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Review Article

The trace fossil record of the Nama Group, Namibia: Exploring the terminal Ediacaran roots of the Cambrian explosion

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A R T I C L E I N F O

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A B S T R A C T

The Ediacaran–Cambrian transition marks one of the most important geobiological revolutions in Earth History, including multiple waves of evolutionary radiation and successive episodes of apparent mass extinction. Among the proposed drivers of these events (in particular the extinction of the latest Neoproterozoic 'Ediacara biota') is the emergence of complex metazoans and their associated behaviors. Many metazoans are thought to have crucial geobiological impacts on both resource availability and the character of the physical environment – 'ecosystem engineering' – biological processes best preserved in the geological record as trace fossils. Here, we review this model using the trace fossil record of the Ediacaran to Cambrian Nama Group of southern Namibia, combining previous published accounts with the results of our own field investigations. We produce a revised ichnostratigraphy for the Nama Group that catalogues new forms, eliminates others, and brings the trace fossil record of the Nama into much closer alignment with what is known from other Ediacaran sections worldwide. We provide evidence for a link between sequence stratigraphy, oxygen, and the emergence of more complex bilaterian behaviors. Lastly, we show that observed patterns of extinction and survival over pulses of Ediacaran extinction are hard to ally with any one specific source of ecological stress associated with bioturbation, and thus a biologically-driven extinction of the Ediacara biota, if it occurred, was more likely to have been driven by some combination of these factors, rather than any single one.

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1. Introduction

The interval spanning the late Ediacaran to early Cambrian (~571–509 million years ago) marks one of the most important geobiological revolutions in Earth History, including major perturbations to global geochemical cycles, the establishment of the first macroscopic and eukaryotic ecosystems, the first major turnover of complex eukaryotic life (the extinction of the enigmatic Ediacara biota), and arguably, the most dramatic evolutionary radiation of the last billion years – the Cambrian Explosion (Erwin et al., 2011; Erwin and Tweedt, 2012; Erwin and Valentine, 2013; Mángano and Buatois, 2016, 2017; Droser et al., 2017; Darroch et al., 2018a; Muscente et al., 2018; Tarhan et al., 2018; Wood et al., 2019, 2020). The paleontological record of this interval thus provides evidence of the Precambrian rise of animals, and is central to understanding both rates and patterns of early metazoan evolution, and the origins of the modern animal-dominated biosphere. Recent work on the Ediacaran-Cambrian transition has identified several distinct bioevents, including one or more pulses of extinction (Amthor et al., 2003; Laflamme et al., 2013; Darroch et al., 2015, 2018a; Muscente et al., 2019), and successive waves of evolutionary radiation (Wood et al., 2019). The ultimate causes of these events, however, are still uncertain, with a wide variety of extrinsic (i.e., environmental) and intrinsic (biological) drivers hypothesized. In this context, understanding rates and patterns of biotic evolution in the latest Neoproterozoic is crucial.

