TRACE FOSSILS WITH SPREITEN FROM THE LATE EDIACARAN NAMA GROUP, NAMIBIA: COMPLEX FEEDING PATTERNS FIVE MILLION YEARS BEFORE THE PRECAMBRIAN–CAMBRIAN BOUNDARY

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ABSTRACT—Here we describe large, complex trace fossils in the late Ediacaran Omkyk Member of the Zaris Formation, Nama Group, southern Namibia. The horizontal trace fossils are preserved on a number of talus blocks from a bedding plane of a cm-thick sandstone lens from a single stratigraphic horizon less than 100 m below an ash bed dated at 547.3 ± 0.7 Ma. The forms consist of overlapping U-shaped spreiten elements with parallel limbs surrounded by an outer tube. Individual U-shaped elements are 0.2 to 1 cm in diameter, the outer tube is less than 3 mm in diameter, and the forms as a whole range from 5 to 30 cm long and 3 to 10 cm wide. The specimens commonly show a change in direction and change in diameter. The morphology of these trace fossils is comparable to backfill structures, particularly specimens of Paleozoic *Zoophycos* from shallow water environments. Here we interpret these horizontal spreiten-burrows to record the grazing of the trace-maker on or below a textured organic surface. The identification of large late Ediacaran trace fossils is consistent with recent reports of backfilled horizontal burrows below the Precambrian–Cambrian boundary and is suggestive of the appearance of complex feeding habits prior to the Cambrian trace fossil explosion.

INTRODUCTION

EDIACARAN STRATA record biological experimentation and expansion that presaged the Cambrian explosion. Along with the classic Ediacaran biota (Narbonne, 2005), calcifying metazoans (Grotzinger et al., 2000), possible metazoan embryos (Xiao and Knoll, 2000), and putative mollusks (Fedonkin and Waggoner, 1997) all make their first appearance in the fossil record during the Ediacaran Period. This rise of macroscopic organisms is coupled with a diversification of microfossils (Cohen et al., 2009a), evidence for predation (Bengtson and Zhao, 1992; Hua et al., 2003), and the first appearance of trace fossils (Jensen et al., 2006). Molecular clock data further predicts that mobile bilaterians capable of complex feeding patterns should have been abundant during the Ediacaran Period (Erwin et al., 2011). However, in comparison to the rich ichnofossil record that complements the great metazoan radiation of the Cambrian (Crimes, 1992; Jensen, 2003), the Ediacaran trace fossil record is sparse, consisting mostly of small, bed-parallel burrows (Jensen et al., 2006). This presents a dilemma as to why the development of complex and abundant trace-making was not only abrupt in the fossil record, but also lagged behind the molecular fossil record that predicts the appearance of trace-making animals (Erwin et al., 2011). It also indicates a potential problem in defining chronostratigraphic boundaries with records of behavior that are potentially taphonomically biased or diachronous (Wilson et al., 2012; but see also Buatois et al., 2013), particularly without direct geochronological constraints and other independent correlation tools. Moreover, these forms could have been developed among many different genera. Indeed, recent discoveries suggest that this critical transition in sediment-organism interactions may have begun to develop in the late Ediacaran (Liu et al., 2010; Chen et al., 2012; Rogov et al., 2012; Macdonald et al., 2013).

The burgeoning record of complex Ediacaran trace fossils has important implications for mixing at the sediment-water interface prior to the Cambrian Period. For example, in modern settings, bioturbation can affect sediment column redox zonation and the localized recycling of organic matter (Aller, 1994; Ziebis et al., 1996; Meysman et al., 2006). It has long been recognized that the transition from firm-ground substrates of the Proterozoic to the more soupy, well-mixed upper sedimentary layers of the Phanerozoic had critical biogeochemical and ecological impacts (McIlroy and Logan, 1999; Bottjer et al., 2000; Droser et al., 2002; Seilacher et al., 2005; Canfield and Farquhar, 2009). Recent reports of bioturbation in late Ediacaran strata (e.g., Rogov et al., 2012; Carbone and Narbonne, 2014) suggest that extensive infaunal activity preceded the 'Cambrian Explosion' but post-dated the Shuram carbon isotope excursion (Grotzinger et al., 2011). Here we describe previously unreported complex trace fossils from late Ediacaran strata in the Omkyk Member of the Nama Group of southern Namibia that occur stratigraphically below ash beds dated at 547.3 ± 0.7 Ma (Grotzinger et al., 1995; all dates reported herein are U/Pb CA-ID-TIMS on zircons recalculated by Schmitz, 2012), but immediately above a large negative carbon isotope excursion that has been correlated globally with the pre-551 Ma Shuram excursion (Condon et al., 2005). We then discuss implications for the expansion of complex infaunal activity and biogeochemical cycling.

GEOLOGIC SETTING

The terminal Ediacaran to Terreneuvian Cambrian Nama Group was deposited in a foreland basin on the northern margin of the Kalahari Craton in response to the Pan-African Damaran orogeny (Germs, 1972; Germs and Gresse, 1991; Grotzinger and Miller, 2008). The age of the Nama Group is well constrained by U-Pb CA-ID-TIMS zircon ages from interbedded ashes, with deposition spanning a period of ~15 Ma from 550–535 Ma (Grotzinger et al., 1995; Grotzinger and Miller, 2008). In the northerly sub-basin, near Hauchabfontein Farm, the Dabis Formation (Kuibis Subgroup, Nama Group) overlies Paleoproterozoic crystalline basement and consists of coarse-grained sandstone and conglomerate (Fig. 1), which preserve soft-bodied Ediacaran biota (Germs, 1972; Narbonne et al., 1997).
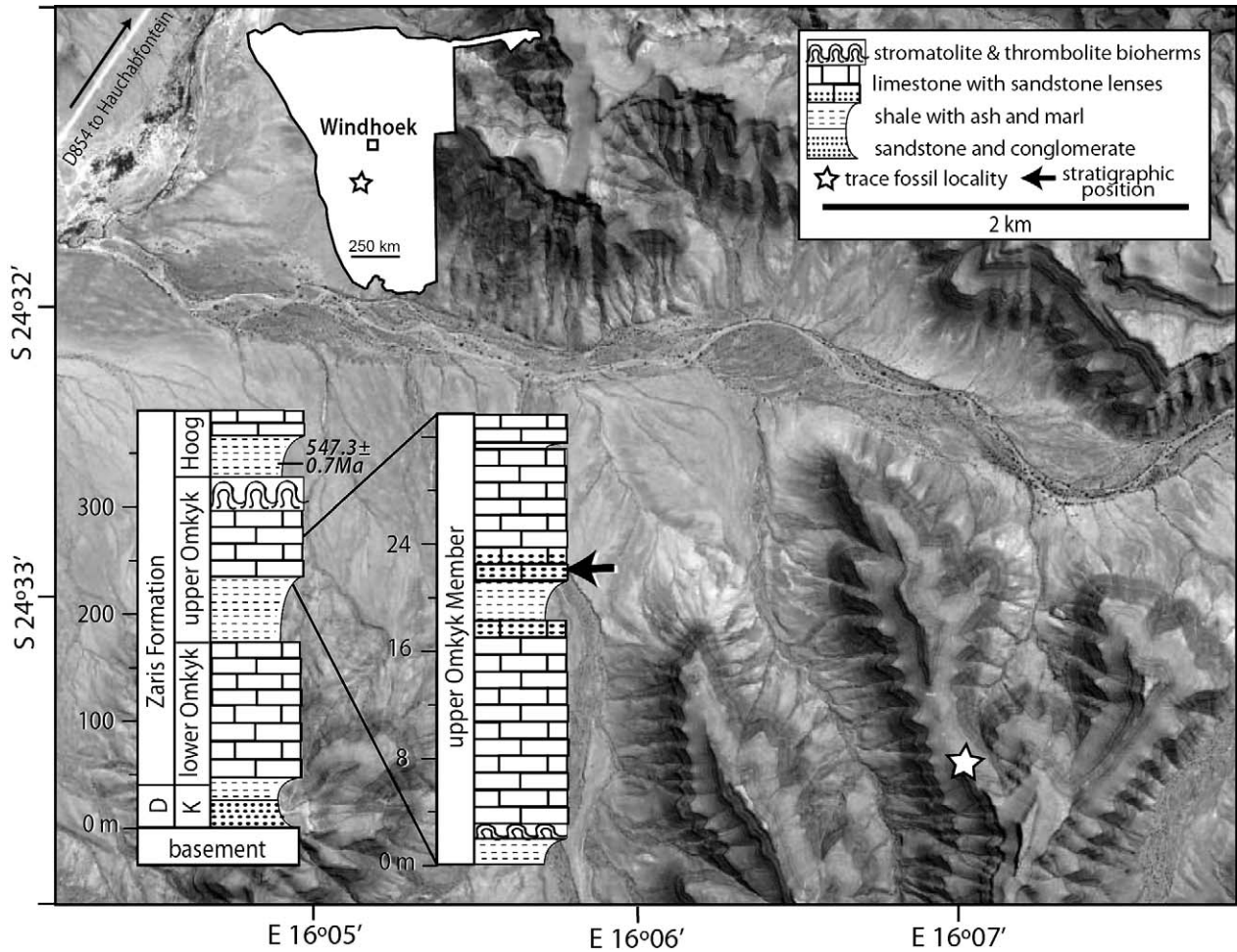
FIGURE 1—Google Earth image of Hauchabfontein Farm with insets of a location map, the generalized stratigraphy of the Kuibis Subgroup, and the detailed stratigraphy of units bounding the trace fossil. Arrow points to the stratigraphic horizon of the sandstone bed that hosts the trace fossils. 'Marl' is shorthand for carbonate-rich shale and calcisiltite. 'Ma' is million years ago.

