Trace fossils versus body fossils: *Oldhamia recta* revisited

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**Abstract**

New discoveries in North Carolina’s Neoproterozoic Carolina Terrane, combined with a reexamination of the holotype of *Oldhamia recta* and other material from the Yale Peabody Museum, reveal these specimens as body fossils of a rod-like organism, rather than ichnofossils. Close examination of fossils originally identified as *O. recta* lack: levees made by movement of a tracemaker through a sediment; internal structures indicating backfilling or fecal material; scratch marks (denoting a recumbent lifestyle); or evidence of peristaltic movement. Crossovers of rods in some instances also indicate rigidity in the fossils. Most importantly, quantitative analyses indicate Gaussian size distributions and narrow ranges of alignment for the fossils, with each respective line of evidence interpreted as body fossils aligned by currents. Because this newly discerned evidence favors a body fossil origin for these specimens, we propose that *O. recta* is invalid as an ichnospecies. Our research supports more quantitative approaches to augment qualitative descriptions when evaluating whether Ediacaran-age structures are trace or body fossils.

**1. Introduction**

Discerning Neoproterozoic trace fossils from body fossils is crucial to understanding their diversity, evolution and behavior. The task is complicated by fundamental differences in Neoproterozoic paleoecology as compared to that of the Phanerozoic (Droser et al., 2006). A critical step in understanding these fossils is recognition of how microbial mats affected the sediment–water interface, which along with other factors, vertically restricted bioturbation to horizontal planes (Seilacher and Pflüger, 1994; Seilacher, 1999; Bottjer et al., 2000). In this environment, organisms can be thought of as mat encurers, mat stickers, mat scratchers or undermat miners (Seilacher, 1999). Evidence of the mats is oftentimes preserved as微生物ially induced sedimentary structures (MISS) such as "elephant skin" or wrinkles (e.g., Hagadorn and Bottjer, 1997; Noffke et al., 2001). Thus Neoproterozoic trace fossils are often interpreted in the context of how these reflect organismal interactions with microbial mats (e.g., Gehling and Droser, 2009).

Droser et al. (2005) offered several criteria for distinguishing trace from body fossils in Neoproterozoic sediments. For example, if individuals are parallel, this evidence may favor current alignment. Preferred orientations are rare in trace fossils, particularly burrows; the only exceptions are where organisms have aligned their burrows with a flow for suspension feeding (Crimes and Crossley, 1980; Pemberton and Frey, 1984), or burrows are sheared (deformed by a current (Gingras and Bann, 2006). Furthermore, body fossils, reflecting a wide variety of body parts, could show morphological variation along a Gaussian distribution, or could vary noticeably along given linear elements, especially if represented by body fragments. In contrast, trace fossils were made by entire organisms, and normally have consistent widths along their lengths, and regular lengths if made by repeated feeding probes of the same-sized tracemaker. True trace fossils should also show levees and grooves, indicating active pushing aside of sediment. Additionally, trace fossils may indicate active backfilling, or show evidence of material having passed through a gut, such as fecal pellets. All of these criteria need to be taken into account when making an interpretation of a Neoproterozoic fossil. Such methods have led to a recent reappraisal of the Ediacaran trace fossil record (Jensen et al., 2006), as well as other forms that might be mistaken for trace fossils (Gehling and Droser, 2009).

With these caveats in mind, recent discoveries of new body fossils and ichnofossils in the Neoproterozoic Carolina Terrane has prompted a renewed look at their identity and significance (Weaver et al., 2006a,b; Hibbard et al., 2006, 2009; Weaver et al., 2008). Several specimens, acquired by the North Carolina Museum of Natural Sciences through collection and donation, contain fossils identified initially as the ichnospecies *Oldhamia recta*, which had been named from the same Neoproterozoic rocks in North Carolina (Seilacher et al., 2005). Our closer examination, however, reveals that these fossils are more likely attributable to a rod-like body fossil. A newly discovered specimen, NCSM10530 (North Carolina State Museum) was particularly key in our revised identification, but we also examined the holotype and hypotypes of *O. recta* to test its original...
diagnosis. Through a combination of qualitative and quantitative assessments of all examined specimens, we conclude that “Oldhamia recta” is no longer valid as an ichnospecies. Nonetheless, if these specimens are later justified as new taxa, the name may still apply to a body fossil. In particular, we emphasize that similar studies examining the identity of horizontally oriented Ediacaran fossils use orientation data as a primary criterion to test for evidence of current alignment. Our study thus serves as a cautionary tale about the difficulties of separating Ediacaran body fossils from trace fossils (Droser et al., 2005; Cohen et al., 2009).

