diagnostic features such as bulbous ends, interruptions, variable width, narrow ends, and beaded levees to several other trace fossils: “*Archaeonassa*” sp. indet. from the Ediacara Member (550 Ma) of South Australia and Ust’Pinega Formation (558 Ma) of Russia (Jensen, 2003), un-named traces of the Tacuari Formation (585–600 Ma) of Uruguay (Pecoits et al., 2012), and *Myxomitodes stirlingsensis* from the Stirling Range Sandstone (2000–1800 Ma) of Western Australia (Bengtson et al., 2007). Poorly preserved undermat burrows from the 1100 Ma Chorhat Sandstone of India (Seilacher et al., 1998), may also be evidence of a long Precambrian fossil record of mycetozoans, like 1025 Ma body fossils of *Mycosphaeroides aggregatus* from the Neryuenska Formation of Siberia (Hermann and Podkovryov, 2006). The enigmatic Ediacaran fossils *Gaojianshan* and *Palaeopascichnus* have also been attributed to slime molds (Zhuravlev et al., 2009), but show backfill-like structures more complex than formed by living slime molds. Western Australian *Myxomitodes stirlingsensis* and South Australian *Archaeonassa* are in sequences with paleosols and fluvial-intertidal facies (Retallack, 2012, 2013), and *Myxomitodes* is close to the 1900 Ma age of the oldest known marine eukaryote, *Grypania spiralis* (Han and Runnegar, 1992; Schneider et al., 2002). In contrast, the Chorhat, Tacuari, Shibantan and Ust’Pinega fossils are presumed to have been marine (Jensen, 2003; Pecoits et al., 2012; Chen et al., 2013), but like many Precambrian fossil localities have not been examined for paleosols (Retallack, 2013).

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