Above these siliciclastic units, the Kuibis Subgroup continues upwards with as much as 600 m of carbonate-dominated strata of the Zaris Formation. The Kuibis Subgroup is succeeded by approximately 1 km of siliciclastic-dominated strata that spans the ca. 541 Ma Ediacaran–Cambrian boundary (Grotzinger and Miller, 2008).

The Zaris Formation is subdivided into the Lower Omkyk, Upper Omkyk, and Hoogland members (Fig. 1), all of which contain abundant calcifying metazoan fossils (Grotzinger et al., 2000; Wood et al., 2002). At Hauchabfontein Farm, the Lower Omkyk Member consists of 122 m of dark blue-gray limestone that coarsens-upwards from ribbon-bedded lime mudstone to variably recrystallized cloudinid packstone, grainstone, and calcarenite with common scour surfaces and thin sandstone lenses. The sandstone lenses are typically less than 2 cm thick and are laterally continuous for less than 500 m. The Upper Omkyk Member begins with 72 m of shale and calci-siltite with flinty, apple-green colored volcanic tuff interbeds and hetero-lithic storm deposits. These are succeeded by an additional 63 m of dark-colored, trough cross-bedded interclast and ooid grain-stones that are compositionally similar to those of the Lower Omkyk Member. It is near the base of the Upper Omkyk Member that the spreiten trace fossils were discovered within a 0.5–2 cm thick lenticular bed of medium- to coarse-grained sandstone. These sandstone beds and lenses have sharp bases

and are interpreted to represent storm deposits within wave-influenced shoreface facies (Grotzinger and Miller, 2008). The Upper Omkyk Member culminates with tan-colored stromato-lite-thrombolite patch-reefs, which are ~13 m thick at the trace fossil locality. The bioherms are capped with approximately 50 m of recessive shale and marl, which make up the basal Hoogland Member and include a volcanic tuff horizon dated at 547.3 ± 0.7 Ma (Grotzinger et al., 1995).

MATERIALS AND METHODS

All trace fossil specimens were found near the Zebra River in the Ediacaran Kuibis Formation of the Nama Group in southern Namibia. The best-preserved specimen (Fig. 2.1) was discov-ered at S 24°33.341′, E 16°07.058′, and additional trace fossils are present on nearby talus blocks exposed on the privately owned Hauchabfontein farm (Fig. 1). The trace fossils were solely examined in the field because the large size of the talus blocks preserving the trace fossils (approximately 2 m^3 in area) and restrictive Namibian laws regarding Ediacaran fossils precluded their collection.

Despite detailed examination of trace fossils in the Nama Group by previous authors (e.g., Crimes and Germs, 1982; Jensen et al., 2000; Noffke et al., 2002; Cohen et al., 2009b), the narrow geographic range of the facies that preserve these forms likely precluded their earlier discovery. The trace fossils

FIGURE 2—Field photographs of trace fossil on bedding planes from the discovery locality. *1*, large spreiten trace fossil exhibiting an increasing diameter, and displaying: A, U-shaped spreite elements; B, overlapping elements at the margin, indicative of spreiten-style excavation and sediment displacement by an organism; and C, possible tubes at the margin; *2*, close-up of part of trace fossil in *1*, showing a change in direction of the trace and geometry of individual spreite; note the U-shaped spreiten are nested with steeper inner walls, indicating a retrusive form and progression from right to left; *3*, close-up of tube on upper right margin of trace fossil in *1* displaying positive epirelief.

preserved in the Upper Omkyk Member occur in a 1.4 m thick, trough cross-bedded limestone bed with 0.5–2 cm thick orange-stained quartz-rich sandstone lenses. The traces penetrate less than 1 cm into the sandstone lens, and they are found only on bedding plane surfaces. They are isolated to the sandstone lens with no evidence of penetration into the underlying carbonate beds. They were identified on four separate blocks over a lateral distance of approximately 100 m along a single stratigraphic horizon. The trace fossils were observed on talus blocks because this is the only place that bedding planes are exposed, but there is no ambiguity about what bed they came from, as the blocks are displaced less than 10 m directly below the distinctive source bed. Following this bed more than 0.5 km to the southeast revealed that the sandstone lens in which the trace fossils are preserved thickens and becomes less discrete; consequently, bedding planes do not fracture along horizons that display the traces. Following this bed more than 0.5 km to the northwest, the sandstone lens thins and eventually disappears.

DESCRIPTION OF TRACE FOSSILS

The trace fossils consist of arcuate, nested, retrusive U-shaped structures with parallel limbs (Fig. 2.1). These structures minimally penetrate the sediment (less than 1 cm) and show patterns of excavation along the horizontal bedding plane with approximately 5 mm of positive epirelief. There are no obvious lithological differences between lamellae and matrix. Individual U-shaped elements are 0.2 to 1 cm in diameter, overlap at the margins, and thus taper at the ends and change in diameter from one terminus to the other (Fig. 2.2). The trace is outlined by a poorly preserved, eroded 2 to 3 mm diameter tube that is most visible on the upper part of the lower left portion of the trace as imaged (Fig. 2.3). The length of the entire ichnofossil ranges from 5 to 30 cm across a single bedding plane and are 3 to 10 cm wide. These do not represent a maximum or minimum size range for these ichnofossils because few samples were available for analysis and some may be incomplete. The specimens commonly show a change in direction across a single bedding plane.

The horizontal spreiten burrows of the Omkyk Member consist of a series of spreite elements that cover bedding plane surfaces of large talus blocks. None of the traces reported herein are branched. The largest of these traces shows a change in width along the length of the structure (Fig. 2.1, 2.2), and at least part of this change in diameter may be related to slightly oblique cut of the trace fossil along its length. Some of the elements cut across each other and are convexly nested (Fig. 2.1, 2.2), which is consistent with retrusive spreiten.

TAPHONOMY OF TRACE FOSSILS

The trace fossils occur in a 0.5–2 cm thick sandstone lens within a 1.4 m-thick limestone bed (Fig. 3.1). Other thinner sandstone lenses are present within this interval (Fig. 3.1), but these lenses do not break off along flat bedding planes, precluding the preservation of observable trace fossils. On a larger scale, similar sandstone lenses are present at other stratigraphic levels in both the lower and upper Omkyk Member, but the trace fossils were only found at this single horizon. The taphonomic conditions that fostered the preservation of these trace fossils appear to be closely related to textured organic surfaces (TOS) on the sandstone lens, which have been interpreted as microbially-bound bedding surfaces (Droser et al., 2005; Gehling and Droser, 2009; Schieber, 1999). Bedding surfaces associated with horizontal spreiten-burrows preserve TOS; however, these trace fossils cross-cut the TOS fabrics

(Fig. 3.2). TOS fabrics have been described at many horizons in the Nama Group (Bouougri and Porada, 2007) and are present on many bedding planes of sandstone in the Omkyk Member (e.g., Fig. 3.2, 3.3). These include patterned elements that broadly resemble "baggy" forms (Gehling and Droser 2009; Fig. 3.2, 3.3). If the TOS represent the remnants of microbial mats, it is probable that the trace-makers were under-mat miners (Seilacher, 1999).