2. Geologic setting

The Carolina Terrane consists of the remnants of a composite Proterozoic island arc, preserving volcanic and volcaniclastic rocks (Hibbard et al., 2002). Stratigraphy of the Albequerque Group (Conley and Bain, 1965) has been reinterpreted several times (Conley and Bain, 1965; Stromquist and Sundelius, 1969; Milton, 1984). Currently accepted stratigraphy is that of Milton (1984), as verified by Butler and Secor (1991) and Hibbard et al. (2002).

Fossils described herein originated in the Floyd Church Formation of the Albequerque Group in Stanly County, North Carolina (Milton, 1984). Below the Floyd Church Formation lies the Cid Formation, divided into an upper volcanic Flat Swamp Member and a lower unnamed mudstone member. Uranium–lead dating of a metarhyolite from the Flat Swamp Member yields an age of 547 ± 2 Ma (Hibbard et al., 2006), whereas a meta-andesite from the same formation gives a concordant age of 540.6 ± 1.2 Ma (Ingle et al., 2003). Overlying the Floyd Church Formation is the Yadkin Formation, which contains detrital zircons indicating an age that is at least Early Cambrian (Hibbard et al., 2008). The Proterozoic–Cambrian boundary is taken as ca. 542 Ma (Bowring et al., 2007).

This stratigraphy postdates that used in trace fossil work of Gibson (1989), who recognized the McManus Formation, which encompassed what is now named (from youngest to oldest) the Floyd Church Member, and the mudstone member of the Cid Formation. The volcanic Flat Swamp Member of the Cid Formation is now recognized as a prominent stratigraphic marker, resulting in: elevation of the Floyd Church to Formation status; establishment of the Cid Formation; and splitting of the Cid Formation into an upper Flat Swamp Member and a lower unnamed mudstone member. Trace fossils described by Gibson (1989) and discussed herein originated in the upper sections of the former McManus Formation. Based on locality data, these are now considered to be within what is now named the Floyd Church Formation.

The Floyd Church Formation was interpreted by Gibson and Teeter (1984) as deposited under shallow near-shore conditions with tidal influence. The basal Floyd Church Formation in the vicinity of Jacob’s Creek Quarry (Hibbard et al., 2009) contains sedimentary structures consistent with intertidal deposition. Within the Albequerque Group as a whole, the depositional environment of the Floyd Church Formation would be intermediate between that of the graywackes, sands and silts of the overlying Yadkin Formation, and that of the shallow marine mudstones of the Cid Formation.

3. Qualitative and quantitative descriptions of O. recta

In our analysis, we examined the holotype and hypotypes of O. recta from the Yale Peabody Museum (YPM), as well as a new specimen acquired by the North Carolina State Museum (NCSM10530, Fig. 1). Measurements include readily quantifiable sizes and orientations of the rod-shaped fossils. Length and width of rod-like elements were measured directly on the surface of each slab using low-angle incident lighting, a binocular microscope, and an electronic micrometer with an accuracy of ±0.01 mm. All possible differences among populations were examined by measuring both negative- and positive-relief fossils on NCSM10530. Width data from NCSM10530 also allowed for comparison of positive- and negative-relief fossils. Statistics were performed using Microsoft Excel (Table 1). Orientations were measured manually relative to an arbitrary north by laying a digital grid over a digital image or photographs of each slab. Orientation data were displayed and vector statistics calculated using freeware Rose 2.1.0 developed by Todd Thompson (Indiana Geological Survey).

Seilacher et al. (2005) originally described the holotype of O. recta (YPM-204453, Fig. 2) from the Floyd Church Formation as: “Bundles of straight, subparallel, unbranched and closely spaced tunnels oriented parallel to the bedding plane. Tunnels are a few centimeters long and up to 1.5 mm in diameter. Preserved as positive, as well as negative, reliefs on the same bedding plane.” The designated holotype includes all specimens fitting this description on the slab. Seilacher et al. (2005) further interpreted the holotype as “Oldhamia with straight backfilled tunnels parallel to the bedding plane that are arranged in non-intercutting and seemingly unconnected bundles.” In our reexamination of the holotype, accompanying hypotypes, and the new specimen from the Floyd Church Formation (NCSM10530), we applied the original description and interpretation of this ichnospecies to test its diagnostic validity. The resultant modified description then lent to a new interpretation of O. recta, discussed in the following section.