In terms of extrinsic (i.e., environmental) factors, several recent studies identify dynamic and global changes in redox conditions as potential drivers of both pulsed extinction and evolutionary radiation in the latest Neoproterozoic. For example, intervals of ocean anoxia have been suggested as drivers of late Ediacaran extinction (Kimura and Watanabe, 2001; Zhang et al., 2018; Tostevin et al., 2019), while pulses of oxygenation and nutrient supply (or redox fluctuations – see Wood and Erwin, 2017) have long been thought to be responsible for the appearance of more complex metazoan behaviors in the late Neoproterozoic (McFadden et al., 2008; Johnston et al., 2012; Sahoo et al., 2016; Wei et al., 2018; Wood et al., 2019, 2020). However, other studies have suggested that biological factors may have played a crucial role in driving many of these environmental changes and/or patterns of biotic turnover (e.g., Butterfield, 2011). The evolution of key traits, such as the acquisition of the metazoan gut, filter feeding, and the ability to mix the sediment-water interface may have, for example, been responsible for oxygenating the Neoproterozoic oceans (Fike et al., 2006; Butterfield, 2011), increasing seawater sulfate concentrations (Canfield and Farquhar, 2009), and driving the extinction of the Ediacara biota (an informal grouping of soft-bodied organisms, likely comprising both stem- and crown-group animals, as well as extinct groups with no modern representatives – see Xiao and Laflamme, 2009; Laflamme et al., 2013; Darroch et al., 2018a; Dunn et al., 2018; although see Budd and Jackson, 2016 for an alternative viewpoint). Central to this model is the role of early animals as ecosystem engineers (Erwin and Tweedt, 2012; Buatois et al., 2020). Organisms with complex biological organization and behaviors are frequently able to change the habitability of an ecosystem for themselves and other organisms by regulating resource availability and modifying the physical environment. Ecosystem engineers are therefore powerful agents of environmental change that create (or eliminate) niche space for other organisms, and are an important control on local and regional diversity (Jones et al., 1994, 1997; Wright et al., 2002; Hastings et al., 2007).

Among the many proposed geobiological impacts associated with metazoan evolution, the role of animal ecosystem engineers in driving the extinction of the Ediacara biota has been a topic of intense debate (see e.g., Erwin and Tweedt, 2012; Laflamme et al., 2013; Darroch et al., 2015, 2016, 2018a; Smith et al., 2016; Buatois and Mángano, 2016; Schiffbauer et al., 2016; Budd and Jensen, 2017; Tarhan et al., 2018; Muscente et al., 2018, 2019; Wood et al., 2019; Mángano and Buatois, 2020). Certainly, the latest Ediacaran 'Nama' interval (~548-539 Ma; Waggoner, 2003; Boag et al., 2016) is associated with relatively depauperate and potentially ecologically 'stressed' communities of soft-bodied Ediacaran organisms (Darroch et al., 2015, 2018b; Boag et al., 2016; Muscente et al., 2018), coinciding with an apparent increase in the diversity of metazoan behaviors (Erwin and Tweedt, 2012; Darroch et al., 2018a). Although evidence of ecosystem engineering can potentially be recorded in a wide variety of ways in fossils (reviewed in Marenco and Bottjer, 2007, 2011), they are perhaps most easily recognized in trace fossils and the geological record of bioturbation (Buatois et al., 2020). Bioturbation is a crucial ecosystem engineering process, affecting the oxygenation of the water column (Aller, 1982; Erwin and Tweedt, 2012; Mángano and Buatois, 2014, 2020), pore water redox chemistry (Canfield and Farquhar, 2009; Tarhan et al., 2015; Zhang et al., 2017), sediment stability (Rhoads and Young, 1970), and the cycling of marine nutrients (McIlroy and Logan, 1999; Laverock et al., 2011). In this vein, the appearance of metazoan trace fossils in the Ediacaran and the subsequent increase in ichnodiversity and extent of substrate reworking have long been recognized as crucial controls on the character of the marine sediment substrate. Perhaps more importantly, the expansion of ecosystem engineering behaviors marks a permanent geobiological step-change in the strength of coupling between the geosphere and biosphere (Seilacher and Pflüger, 1994; Bottjer et al., 2000; Seilacher et al., 2005; Mángano and Buatois, 2014, 2017; Butterfield, 2011; Buatois et al., 2020). However, the degree to which burrowing activity of emerging metazoans could have caused or contributed to global-scale biotic turnover (and in particular, the extinction of the Ediacara biota) remains unknown (Darroch et al., 2018a; Cribb et al., 2019). Compiling a comprehensive account of Ediacaran trace fossil diversity, alongside analyses of the behaviors they represent and their roles in engineering the Neoproterozoic marine environment, has thus become a key cog in our understanding of the rates and patterns of metazoan evolution, and in evaluating hypothesized biotic drivers of the Ediacaran-Cambrian transition (Buatois et al., 2020).