Various lines of evidence suggest that these structures formed when the quartz-rich sandstone lenses were unlithified and not subsequent to their burial, and lithification. The organization of these forms into discrete spreiten elements implies that this infaunal excavation must have occurred prior to lithification. Furthermore, the presence of these forms below the uppermost sandstone layers is consistent with in situ formation prior to lithification, rather than more recent bioaccumulation of sand by termites or terrestrial insects (Cloud et al., 1980). Moreover, marine deposition ceased in the early Cambrian with the Damaran Orogeny (Germs, 1972; Germs and Gresse, 1991; Grotzinger and Miller, 2008), and since that time, Namibia has been located in an uplifted area of erosion and has not experienced significant submergence and sedimentation (Martin, 1975; Stollhofen et al., 2000), precluding the possibility that these deposits were reworked or generated secondarily.

DISCUSSION

Wave formed structures and body fossil impressions.—Wetzel (1999, 2013) documented a set of abiogenic shallow water structures termed 'tilting traces,' which formed by raking of objects in an oscillatory flow regime. While this mechanism produces structures that are important to consider when interpreting trace fossils, these structures do not closely resemble the forms in the Omkyk Member. Oscillatory raking of a medusa produced spreiten-like structures, but these features lacked an outer tube, contain U-shaped elements of variable size, and do not penetrate the sediment. These aspects of the tilting marks are thus inconsistent with the structures described herein.

Similarly, the Ediacaran *Palaeopascichnus*, which were originally described as meandering trace fossils (Fedonkin, 1977) and have subsequently been interpreted as unusual macroscopic body fossils (Jensen, 2003) perhaps of large foraminifera (Seilacher et al., 2005), share some characteristics with the Omkyk structures. However, the marginal overlapping of spreiten elements, the cross-cutting relationships with TOS, and evidence for sediment displacement allow us to interpret the Omkyk specimens as trace fossils. Although it is possible that what has been called *Palaeopascichnus* is polymorphic and has different origins, to avoid further confusion we refer to the forms described here as horizontal spreiten-burrows.

Interpretation and comparison with existing ichnogenera.— Horizontal to oblique U-shaped spreiten burrows are defined by their total width, length, and outer tube dimensions (Fig. 4). Important features of the Omkyk traces are that the spreiten elements are nested, dip outward, and overlap, and their diameter changes along the length of the trace fossil. The evidence for sediment displacement, in the form of organized spreiten with elements that occasionally cut across each other (Fig. 2.1, 2.2), most likely represents a complex, sediment-mining behavior. These spreiten forms minimally penetrate less than 1 cm into the sandy lenses in which they are preserved and consist of horizontal U-shaped elements of consistent thickness, which are characteristics of infaunal, bedding plane-parallel trace fossils (e.g., Rhizocorallids and traces made by the polychaete worm *Polydora*, Seilacher, 2007, p. 56). These features are consistent with formation as backfill that was generated by a bilaterian via a progressively concave, retrusive pattern (Fig. 4). The traces
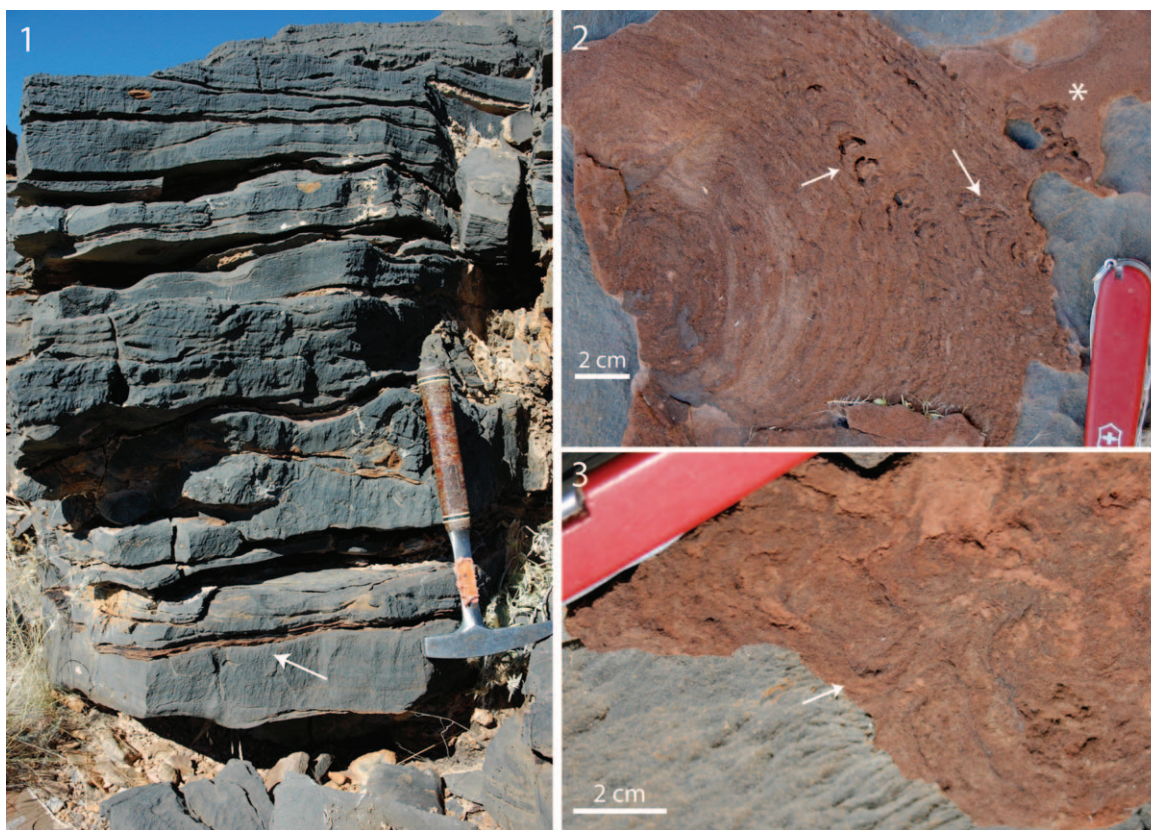
FIGURE 3—*1*, outcrop photograph showing in situ trace fossil-bearing sandstone lenses within thick limestone bed; note that trace fossils are from the thickest lens marked with an arrow, hammer handle is 30 cm long; *2*, two U-shaped trace fossils on bedding planes with textured organic surface (arrows), asterisk shows raised edge of sandstone bed; *3*, close-up of textured organic surfaces common on the sandstone bedding planes. Specimens imaged in *2* and *3* are from talus blocks located ∼100 m northwest of discovery locality.

appear to shallow from bottom to top in the direction of burrowing (Figs. 2.1, 4). Similar features have also been observed in the Paleozoic *Zoophycos* and *Spirophyton* (Miller, 1991; Sappenfield et al., 2012; Fig. 5), traces with "ambivalent backfill" in which centrifugal cross lamination of the spreiten elements is not readily apparent (Seilacher, 2007). Although portions of the structure compare favorably to *Rhizocorallium*, the less distinct outer tube and changing diameter precludes defining a closer relationship between these Omkyk traces and *Rhizocorallium*, but does not eliminate their similarities. In other ways, such as the pronounced change in the large trace diameter across a single bedding plane, this form is more similar to that of Paleozoic *Zoophycos* (Fig. 5). Importantly, like the Omkyk trace fossils, Paleozoic *Zoophycos* is distinct from Mesozoic and Cenozoic *Zoophycos*, in that they lack "perfection" of form and are preserved in shallow water sandstone beds (Miller, 1991). Because these comparisons are imperfect and because this trace shares qualities of both of these Phanerozoic trace fossils, we refrain from assigning these forms to a particular ichnotaxon, but instead refer to the Omkyk traces as horizontal spreiten-burrows.

Carbon isotope chemostratigraphy.—Carbon isotope chemostratigraphy potentially provides an independent method of testing correlations between ichnozones. For example, trace fossils of the Nama Group, including those described herein from the Omkyk member, occur above a carbonate carbon isotope excursion (Grotzinger et al., 1995) that has been correlated with the Shuram excursion in Oman (Burns and Matter, 1993; Grotzinger et al., 2011). In Oman, the Shuram excursion occurs directly below the Ara Group, which contains ashes that have been dated between 546.7 ± 0.7 Ma and the Ediacaran–Cambrian boundary at 541.0 ± 0.6 Ma (Amthor et al., 2003; Bowring et al.,

2007). We refer to Ediacaran large negative carbon isotopic exursions as 'Shuram-like' (Fig. 6) because their direct global correlation is still in question, as it is unclear if there is one isochronous excursion or multiple carbon isotope excursions during the late Ediacaran Period (Macdonald et al., 2013). Nonetheless, under the assumption that the Shuram excursion is isochronous, below we use the excursion to evaluate the synchroneity of Ediacaran ichnozones.