From the start, the original description of the holotype of O. recta is problematic in its application of the term “tunnel,” rather than our preferred, more neutral terms, “rod” or “tube.” The distinction between a “rod” and “tube” is related to morphology and preservational modes. Tubes would have been hollow originally, having outer walls or linings and open interiors, whereas rods are solid, while allowing for the possibility that “rods” could also consist of sediment-filled tubes. With this stipulation in mind, we currently describe the Floyd Church Formation fossils as rods, rather than tubes, owing to their lack of evidence for walls or linings. Positive and negative reliefs of specimens on bedding planes both indicate relative rigidity. We saw no evidence of collapsed tubes, such as some described from the Ediacaran of South Australia (e.g., “Aulozoon”: Gehling et al., 2005). Additionally, fossil burrows, regardless of their trace makers, are often termed by orientations such as vertically aligned “shafts” or horizontally aligned “tunnels” (Ekdale and Bromley, 2003; Haszprunar et al., 2007). Nevertheless, either term used in a description presumes that the described specimen is a trace fos-
sil, which may not always be the case with Ediacaran fossils (Droser et al., 2005; Cohen et al., 2009; Gehling and Droser, 2009). We also saw no evidence of backfilling in the fossils, as asserted by Seilacher et al. (2005): meniscate fills, fecal pellets, and other such traits of an animal actively packing a burrow behind it (sensu Bromley, 1996) are lacking. Although such traits may not be readily visible owing to the small size of the fossils, their apparent absence means that an interpretation of backfilling is only supported by assertion and presumption.

Another point of contention in the holotype description is related to the occurrence of rods as “bundles,” which may imply that rods are connected or bound with one another. We find no evidence that specimens are actually tied together or otherwise directly connected (explained in more detail later). Thus we prefer to say that they are “clustered” (i.e., more than one rod in close association with one another). Accordingly, these clusters were examined for whether they were unbranched or branched, which in the latter instance would show direct connections. In most examples, we could find no evidence of branching, although several clusters from the holotype, hypotypes, and NCSM10530, rods apparently project from single, narrow points, analogous to a cluster of needles from a pine tree. Although other trace fossils have been interpreted as deposit-feeding burrows that emanate from a single burrow axis (e.g., Chondrites, Asterosoma: Ekdale, 1992), we know of no examples in which branches join in narrow points. “Tunnels” that taper in tandem to a point are also odd for a trace fossil: except for variations imparted by peristaltic movement or growth of a trace maker, invertebrate burrows tend to maintain near-constant diameters along their lengths (Bromley, 1996). Furthermore, we could find no evidence that points were caused by clusters converging and dipping vertically downward below a horizontal bedding plane, which would cause a false sense of tapering.

Through orientation analyses of the holotype, hypotypes, and NCSM10530, we also tested the assertion that linear elements of O. recta are subparallel. Holotype (Fig. 2) and hypotype specimens from the Peabody Museum do show an apparent alignment (Fig. 3); orientation measurements of individual rods show consistency ratios of 0.92–0.96, with 1.0 in perfect alignment (n = 316). Hence, we would amend the description of O. recta as “near-parallel,” as opposed to subparallel. Interestingly, one senses a preferred orientation of the fossils on NCSM10530, but these are actually more bimodal (Fig. 4). Their overall consistency ratio is only 0.77 (n = 213), but when split into two groups, each has a ratio of 0.94 and vector means of 318 ± 20° (N42W, n = 132) and 35 ± 24° (N35E, n = 81). The hypothesis that these are separate groups holds at the 1σ level but not at the 2σ level (Fig. 4).