Against this backdrop, we review the Ediacaran trace fossil record of the Nama Group of southern Namibia, which preserves Ediacaran- to Cambrian-aged fossiliferous sediments in unparalleled lateral extent. We collate trace fossil summaries for the Nama Group produced by previous workers, compare this with the results of our own fieldwork and exploration (comprising 5 separate field seasons undertaken between 2008 and 2019), and compare the stratigraphic ranges of specific ichnotaxa and their respective behaviors with other Ediacaran-Cambrian sections worldwide. Lastly, we assess the potential ecosystem engineering impacts of these behaviors, and discuss if and how the emergence of a Cambrian-type evolutionary fauna may have plausibly caused the first major turnover in macroscopic and eukaryotic life.

1.1. Invertebrate bioturbation as ecosystem engineering

Bioturbating animals act as ecosystem engineers by altering resource flows and modifying the physical environment (Fig. 1; Jones et al., 1994; Meysman et al., 2006), and can be divided into two types of sediment mixing: biomixing and bioirrigation (see also Kristensen et al., 2012). Biomixing refers to the mixing of solid sediment particles, whereas bioirrigation refers to the mixing of pore water solutes with the sediment-water interface and is most effective at introducing oxygen into the sediment. Interactions between bioturbating benthic meio-/macrofauna and microbes living in the sediment result in changes to the biogeochemistry of the sediment and overlying water, particularly by influencing biogeochemical processes and nutrient cycling. Sediment mixing and the construction of penetrative burrows modifies the flow of resources to microbial communities by changing particle and solute transport. Critically, bioirrigation both shifts redox gradients (Rosenberg et al., 2001) and directly controls the availability of redox-sensitive elements, for example sulfur and iron redox cycling (see e.g., Canfield and Farquhar, 2009; Tarhan et al., 2015; van de Velde and Meysman, 2016), to microbial communities in the sediment. Bioirrigation flushes

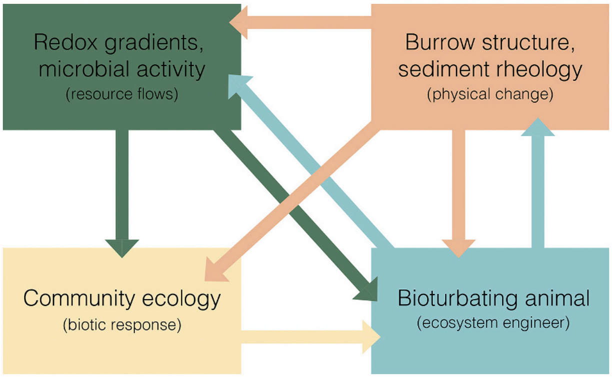

Fig. 1. Flow-chart illustrating ecosystem engineering processes and effects. Bioturbation directly impacts resource flows and physical abiotic factors in the ecosystem (blue arrows), and these changes can affect the bioturbating animal itself (diagonal green and vertical orange arrows). Some physical changes can also impact resource flows (horizontal orange arrow). Finally, these changes in resource flows and the physical environment ultimately cause a biotic response at the community level (vertical green and diagonal orange arrows), and this biotic response impacts the bioturbating animal (yellow arrow).
Adapted from Jones et al. (2010).