In South China, a maximum age constraint on Shuram-like excursions is provided by a 551.1 ± 1.0 Ma date from unit D of the Doushantuo Formation (Condon et al., 2005), which marks a return to positive $\delta^{13}C_{carb}$ values stratigraphically below the first occurrence of *Planolites* trace fossils (Zhou and Xiao, 2007). Similarly, a Shuram-like excursion occurs at the base of the Nama Group below an ash bed dated at 547.3 ± 0.7 Ma (Grotzinger et al., 1995). Coupled with these dates, Shuram-like isotope excursions can be used to construct an age model for fossiliferous sections in Australia, northwestern Canada, and Siberia, all of which do not have direct geochronological age constraints on Ediacaran strata (Fig. 6). Although trace fossils in Newfoundland and the White Sea region of Russia are in siliciclastic-dominated successions that lack carbonate strata for chemostratigraphy, direct geochronological constraints within these sections suggest they were formed during or before the Shuram-like excursions (Fig. 6).

Ediararan ichnozones.—Crimes (1987) distinguished a three stage trace fossil zonation for the upper Ediacaran (559–541 Ma; Narbonne et al., 2012), each displaying increasing complexity. These zones were later refined by Jensen (2003) and modified (Jensen et al., 2006) to match the Ediacaran macrofossil
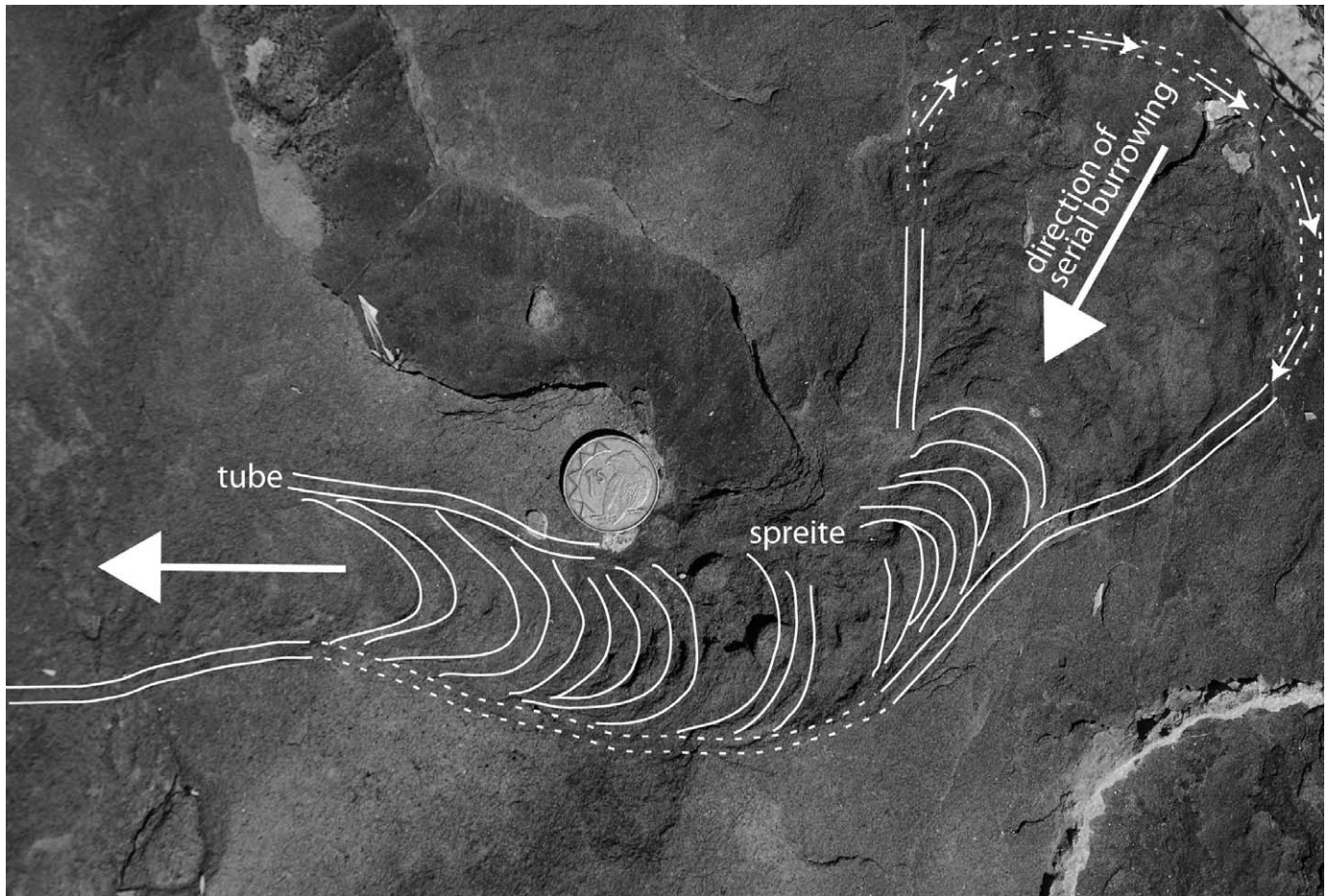
FIGURE 4—Schematic representation of the creation of a single trace fossil overlain on an image of the specimen. Small arrows show the direction of movement of the trace-maker to form one spreite. When the trace-maker backtracks this track will be partially overlapped such that only the outer tube diameter would remain consistent. Large arrow shows the serial progression of the trace-maker, which can be inferred from the steeper inner walls of the U-shaped spreiten and their convex nesting with cross-cutting relations.

assemblages (Avalon, White Sea, and Nama; Waggoner, 2003; Narbonne, 2005). These assemblages lack abundant geochronological constraints, and independent biostratigraphic control, so it remains unclear if these biozones are distinct chronozones or if they potentially reflect taphonomic and environmental differences.

Jensen et al. (2006) described the lowest ichnozone, equivalent to the ca. 579–559 Ma Avalon assemblage, to be devoid of definitive trace fossils. This assumption has been challenged with the recent discovery of putative trace fossils in Newfoundland that are ∼50 m above an ash that has been dated at 565.0 ± 3.0 Ma (Benus, 1988; Liu et al., 2010). These structures have leveed margins and crescentic internal divisions that potentially represent simple backfill (Liu et al., 2010).

The second Ediacaran ichnozone, equivalent to the ca. 558–550 Ma White Sea Assemblage, consists of unbranched horizontal trace fossils exemplified by *Helminthoidichnites*, Dickinsonid imprints, and raspings (Jensen et al., 2006). In the White Sea succession of Russia, trace fossils such as *Archaeonassa* and *Aulichnites*, have been described in the same section with a possible mobile metazoan, *Kimberella*, and some are below an ash bed dated at 552.9 ± 2.6 Ma (Martin et al., 2000). The White Sea Assemblage and its ichnofossils have been previously correlated with macro- and ichnofossils from the Rawnsley Quartzite of Australia and the Blueflower Formation of northwestern Canada (Jensen et al., 2006; Narbonne et al., 2012; Carbone and Narbonne, 2014).

In Australia, many tubular forms, previously interpreted as trace fossils (Glaessner, 1969), have been reinterpreted as body fossils (Gehling and Droser, 2009; Sappenfield et al., 2011). Only simple trace fossils with levees, referred to as *Helminthoidichnites*, *Aulichnites*, *Radulichnus*, and *Spirorhaphe involuta*, have withstood recent scrutiny (Gehling and Droser, 2009; Jensen et al., 2006). Although a direct age constraint on the Rawnsley Quartzite is not available, the traces are present hundreds of meters below a sub-Cambrian unconformity and above a Shuram-like carbon isotope excursion in the Wonoka Formation (Pell et al., 1993; Calver, 2000; Husson et al., 2012). This appears to contradict the correlation with the White Sea Assemblage at the eponymous locality, which was deposited at ca. 553 Ma, during or before the Shuram-like excursions (Fig. 6). Indeed, Ediacaran assemblages may not represent strict chronostratigraphic tie points as both facies assemblages and depositional environments may also represent a major control on the distribution of Ediacara-type fossils and trace fossils, as is seen in South Australia (Gehling and Droser, 2013).