We performed a comprehensive accounting of widths and lengths of rods in all examined specimens. In the holotype (YPM-204453), the mean width was 1.20 ± 0.39 mm; mean length was more variable, at 11.24 ± 7.17 mm (n = 85). Hypotypes of O. recta from the Yale Peabody Museum collection showed similarly narrower distributions in width measurements and greater variability in lengths (Table 1). Mean widths ranged from 1.08 ± 0.36 mm (YPM-212764, n = 85) to 1.55 ± 0.74 mm (YPM-204458, n = 24), whereas mean lengths were 8.17 ± 4.07 mm (YPM-204457, n = 35) to 19.35 ± 5.96 mm (YPM-204458). Combined data of the YPM specimens (including the holotype) also reflect consistency in mean width but high variation in lengths: 1.20 ± 0.42 mm for the width and 11.24 ± 7.17 mm for length (n = 316). Mean width of NCSM10530 is similar to that of the pooled YPM ones (Fig. 5), 1.47 ± 0.36 mm, although mean length is shorter overall and less variable, at 8.51 ± 3.56 mm (n = 249). The analysis indicates that the original general description of dimensions for O. recta (“...a few centimeters long and up to 1.5 mm in diameter...”) holds up reasonably well to our quantitative analysis, although we think that it should have emphasized the great variability in rod lengths (Fig. 6). Deformation of soft-bodied forms as a possible source of error was taken into consideration (e.g., Dzik and Ivantsov, 2002), yet the width of positive- and negative-relief fossils are identical within 1σ error (Fig. 7).

As a result, we would modify the description of the holotype of O. recta to say that the fossils are unbranched, mostly straight clusters of rods with near-constant widths but variable lengths, oriented more-or-less parallel to bedding, and with a high degree of parallelism that may also show a bimodal distribution. This altered description lends to a new diagnosis of these fossils, one that also differs from the one offered by Seilacher et al. (2005): “Oldhamia with straight backfilled tunnels parallel to the bedding

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*Fig. 2. Alignment of rod-shaped fossils in the holotype of “Oldhamia recta,” YPM-204453.*
Fig. 3. Rose diagrams of the orientation of fossils in holotype and hypotype specimens from the Peabody Museum. “North” is arbitrary for each specimen. Consistency ratios (C.R.) and number of data points (N) are given in the figure. The high degree of alignment is interpreted as the result of current.

plane that are arranged in non-intercutting and seemingly unconnected bundles.” Based on our evidence, we disagree with all but the assertions that the fossils are “parallel to the bedding plane” and “unconnected bundles” (the latter we amend as “clusters”). Because we see no apparent evidence of backfill structures, we also disagree with the diagnosis as “backfilled tunnels” (Seilacher et al., 2005). An interesting detail about the diagnosis (but not in the original description) of *O. recta* is of the “tunnels...arranged in non-intercutting...bundles.” Hence we also tested this qualitative aspect of the specimens, looking for examples of where individual rod-like elements of the fossils seemed to intercut or were otherwise overlapping one another.

Closer examination of one specimen (YPM-204454/212764, which will be referred to as 204454 for brevity) revealed further evidence that the “tunnels” are actually rods. In more than one instance, a rod had compressed two underlying rods, leaving a negative-relief impression on two positive-relief “tunnels” (Fig. 8, elements b and c). This indicates that rather than cross-cutting (as a burrow would have done), a rod-like element left its mark on two others of its kind as a solid object, not as a trace fossil. To further make this point, elsewhere on the same slab is a definite trace fossil (an unnamed trail, noted as element a in Fig. 8) that cross-cuts negative-relief impressions made by a cluster of three rod-like elements (Fig. 8, elements d and e). Such impressions are not necessarily the result of behavior, but more likely from objects that imparted their outlines to the substrate surface. These objects were then plucked from the surface and their impressions were later crossed by a tracemaker.

4. Why “*Oldhamia recta*” is a body fossil, and not a trace fossil

In terms of qualitative characteristics, the Floyd Church Formation specimens lack the following features expected in ichnofossils, as suggested by Droser et al. (2005) and Jensen et al. (2006): (1) levees, or similar sediment displacements made by movement of a tracemaker through a sediment; (2) internal structures indicating backfilling, fecal material, or a combination of the two; (3)
external or internal ornamentation, such as scratch marks associated with “burrow shafts” (i.e., tubes), thus denoting a recumbent lifestyle (Jensen et al., 2002); or (4) evidence of peristaltic movement, such as slight variations in diameter along the length of each tube. Additionally, we found instances where rods cross on top of one another in places, despite a stated absence of such intersections (“intercuttings”) in the holotype of “O. recta” and hypotypes from the Yale Peabody Museum (Seilacher et al., 2005). Moreover, rod crossovers indicate rigidity in the fossils, rather than cross-cutting relationships that might be expected from multiple burrows. In one example, where a positive-relief rod overlies two others, the convexity of the underlying ones is expressed, implying compression of the overlying rod.