reduced pore water sulfides out of the sediment and into the water column where they are oxidized into sulfates, which has been hypothesized to have caused a seven-fold increase in seawater sulfate concentrations in the early Paleozoic (Canfield and Farquhar, 2009; although see Ries et al., 2009). Bioturbation can also increase the availability of oxidants and organic matter critical for respiration metabolisms, which is thought to influence microbial diversity and community structure and may have significant effects on biogeochemical processes and benthic nutrient cycling (Bertics and Ziebis, 2009). Finally, bioirrigation may increase the bioavailability of redox-sensitive metals that are required in key metalloenzymes responsible for catalyzing major biogeochemical reactions. Many microbes have obligate requirements for metal co-factors that are insoluble in anoxic sediments and pore waters due to precipitation as sulfide minerals (Glass et al., 2018). For example, iron (→ pyrite), copper (→ chalcopyrite), and molybdenum (→ thiomolybdate) are important cofactors in nitrogen cycle enzymes (Godfrey and Glass, 2011). Increasing the oxidant content of the sediment, particularly through bioirrigation, may thus increase the bioavailability of these metal ion cofactors and influence sedimentary biogeochemical processes.

Bioturbation modifies the physical environment of the ecosystem by controlling the sediment rheology or the mechanical properties of the substrate. Bioturbation, either by biomixing or bioirrigation, decreases sediment stability by introducing water into the sediment (Rhoads et al., 1978; de Deckere et al., 2001) or by disrupting sediment-stabilizing biogenic structures such as microbial mats (Seilacher, 1999; Bottjer et al., 2000; Mángano and Buatois, 2017). Concordantly, many benthic organisms are sensitive to alteration of substrate composition or of interstitial microbial communities (e.g. see Lambshead et al., 2001; Smit et al., 2008), both of which can strongly influence recruitment and settling (e.g. Rhoads and Young, 1970; Kirchman et al., 1982; Dahms et al., 2004). Additionally, by mixing sediment to or at the sediment-water interface, bioturbation increases the resuspension of sediment particles, which can have significant effects on the ecology of infaunal macrofauna (Rhoads and Young, 1970; Fig. 1).

2. Geological setting and stratigraphy

The Nama Group in Namibia occurs in the areas south of Windhoek and in the Witvlei area east of Windhoek. Only the Nama Group south of Windhoek is the subject of this trace fossil study, where it records a >3000 m thick accumulation of sediments deposited in a foreland basin on the northwestern margin of the Kalahari Craton during convergence of the Damara and Gariep deformational belts (Germs, 1983; Germs and Gresse, 1991; Stanistreet et al., 1991; Saylor et al., 1995). Sediments in lower parts of the Nama Group were largely sourced from the Kalahari Craton to the east, and comprise a shallow siliciclastic-carbonate succession that prograded basinward (Germs, 1972a, 1983; Dibenedetto and Grotzinger, 2005). Material from the upper Nama Group, in contrast, was mainly sourced from the Damara and Gariep orogenic belts to the north and west (Germs, 1983).

The Nama Group south of Windhoek is divided into two Sub-basins – the Zaris Sub-basin in the north, and the Witputs Sub-basin in the south (Fig. 2; Germs, 1972a, 1983). The Zaris Sub-basin is separated from the Witputs Sub-basin by the Osis Arch, which, during deposition of the Zaris and lower-mid Schwarzrand subgroups at least, represented an ENE-trending paleo-topographic high and likely a peripheral bulge of the foreland basin (Germs and Gresse, 1991; Grotzinger and Miller, 2008). Both basins are subdivided into three Subgroups, in ascending stratigraphic order, the Kuibis, the Schwarzrand, and the Fish River (Fig. 2). Sediments in both basins can broadly be split into two sedimentary successions – one a siliciclastic-carbonate succession comprising the Kuibis Subgroup, and the second a (broadly) siliciclastic succession comprising the Schwarzrand Subgroup (including the Nomtsas and Vergesig formations). Stratigraphic correlations between the two basins were established by Germs (1983) and Germs and Gresse (1991), although the relationship between the Nomtsas and Vergesig formations in some areas north of the Osis Arch is still uncertain (Germs et al., 2010).