In northwestern Canada, trace fossils first appear and are abundant in the basal beds of the Blueflower Formation (Narbonne and Aitken, 1990; Carbone and Narbonne, 2014), although at Sekwi Brook these were previously assigned to the uppermost Gametrail Formation (Macdonald et al., 2013;
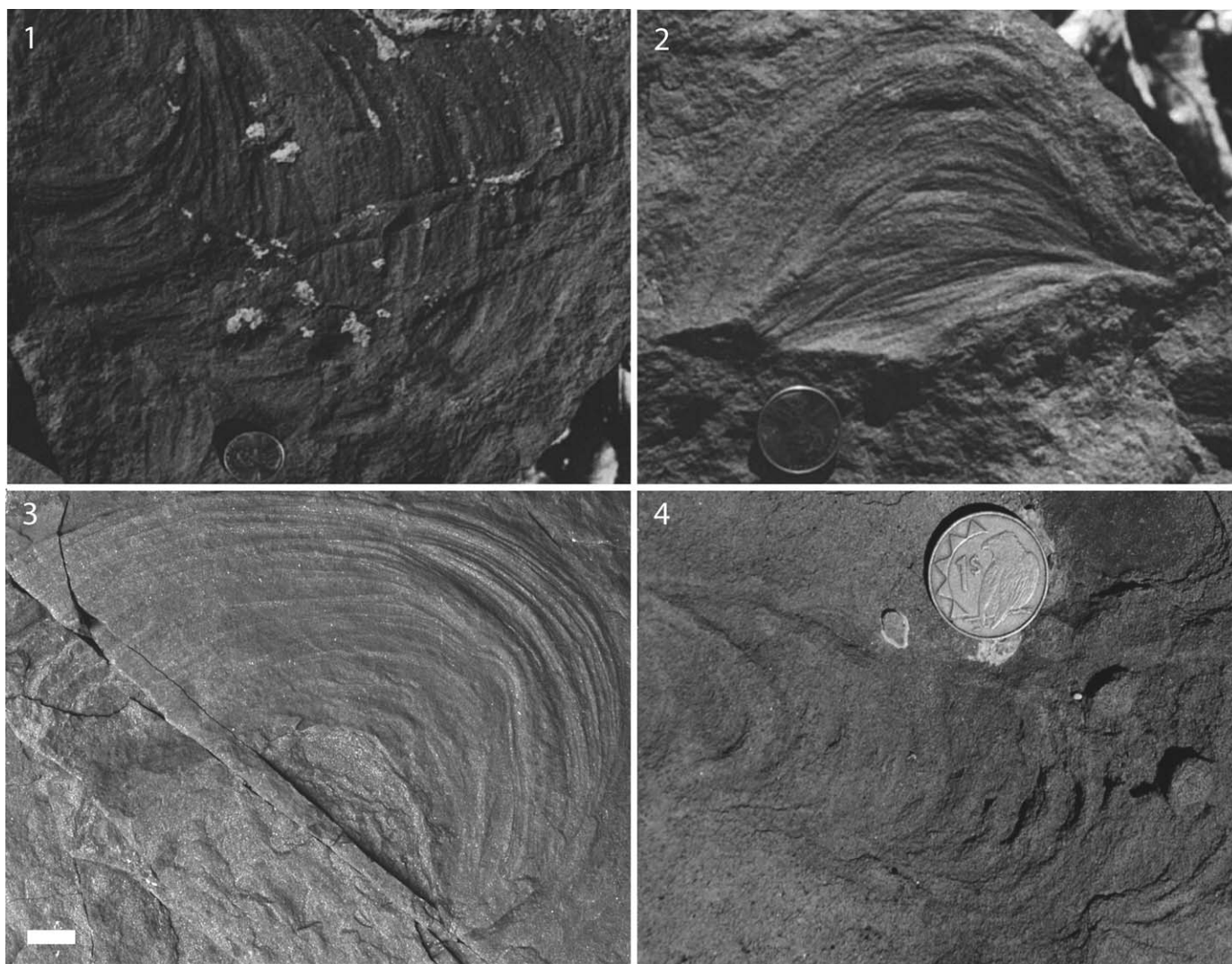
FIGURE 5—*1, 2*, Paleozoic *Zoophycos* from the Devonian Catskill delta storm-dominated shallow marine deposits, New York, modified from Miller (1991) with permission of M. F. Miller; *3*, Paleozoic *Zoophycos* from the Cambrian Woods Canyon Formation in the Nopah Range of California (Sappenfield et al., 2010), image courtesy of A. Sappenfield; *4*, Ediacaran horizontal spreiten described in this paper for comparison with *3*. Coin is 2 cm in *1, 2*, and *4*; scale bar = 1 cm in *3*. Note that these Paleozoic *Zoophycos* trace fossils are developed in sandstone beds and display both overlapping spreiten elements and changes of width along the trace.

MacNaughton and Narbonne, 1999). The Blueflower Formation contains a trace fossil assemblage that includes the forms *Aulichnites*, *Helminthoidichnites*, and multiple types of *Helminthoida*, *Planolites*, and *Torrowangea rosei* (MacNaughton and Narbonne, 1999; Narbonne and Aitken, 1990), which display an increase in complexity up-section from simple surface trails to 3D burrows with evidence of filter-feeding and putative avoidance behavior (Carbone and Narbonne, 2014). These trace fossils are preserved between large carbon isotope excursion in the Gametrail and Risky formations that are potentially correlative with the Shuram and Ediacaran–Cambrian boundary carbon isotope excursion, respectively (Macdonald et al., 2013). Again, the stratigraphic position above a Shuram-like excursion is inconsistent with the correlation with the White Sea Assemblage and presents an additional challenge for Ediacaran fossil assemblages and ichnozones. Instead, chemostratigraphy would suggest that the putative White Sea Assemblages of northwestern Canada and Australia are broadly coeval with the Nama Assemblage elsewhere (Fig. 6).

Previously described trace fossils in the eponymous Nama Group of the ca. 549–542 Ma Nama Assemblage include *Chondrites*, *Nereites*, *Paleophycus sp.*, *Skolithos*, and *Trichophycus tripleurum* (Jensen et al., 2006; Jensen et al., 2000). The appearance of treptichnids and trace fossils with three-lobed lower surfaces are thought to be characteristic of this zone (Jensen et al., 2006; Jensen et al., 2000). The Nama Assemblage has been correlated with the Khatyspyt and Turkut formations of Siberia and the Dengying Formation of South China (Narbonne et al., 2012), which is consistent with existing geochronological constraints and chemostratigraphic correlations (Fig. 6).