Seilacher et al. (2005) originally interpreted YPM specimens of “Oldhamia recta” from the Floyd Church Formation of North Carolina as trace fossils on the basis of the following identified traits: (1) clusters (“bundles”) of straight, unbranched tunnels proximal and subparallel to one another; (2) positive- and negative-relief expression on the same bed surface; and (3) absence of cross-cutting (“intercutting”) or other connections in bundles. Furthermore, Seilacher et al. (2005) interpreted these as backfilled burrows. This conclusion was seemingly made only on the basis of the positive and negative relief of the fossils, rather than on any direct evidence of backfilling; undermat mining is also assumed in this interpretation. Without direct evidence of backfilling, such statements can only be regarded as arguments by assertion. In short, body fossils could likewise be preserved in positive and negative relief, whereas no body fossil would show internal menisci, or fecal pellets within menisci. The lack of evidence for active fills also renders interpretations of undermat mining in “O. recta” problematic. An alternative explanation for the positive-relief expression of these structures would be passive filling of burrows by sediment from above the mat surface. This situation, however, would have required an open connection to the
sitting–water interface, which also belies an undermat-mining scenario.

A trace fossil interpretation of “O. recta” for these specimens also prompts several rhetorical questions. How does a burrow origin necessarily follow from the specimens being straight, subparallel to one another, unbranched (but closely spaced), and parallel to the bedding plane? These traits are equally applicable to elongate body fossils that are clustered, subparallel to one another, and parallel to the bedding plane (horizontally oriented) because of post-mortem (biostratigraphic) processes, such as current alignment or depositional flattening (Brandt, 1989; Droser and Gehling, 2008). Additionally, given the preferred alignment of specimens (hinted in the original description of “O. recta” through the descriptor “subparallel”: Seilacher et al., 2005), why didn’t a undermat miner burrow within such narrow horizontal ranges? Were these heterozoans so advanced in their sensory abilities that they were exhibiting the effects of group behavior (e.g., Martin and Rindsberg, 2006), but as infauna? Furthermore, a fluid can transmit odors and other chemotaxic cues above a sediment surface to guide animal foraging, whereas a lack of flow within a sediment means that such behaviors would be more random (Koy and Plotnick, 2007). The undermat-mining interpretation, combined with active backfilling, is also difficult to reconcile with the variable horizontal extent of the structures.

The conclusions we draw from these qualitative assessments are further supported by quantitative analyses of the fossils themselves and their perceived alignment. With regard to size-frequency distributions, some trace fossils, particularly burrows, can demonstrate tight distributions of size parameters, which oftentimes reflect tracer body size (Kowaleski and Demko, 1996; Martin, 2006). The rods measured in this study are extremely regular in width, as well as showing Gaussian distributions for lengths (despite their high variability). Unless burrow length is directly correlated with tracer body length or some other limiting anatomical trait of the tracer, the normal distribution shown by the lengths of “O. recta”, coupled with the narrow distribution of widths, is more readily explainable from body fossils with regular dimensions. Moreover, preferential alignments of rods, with narrow ranges of alignment, are here interpreted as a result of current alignment, which again is more likely with body fossils. Although some burrows can show preferred orientations as a result of current alignment (Crimes and Crossley, 1980; Pemberton and Frey, 1984) or even current sheet (Gingras and Bann, 2006), we fail to understand how currents could have influenced undermat miners to burrow in preferred directions. The only alternative explanation is that such tracemakers were under the influence of some sort of chemotaxis (Rindsberg and Martin, 2003; Koy and Plotnick, 2007). This possibility, however, was not proposed in the original diagnosis of O. recta (Seilacher et al., 2005) and again is less likely under the scenario of the tracemakers as undermat miners (Koy and Plotnick, 2007).

Yet another objection to the description of these fossils as an ichnospecies of Oldhamia is based on broader circumstances, such as their paleoenvironmental setting. Seilacher et al. (2005) interpreted these trace fossils as indicators of deeper-water conditions in the Abermarle Group, conforming to deep-water interpretations for Cambrian examples of Oldhamia (McNaughton, 2007). A deep-water paleoenvironmental setting for the Abermarle Group, however, is contradicted by other geologic data indicating that it was originally composed of shallow-water sediments (Gibson and Teeter, 1984; Hibbard et al., 2009). Such an inconsistency is more easily explained by the presence of shallow-water body fossils in the Abermarle Group (Floyd Church Formation), rather than anomalous shallow-water Oldhamia.