In the Witputs Sub-basin, the Nomtsas Formation cuts down through the Ediacaran-aged Spitskop and Feldschuhhorn members (commonly forming valley-fill profiles) of the Urusis Formation (Germs, 1972a, 1983; Saylor et al., 1995; Saylor and Grotzinger, 1996; Saylor, 2003; Wilson et al., 2012), and is recognized as Cambrian based on abundant *Treptichnus pedum*, as well as ages derived from U-Pb zircon grains in tuffs that have recently been re-dated, and which yield an age of 538.58 ± 0.19 Ma (Linnemann et al., 2019). Ash beds from the underlying Spitskop Member also have been re-dated yielding updated ages between 540.095 ± 0.099 Ma and 538.99 ± 0.21 Ma (Linnemann et al., 2019). The Spitskop Member preserves soft-bodied Ediacara biota – below and above these dated ash horizons – and, thus, much of this unit has been interpreted to be latest Ediacaran in age (Grotzinger et al., 1995; Narbonne et al., 2012). The Ediacaran-Cambrian boundary in the Witputs Sub-basin was traditionally placed at the erosive unconformity where the Nomtsas Formation cuts down into the Spitskop Member (Germs, 1972a; Germs, 1983; Saylor et al., 1995; Saylor, 2003). Recently, Linnemann et al. (2019) have placed the boundary near the top of the Spitskop Member at Farm Swartpunt. This stratigraphic placement relies on the identification of a specimen compared with *T. pedum* together with *Streptichnus narbonnei*, an ichnotaxon of similar complexity to *T. pedum* (Jensen and Runnegar, 2005). However, the presence of the skeletonized Ediacaran index taxa *Cloudina* and *Namacalathus* in the overlying carbonates at the top of the Spitskop Member at Farm Swartpunt argues for positioning the boundary upwards in the succession. Based on the most recent dates from Linnemann et al. (2019), the Ediacaran-Cambrian boundary in Namibia would then be placed at 539-538 Ma, if the boundary is located (as it has historically been thought) at the unconformity between the Spitskop Member and the Nomtsas Formation.

In the Zaris Sub-basin, a precise stratigraphic location of the Ediacaran-Cambrian boundary has not been determined; an ash bed from the Hoogland Member (Kuibis Subgroup) in the vicinity of Zebra River Farm yields a revised U-Pb zircon age of 547.32 ± 0.65 Ma (Grotzinger et al., 1995; Schmitz, 2012), but no other Ediacaran or Cambrian radiometric ages exist in this Sub-basin. The overlying Fish River Subgroup contains *T. pedum* and has been identified as definitively Cambrian (Germs, 1972a, 1983; Geyer, 2005). Moreover, the presence of the tubular taxon *Shaanxilithes* and *Aspidella* in the upper