Evidence for significant bioturbation has recently been reported in the Ediacaran Khatyspyt Formation of Siberia and attributed exclusively to the trace fossil *Nenoxites* (Rogov et al., 2012). Specimens of *Nenoxites* preserve meniscate backfill and a pronounced horizontal component that has been attributed to a bilaterian trace maker (Rogov et al., 2012; however, see Brasier et al., 2013 for an alternative interpretation). Despite disagreement on the genesis of these interesting forms, the Khatyspyt Formation and underlying Maastakh Formation rest unconformably above a
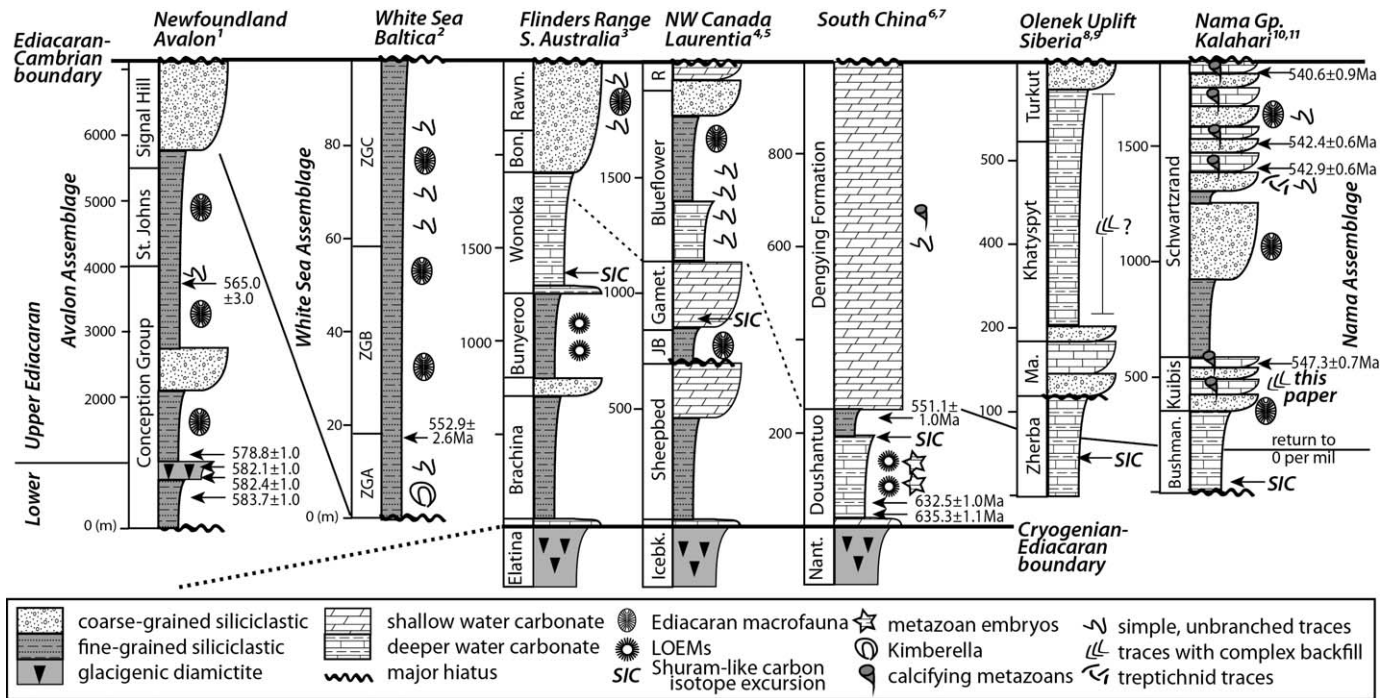
FIGURE 6—Schematic Ediacaran trace fossil record from localities described within the text. Physical-, bio-, and chrono-stratigraphy from: *1*, Liu et al. (2010); *2*, Martin et al. (2000); *3*, Gehling and Droser (2009); *4*, Macdonald et al. (2013); *5*, Narbonne and Aitken (1990); *6*, Zhou and Xiao (2007); *7*, Condon et al. (2005); *8*, Rogov et al. (2012); *9*, Pelechaty et al. (1998); *10*, Jensen et al. (2000); *11*, this paper. Abbreviations: LOEM=Large ornamented Ediacaran microfossils; ZGA, ZGB, and ZBC = Zimnie Gory section units A, B, and C. Ages recalculated by Schmitz (2012).

Shuram-like excursion in the Zherba Formation, and below a sub-Cambrian unconformity (Pelechaty, 1998). Consequently, the age of these possible fabric-destructive burrows is only vaguely resolved between ca. 551 and 542 Ma and could represent the latest portion of the Ediacaran. Moreover, bioturbation of this degree has not been previously reported within the Khatyspyt Formation and appears to be a somewhat localized feature geographically.

Complex feeding patterns and sediment oxygenation.—The horizontal spreiten-burrows of the Zaris Formation reflect a complexity of behavior that conflicts with conventionally defined Ediacaran ichnozones; yet, it is consistent with other recently reported complex backfill structures described from the Ediacaran of Siberia (Rogov et al., 2012). Until this report, the earliest known spreiten trace fossils were from the early Cambrian Gross Aub Formation of Namibia (Geyer and Uchman, 1995) and the late Tommotian or early Atdabanian of central Siberia (Dzik, 2005). Spreiten structures represent some of the earliest innovations in trace making and the presence of spreiten trace fossils in later Ediacaran strata of Namibia indicates that this type of complex behavior evolved earlier than previously suspected. It must be noted, however, that although the Omkyk horizontal spreiten burrows display a more complex under-mat feeding pattern, it is still a bed-parallel form that minimally penetrates the sediment; only the *Nenoxites* of Siberia (Rogov et al., 2012), if correctly interpreted (Brasier et al., 2013), produces beds with an ichnofabric index greater than 2 (sensu Droser and Bottjer, 1993).

Bioturbation and the carbon cycle are directly linked through the respiration of organic matter by introducing oxygen-rich waters into the sediment. Negative carbon isotope excursions as extreme as the pre-551 Ma Shuram excursion do not occur later in Earth history (Grotzinger et al., 2011), suggesting that the late Ediacaran was an interval during which the carbon cycle, and by inference, sedimentary systems, operated in a fundamentally different way. Although simple trace fossils may have appeared

with the ca. 579–559 Ma Avalon Assemblage (Liu et al., 2010), and were certainly preserved in the ca. 558–550 Ma White Sea Assemblage (Jensen et al., 2006), more complex feeding patterns emerged during the ca. 549–542 Ma Nama Assemblage, as highlighted by the spreiten forms reported herein and in the Khatyspyt Formation of Siberia (Rogov et al., 2012). The evolution of more complex feeding patterns and associated bioturbation likely had an impact on remineralization rates in marine sediments (e.g., Canfield and Farquhar, 2009; McIlroy and Logan, 1999). Sediment mixing by metazoan infaunal activity can affect both redox zonation in the sediment column and the cycling of organic matter by supplying oxidants to otherwise anoxic pore waters (Aller, 1994; Aller et al., 2010; Meysman et al., 2006; Ziebis et al., 1996). Importantly, using diffusion modeling, Aller et al. (2010) argue that discrete cm-scale bed penetration is more important for initiating sediment column oxygenation than whole-scale mixing because reaction rates are far higher where there are concentration gradients of oxidants between burrows. The ca. 550 Ma increase in aerobic respiration associated with the expansion of bioturbation would have decreased anaerobic respiration pathways, and inhibited the precipitation of authigenic carbonate by increasing the acidity generated through the oxidation of reduced compounds (C_{org}, H_2S, Fe^{2+}) (e.g., Higgins et al., 2009). The suggestion that large carbon isotope excursions are related to authigenic carbonate formation in unventilated, anoxic sediments (Schrag et al., 2013) potentially provides a link between the trace fossil record and global biogeochemical cycles (Macdonald et al., 2013). Particularly, the transition from dominantly anaerobic respiration to aerobic respiration of organic matter marked the onset of the modern carbon cycle in which the carbon isotope composition of seawater and oxygen levels in the atmosphere were directly linked and controlled primarily by the fractional burial of organic matter.

The documentation of complex trace fossils during the late Ediacaran suggests that ventilation of the sediment-water interface may have pre-dated the Cambrian explosion. Even the small-scale penetration of the Omkyk traces could have had profound impacts on local remineralization. However, it remains to be determined if the patchy distribution of these earliest complex trace-makers reflects a narrow taphonomic window or a more localized distribution of bioturbation in an increasingly oxygenated world.

CONCLUSIONS

The new trace fossils reported here from the upper Omkyk Member of the Zaris Formation, Nama Group, show evidence for sediment displacement in the form of U-shaped spreiten. Like other recently reported forms (Chen et al., 2012; Liu et al., 2010; Rogov et al., 2012), these trace fossils indicate that the ichnological record preserved in Ediacaran strata worldwide may preserve an array of complex behavior more consistent with molecular clock and macrofossil data. The trace-maker is unknown, but we infer that a bilaterian that had the ability to actively mine the sediment for food was responsible for the trace and that it exhibited a specialized and complex behavior normally not seen until the Cambrian Period. The expansion of infaunal feeding patterns during the late Ediacaran Period likely had a profound impact on global biogeochemical cycles.

REFERENCES

ALLER, R. C. 1994. Bioturbation and remineralization of sedimentary organic matter: Effects of redox oscillation. Chemical Geology, 114:331–345.

ALLER, R. C., V. MADRID, A. CHISTOSERDOV, J. Y. ALLER, AND C. HEILBURN. 2010. Unsteady diagenetic processes and sulfur biogeochemistry in tropical deltaic muds: Implications for oceanic isotope cycles and the sedimentary record. Geochimica et Cosmochimica Acta, 74:4671–4692.

AMTHOR, J. E., J. P. GROTZINGER, S. SCHROEDER, S. A. BOWRING, J. RAMEZANI, M. W. MARTIN, AND A. MATTER. 2003. Extinction of Cloudina and Namacalathus at the Precambrian–Cambrian boundary in Oman. Geology, 31:431–434.

BENGTSON, S. AND Y. ZHAO. 1992. Predatorial borings in late Precambrian mineralized exoskeletons. Science, 257:367–369.