Oldhamia as an ichnogenus extended to the Ediacaran has previously provoked disagreements about its possible body fossil identity. As noted by Vickers-Rich and Fedonkin (2007), Oldhamia was originally questioned as an Ediacaran trace fossil by Runnegar (1992), who affiliated it with the body fossil Aspidella. McNaughton (2007) also noted that debate over the trace fossil identity of Oldhamia in general persisted well into the 20th century, but is now widely acknowledged as the product of a small, vermiciform deposit feeder. Nonetheless, McNaughton (2007) also pointed out how the potential use of Oldhamia for biostратigraphy has been more for the Cambrian; this utility has been recognized since the 19th century. In other words, Precambrian examples of Oldhamia are evidently exceptional, and thus should be regarded with greater skepticism.

The distinction of a trace fossil versus a body fossil origin of O. recta may seem trivial to argue. Our reasons for exploring this point in depth are threefold. One is that Ediacaran fossil-bearing strata are filled with odd structures, fossil and otherwise, that defy easy classification compared to those from the Phanerozoic. Yet we still must try to distinguish these structures. To simply say that all such analyses of Oldhamia and other problematic structures will be subjective, and that interpretations will vary, is as unacceptable as saying that a bivalve shell could also be a trace fossil. Secondly, Oldhamia has been proposed as an ichnogenus that could help with better understanding Ediacaran-Cambrian stratigraphy, and has even been interpreted in terms of an evolutionary history (Seilacher, 1974; Lindholm and Casey, 1990; Seilacher et al., 2005; McNaughton, 2007). Hence its misidentification will result in faulty reconstructions of broader trends in the ichnogenus, whether temporally or paleogeographically. Third, Oldhamia is regarded as an ichnogenus indicating deep-water environments (Seilacher et al., 2005; Aceñolaza and Aceñolaza, 2007; McNaughton, 2007). If this paleoenvironmental interpretation continues to hold, its mistaken identity may result in misleading assessments of Ediacaran and Cambrian paleoenvironments.

Although we do not consider our work as the final word on the status of “Oldhamia recta,” we hereby submit that it is incumbent on future researchers to test and disprove our designation of it as a body fossil. Such disproof could be easily accomplished by providing further evidence supporting its trace fossil origin, such as active backfill structures and other ichnological features unknown to body fossils. Indeed, we fully expect that some researchers will continue to use “Oldhamia recta” as an ichnospecies, particularly for Ediacaran occurrences. In an example of how science works, though, we should point out how this ichnospecies remains unidentified in any other Ediacaran deposit, or in Cambrian strata, despite its widespread occurrence as an ichnogenus (McNaughton, 2007). In other words, specimens of “Oldhamia recta” from the Floyd Church Formation would be the only known examples in the world; more Ediacaran examples from other localities would also help to clarify its identity and potentially disprove our new hypothesis. Regardless, a lack of caution in the face of the data we have presented here may cause further confusion about the identity of other Ediacaran fossils, which admittedly are composed of a bewildering assortment of body fossils, trace fossils, and pseudofossils.

5. Summary

In short, a closer examination of the YPM specimens of “Oldhamia recta” (including its holotype), show these fossils lack key traits confirming a trace fossil origin. Additionally, and most importantly, the quantitative data of size distributions and orientation data argue strongly for body fossil origin and subsequent alignment by currents along bedding plane surfaces. Furthermore, the new examples described from the Floyd Church Formation in this study (particularly NCSM10530) affirm the preceding data, and again favor a body fossil origin for “O. recta.” This affirmation is also supported by the paleoenvironmental setting of the Floyd Church...
Formation as a shallow-water deposit, as opposed to the deeper-water setting associated with other ichnospecies of Oldhamia. We propose that these specimens are body fossils of a yet-undescribed rod-like organism that deserves more study. Our study also supports the use of more quantitative approaches when evaluating whether Ediacaran-age structures are trace fossils or body fossils, which potentially can illuminate broader aspects of fossil identity that supersede arguments over enigmatic structures based only on morphology. The fundamental question – is this a body fossil or a trace fossil? – always should be asked when encountering such anomalous structures, some of which oftentimes have no facile Phanerozoic parallels (Droser et al., 2005; Cohen et al., 2009; Gehling and Droser, 2009).

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