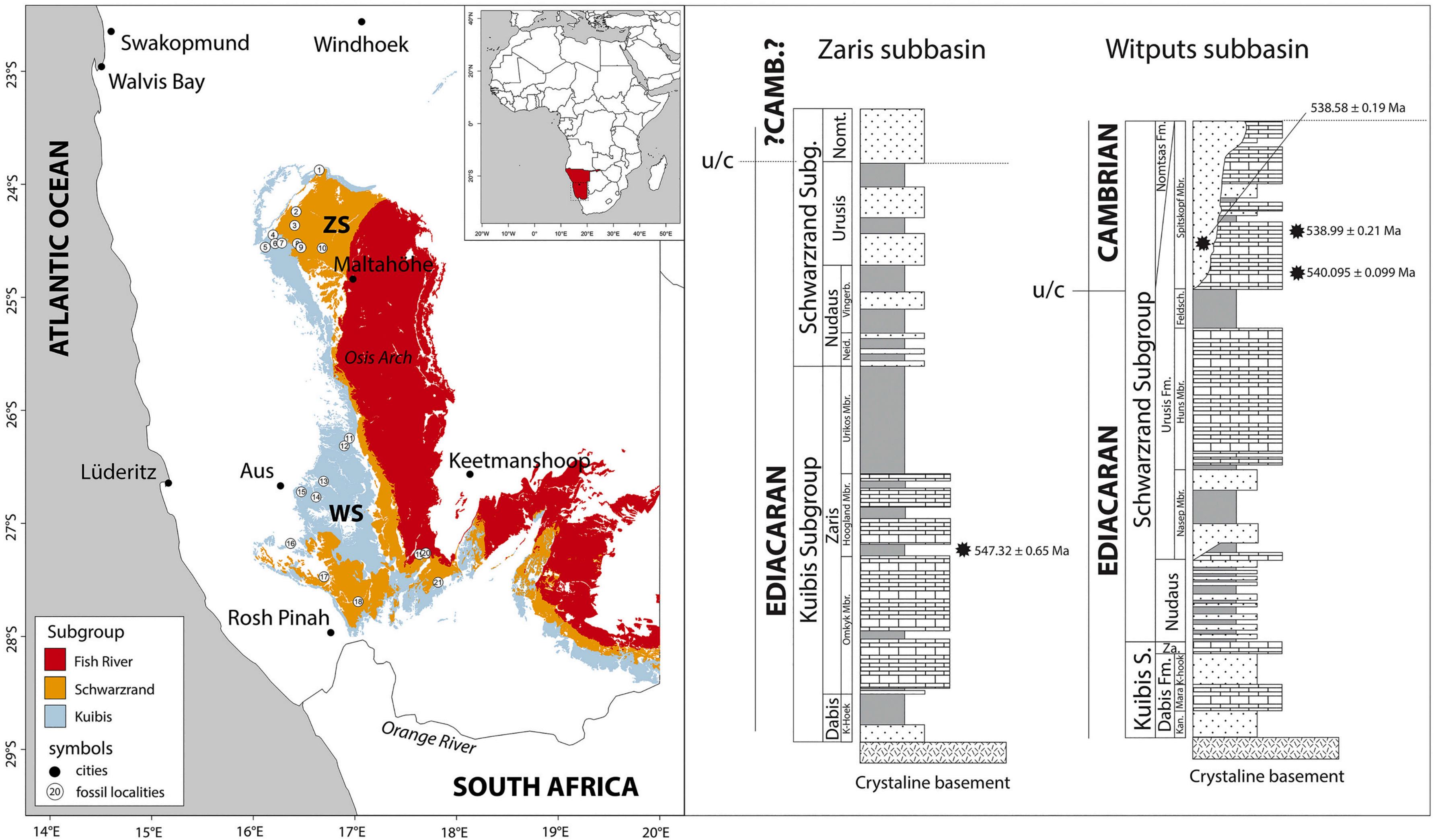

Fig. 2. Map of the Nama Group south of Windhoek, showing the locations of the Zaris ('ZS') and Witputs ('WS') Sub-basins (separated by the Osis Arch), along with the localities (numbered) investigated over the course of this work. Localities are: 1. Farm Driedoornvlatke; 2. Farm Berghoek; 3. Farm Haruchas; 4. Farm Neuras; 5. Farm Hauchabfontein; 6. Farm Donkergange; 7. Zebra River; 8. Farm Nudaus; 9. Farm Kamkas; 10. Farm Urusis; 11. Farm Zuurburg; 12. Farm Hansburg; 13. Farm Weltevrede; 14. Farm Tsachanabis; 15. Farm Aar; 16. Farm Grens; 17. Farm Swartpunt; 18. Farm Arimas; 19. Farm Sontaagsbrunn; 20. Koelkrans Camp; 21. Canyon Roadhouse. Geochronological dates after Linnemann et al. (2019).

Schwarzrand Subgroup (Darroch et al., 2016; although see section on 'Pseudofossils and problematica' for discussion of *Shaanxilithes* in the Nama) suggest that the Ediacaran-Cambrian boundary may occur at the contact between the Urusis and Nomtsas formations (i.e., similar to its interpreted position in the Witputs).