BENUS, A. P. 1988. Sedimentological context of a deep-water Ediacaran fauna (Mistaken Point, Avalon Zone, eastern Newfoundland), p. 8–9. *In* E. Landing, G. M. Narbonne, and P. M. Myrow (eds.), Trace fossils, Small Shelly Fossils and the Precambrian–Cambrian Boundary. Volume New York State Museum Bulletin 463.

BOTTJER, D. J., J. W. HAGADORN, AND S. Q. DORNBOS. 2000. The Cambrian substrate revolution. GSA Today, 10:1–7.

BOUOUGRI, E. H. AND H. PORADA. 2007. Siliciclastic biolaminites indicative of widespread microbial mats in the Neoproterozoic Nama Group of Namibia. Journal of African Earth Sciences, 48:2007.

BOWRING, S. A., J. P. GROTZINGER, D. J. CONDON, J. RAMEZANI, AND M. NEWALL. 2007. Geochronologic constraints on the chronostratigraphic framework of the Neoproterozoic Huqf Supergroup, Sultanate of Oman. American Journal of Science, 307:1097–1145.

BRASIER, M. D., D. MCILROY, A. G. LIU, J. B. ANTECLIFFE, AND L. R. MENON. 2013. The oldest evidence of bioturbation on Earth: Comment. Geology, 41: e289–e289.

BUATOIS, L. A., J. ALMOND, AND G. J. B. GERMS. 2013. Environmental tolerance and range offset of Treptichnus pedum: Implications for the recognation of the Ediacaran–Cambrian boundary. Geology, 41:519–522.

BURNS, S. J. AND A. MATTER. 1993. Carbon Isotopic record of the latest Proterozoic from Oman. Ecologae Geologicae Helvetiae, 86:595–607.

CALVER, C. R. 2000. Isotope stratigraphy of the Ediacaran (Neoproterozoic III) of the Adelaide Rift Complex, Australia, and the overprint of water column stratification. Precambrian Research, 100:121–150.

CANFIELD, D. E. AND J. FARQUHAR. 2009. Animal evolution, bioturbation, and the sulfate concentration of the oceans. Proceedings of the National Academy of Sciences, 106:8123–8127.

CARBONE, C. AND G. M. NARBONNE. 2014. When life got smart: the evolution of behavioral complexity through the Ediacaran and early Cambrian of NW Canada. Journal of Paleontology, 88:309–330.

CHEN, Z., C. ZHOU, M. MEYER, K. XIANG, J. D. SCHIFFBAUER, X. YUAN, AND S. XIAO. 2012. Trace fossil evidence for Ediacaran bilaterian animals with complex behaviors. Precambrian Research 224:690–701.

CLOUD JR., P. E., L. B. GUSTAFSON, AND J. A. L. WATSON. 1980. The works of living social insects as pseudofossils and the age of the oldest known metazoa. Science, 210:1013–1015.

COHEN, P. A., A. H. KNOLL, AND R. B. KODNER. 2009a. Large spinose microfossils in Ediacaran rocks as resting staes of early animals. Proceedings of the National Academy of Sciences, 106:6519–6524.

COHEN, P. A., A. S. BRADLEY, A. H. KNOLL, J. P. GROTZINGER, S. JENSEN, J. ABELSON, K. HAND, G. D. LOVE, J. METZ, N. MCLOUGHLIN, P. MEISTER, R. SHEPARD, M. TICE, AND J. P. WILSON. 2009b. Tubular compression fossils from the Ediacaran Nama Group, Namibia. Journal of Paleontology, 83: 110–122.

CONDON, D. J., M. ZHU, S. A. BOWRING, W. WANG, A. YANG, AND Y. JIN. 2005. U-Pb ages from the Neoproterozoic Doushantuo Formation, China. Science, 308:95–98.

CRIMES, T. P. 1987. Trace fossils and correlation of late Precambrian and early Cambrian strata. Geological Magazine, 124:97–119.

CRIMES, T. P. 1992. The record of trace fossils across the Proterozoic–Cambrian boundary, p. 177–202. *In* J. H. Lipps and P. W. Signor, III (eds.), Origin and Early Evolution of the Metazoa. Plenum, New York.

CRIMES, T. P. AND G. J. B. GERMS. 1982. Trace fossils from the Nama Group (Precambrian–Cambrian) of Southwest Africa (Namibia). Journal of Paleontology, 56:890–907.

DROSER, M. L. AND D. J. BOTTJER. 1993. Trends and patterns of Phanerozoic ichnofabrics. Annual Review of Earth and Planetary Sciences, 21:205–225.

DROSER, M. L., J. G. GEHLING, AND S. JENSEN. 2005. Ediacaran trace fossils: True and false, p. 125–138. *In* D. E. G. Briggs (ed.), Evolving Form and Function: Fossils and Development. Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

DROSER, M. L., S. JENSEN, AND J. G. GEHLING. 2002. Trace fossils and substrates of the terminal Proterozoic–Cambrian transition: Implications for the record of early bilaterians and sediment mixing. Proceedings of the National Academy of Sciences, 99:12, 572–12,576.

DZIK, J. 2005. Behavioral and anatomical unity of the earliest burrowing animals and the cause of the "Cambrian explosion." Paleobiology, 31:503–521.

ERWIN, D. H., M. LAFLAMME, S. M. TWEEDT, E. A. SPERLING, D. PISANI, AND K. J. PETERSON. 2011. The Cambrian conundrum: Early divergence and later ecological success in the early history of animals. Science, 334:1091–1097.

FEDONKIN, M. A. 1977. Precambrian–Cambrian ichnocoenoses of the East European Platform, p. 183–194. *In* T. P. Crimes and T. P. Harper (eds.), Trace Fossils 2. Geological Journal Special Issue, Volume 9.

FEDONKIN, M. A. AND B. M. WAGGONER. 1997. The late Precambrian fossil Kimberella is a mollusc-like bilaterian organism. Nature, 388:868–871.

GEHLING, J. G. AND M. L. DROSER. 2009. Textured organic surfaces associated with the Ediacara biota in South Australia. Earth-Science Reviews, 96:196–206.

GEHLING, J. G. AND M. L. DROSER. 2013. How well do fossil assemblages of the Ediacara Biota tell time? Geology, 41:447–450.

GERMS, G. J. B. 1972. The stratigraphy and paleontology of the lower Nama Group, South West Africa. Bulletin, University of Cape Town, Department of Geology, Chamber Mines Precambrian Research Unit 12, 250 p.

GERMS, G. J. B. AND P. G. GREESE. 1991. The foreland basin of the Damara and Gariep Orogens in Namaqualand and southern Namibia: Stratigraphic correlations and basin dynamics. South African Journal of Geology, 94: 159–169.

GEYER, G. AND A. UCHMAN. 1995. Ichnofossil assemblages from the Nama Group (Neoproterozoic–lower Cambrian) in Namibia and the Proterozoic–Cambrian boundary problem revisited. Beringeria Special Issue 2, p. 175–202.

GLAESSNER, M. F. 1969. Trace fossils from the Precambrian and basal Cambrian. Lethaia, 2:369–393.

GROTZINGER, J. P., S. A. BOWRING, B. Z. SAYLOR, AND A. J. KAUFMAN. 1995. Biostratigraphic and geochronologic constraints on early animal evolution. Science, 270:598–604.

GROTZINGER, J. P., D. A. FIKE, AND W. W. FISCHER. 2011. Enigmatic origin of the largest-known carbon isotope excursion in Earth's history. Nature Geoscience, 4:285–292.

GROTZINGER, J. P. AND R. M. MILLER. 2008. The Nama Group, p. 13229–13272. *In* R. M. Miller (ed.), The Geology of Namibia. Volume 2. Geological Survey of Namibia, Windhoek, Namibia.

GROTZINGER, J. P., W. A. WATTERS, AND A. H. KNOLL. 2000. Calcified metazoans in thrombolite-stromatolite reefs of the terminal Proterozoic Nama Group, Namibia. Paleobiology, 26:334–359.

HIGGINS, J. A., W. W. FISCHER, AND D. P. SCHRAG. 2009. Oxygenation of the ocean and sediments: Consequences for the seafloor carbonate factory. Earth and Planetary Science Letters, 284:25–33.

HUA, H., B. R. PRATT, AND L.-Y. ZHANG. 2003. Borings in Cloudina shells: Complex predator-prey dynamics in the terminal Neoproterozoic. Palaios, 18:454–459.

HUSSON, J. M., A. C. MALOOF, AND B. SCHOENE. 2012. A syn-depositional age for Earth's deepest δ13C excursion required by isotope conglomerate tests. Terra Nova, 24:318–325.

JENSEN, S. 2003. The Proterozoic and earliest Cambrian trace fossil record: Patterns, problems and perspectives. Integrative and Comparative Biology, 43:219–228.

JENSEN, S., M. L. DROSER, AND J. G. GEHLING. 2006. A critical look at the Ediacaran trace fossil record, p. 115–157. *In* S. Xiao and A. J. Kaufman (eds.), Neoproterozoic Geobiology and Paleobiology. Volume 27. Springer, New York, New York.

JENSEN, S., B. Z. SAYLOR, J. G. GEHLING, AND G. J. B. GERMS. 2000. Complex trace fossils from the terminal Proterozoic of Namibia. Geology, 28:143–146.

LIU, A. G., D. MCILROY, AND M. D. BRASIER. 2010. First evidence for locomotion in the Ediacara biota from the 565 Ma Mistaken Point Formation, Newfoundland. Geology, 38:123–126.

MACDONALD, F. A., J. V. STRAUSS, E. A. SPERLING, G. P. HALVERSON, G. M. NARBONNE, D. T. JOHNSTON, M. KUNZMANN, D. P. SCHRAG, AND J. A. HIGGINS. 2013. The stratigraphic relationship between the Shuram carbon isotope excursion, the oxidation of Neoproterozoic oceans, and the first appearance of the Ediacara biota and bilaterian trace fossils in northwestern Canada. Chemical Geology, doi: 10.1016/j.chemgeo.2013.05.032.

MACNAUGHTON, R. B. AND G. M. NARBONNE. 1999. Evolution and eology of Neoproterozoic–lower Cambrian trace fossils, NW Canada. Palaios, 14:97–115.

MARTIN, H. 1975. Structural and palaeogeographical evidence for an upper Palaeozoic sea between southern Africa and South America. Proceeding Papers IUGS 3rd Gondwana Symposium, Canberra, Australia, p. 37–51.

MARTIN, M. W., D. V. GRAZHDANKIN, S. A. BOWRING, M. A. FEDONKIN, AND J. L. KIRSCHVINK. 2000. Age of Neoproterozoic bilatarian body and trace fossils, White Sea, Russia: Implications for metazoan evolution. Science, 288:841–845.

MCILROY, D. AND G. A. LOGAN. 1999. The impact of bioturbation on infaunal ecology and evolution during the Proterozoic–Cambrian transition. Palaios, 14:58–72.

MEYSMAN, F. J. R., J. J. MIDDELBERG, AND C. H. R. HEIP. 2006. Bioturbation: A fresh look at Darwin's last idea. Trends in Ecology and Evolution, 21:688–695.

MILLER, M. F. 1991. Morphology and paleoenvironmental distribution of Paleozoic Spirophyton and Zoophycos: Implications for the Zoophycos ichnofacies. Palaios, 6:410–425.

NARBONNE, G. M. 2005. The Ediacara biota: Neoproterozoic origin of animals and their ecosystems. Annual Review of Earth and Planetary Sciences, 33:421–442.

NARBONNE, G. M. AND J. D. AITKEN. 1990. Ediacaran fossils from the Sekwi Brook area, Mackenzie Mountains, northwest Canada. Palaeontology, 33:945–980.

NARBONNE, G. M., B. Z. SAYLOR, AND J. P. GROTZINGER. 1997. The youngest Ediacaran fossils from southern Africa. Journal of Paleontology, 71:953–967.

NARBONNE, G. M., S. XIAO, AND G. SHIELDS-ZHOU. 2012. Ediacaran Period, p. 427–449. *In* F. Gradstein, J. Ogg, M. D. Schmitz, and O. G. (eds.), Geologic Timescale 2012. Elsevier, Oxford.

NOFFKE, N., A. H. KNOLL, AND J. P. GROTZINGER. 2002. Sedimentary controls on the formation and preservation of microbial mats in siliciclastic deposits: A case study from the upper Neoproterozoic Nama Group, Namibia. Palaios, 17:533–544.

PELECHATY, S. M. 1998. Integrated chronostratigraphy of the Vendian System of Siberia: Implications for a global stratigraphy. Journal of the Geological Society of London, 155:957–973.

PELL, S. D., D. M. MCKIRDY, J. JANSYN, AND R. J. F. JENKINS. 1993. Ediacaran carbon isotope stratigraphy of South Australia—An initial study. Transactions of the Royal Society of South Australia, 117:153–161.

ROGOV, V., V. MARUSIN, N. BYKOVA, Y. GOY, K. E. NAGOVITSIN, B. B. KOCHNEV, G. KARLOVA, AND D. V. GRAZHDANKIN. 2012. The oldest evidence of bioturbation on Earth. Geology, 40:395–398.

SAPPENFIELD, A., M. L. DROSER, AND J. G. GEHLING. 2011. Problematica, trace fossils, and tubes within the Ediacara member (South Australia): Redefining the Ediacaran trace fossil record one tube at a time. Journal of Paleontology, 85:256–265.

SAPPENFIELD, A., M. L. DROSER, M. J. KENNEDY, AND R. MCKENZIE. 2012. The oldest *Zoophycos* and implications for early Cambrian deposit feeding. Geological Magazine, 149:1118–1123.

SCHIEBER, J. 1999. Microbial mats in terrigenous clastics: The challenge of identification in the rock record. Palaios, 14:3–12.

SCHMITZ, M. D. 2012. Radiometric ages used in GTS2012, Appendix 2, p. 1045–1082. *In* F. Gradstein, J. Ogg, M. D. Schmitz, and G. Ogg (eds.), Geologic Timescale 2012. Elsevier.

SCHRAG, D. P., J. A. HIGGINS, F. A. MACDONALD, AND D. T. JOHNSTON. 2013. Authigenic carbonate and the history of the global carbon cycle. Science, 339:540–543.

SEILACHER, A. 1999. Biomat-related lifestyles in the Precambrian. Palaios, 14:86–93.

SEILACHER, A. 2007. Trace Fossil Analysis. Springer, Berlin.

SEILACHER, A., L. A. BUATOIS, AND M. G. MANGANO. 2005. Trace fossils in the Ediacaran–Cambrian transition: Behavioral diversification, ecological turnover and environmental shift. Palaeogeography, Palaeoclimatology, Palaeoecology, 227:323–356.

STOLLHOFEN, H., I. G. STAINSTREET, B. BANGERT, AND H. GRILL. 2000. Tuffs, tectonism and glacially related sea-level changes, Carboniferous–Permian, southern Namibia. Palaeogeography, Palaeoclimatology, Palaeoecology, 161:127–150.

WAGGONER, B. M. 2003. The Ediacaran biotas in space and time. Integrated Comparative Biology, 43:104–113.

WETZEL, A. 1999. Tilting marks: A wave-produced tool mark resembling a trace fossil. Palaeogeography, Palaeoclimatology, Palaeoecology, 145:251–254.

WETZEL, A. 2013. Tilting marks: Observations on tool marks resembling trace fossils and their morphological varieties. Sedimentary Geology, 288:60–65.

WILSON, J. P., J. P. GROTZINGER, W. W. FISCHER, K. P. HAND, S. JENSEN, A. H. KNOLL, J. ABELSON, J. M. METZ, N. MCLOUGHLIN, AND P. A. COHEN. 2012. Deep-water incised valley deposits at the Ediacaran–Cambrian boundary in southern Namibia contain abundant treptichnus pedum. Palaios, 27:252–273.

WOOD, R. A., J. P. GROTZINGER, AND J. A. D. DICKSON. 2002. Proterozoic modular biomineralized metazoan from the Nama Group, Namibia. Science, 296:2383–2386.

XIAO, S. AND A. H. KNOLL. 2000. Phosphatized animal embryos from the Neoproterozoic Doushantuo Formation at Weng'an, Guizhou, South China. Journal of Paleontology, 74:767–788.

ZHOU, C. AND S. XIAO. 2007. Ediacaran δ13C chemostatigraphy of South China. Chemical Geology, 237:107–126.

ZIEBIS, W., S. FORSTER, M. HUETTEL, AND B. B. JORGENSEN. 1996. Complex burrows of the mud shrimp Callianassa truncata and their geochemical impact in the sea bed. Nature, 382:619–622.