2.1. Paleoenvironments

The Nama Group records a wide variety of paleoenvironments, ranging from fluvial and marginal marine to shallow marine wave- and tide-dominated siliciclastic and carbonate settings (Germs, 1972a, 1983; Saylor et al., 1995, 1998; Saylor, 2003; Dibenedetto and Grotzinger, 2005; Grotzinger and Miller, 2008; Maloney et al., 2020), including extensive stromatolitic and/or thrombolitic reef tracts. Broadly, the Kuibis, Schwarzrand, and Fish River subgroups consist of fluvial, deltaic, and shallow-marine conglomerate, sandstone, and siltstone formed during lowstand and highstands, and shallow-marine sandstone, siltstone, shale and limestone formed during transgressions (Germs, 1983; Saylor et al., 1995; Saylor, 2003; Grotzinger and Miller, 2008). North of the Osis Arch, proximal sandstone and limestone in the east deepen northwestwards into platform carbonate and shale, whereas south of the Osis arch, the changing thickness of units suggests a deepening westward (Grotzinger and Miller, 2008). Structures interpreted as glacial grooves and pavements are potential evidence for a glaciogenic event that occurred during deposition of the basal Vingerbreek Member (Schwarzrand Subgroup – Germs, 1972a, 1995; Germs and Gaucher, 2012), with a second such event also suggested to have taken place during deposition of the upper Schwarzrand (Germs, 1972a, 1995). However, these interpretations have been questioned by Saylor et al. (1995, 1998) and Grotzinger and Miller (2008).

Sequence stratigraphic work by Saylor et al. (1995, 1998) recognized seven depositional sequences in the Kuibis and Schwarzrand subgroups separated by unconformities (or correlative conformities), with relative sea level controlled broadly by the tectonic evolution of the basin, with equivocal evidence for glaciogenic sea level rise and fall (Grotzinger and Miller, 2008). Mixed microbial-metazoan reefs are well developed in the Omkyk Member (Zaris Sub-basin) and towards the top of the Huns Member (Witputs Sub-basin), and exhibit a variety of biostrome, patch reef, and pinnacle geometries (Saylor et al., 1995, 1998; Grotzinger et al., 2000, 2005).

3. Body fossils

Although this review is focused on trace fossils, a brief summary of

Fig. 3. a–f) Soft bodied Ediacara biota from the Witputs Sub-basin: a–b) *Swartpuntia germsi* (Farm Swartpunt); c) *Pteridinium simplex* (Farm Swartpunt); d–e) In-situ accumulations of *Ernietta plateauensis* (Farms Hansburg and Kuibis); f) *Rangea scheiderhoehni* (Farm Hansburg). g–k) *Aspidella* holdfasts from the Zaris Sub-basin; note the large size and tight clustering of holdfast structures in k) (Farms Nudaus and Kamkas). Body fossils in a–c) and i–k) preserved on bed tops, with *Ernietta* in d-e exposed on bed bases. *Rangea* in f) found in float. Filled scale bars 1 cm.

the body fossils found in the same succession helps to provide context for the broader ecosystem present in the Nama Group, and is crucial to assessing the character and tempo of the Ediacaran-Cambrian transition. The Nama Group preserves a typical late Ediacaran ('Nama'-type) assemblage of soft-bodied Ediacara biota (see Laflamme et al., 2013; Boag et al., 2016; Muscente et al., 2018), alongside calcifying metazoans, a collection of organic-walled (or weakly mineralized) tube-like organisms, and possible algae (also reviewed in Germs, 1995; Pickford, 1995; and Grotzinger and Miller, 2008) (Fig. 3).

Ediacara biota are distributed throughout the Ediacaran portions of the Nama Group, and overwhelmingly belong to either the Rangeomorpha or Erniettomorpha (Fig. 3a–f). Some of the oldest historical reports of Ediacaran macrofossils from anywhere in the world come from Namibia; Gürich (1929, 1930a, 1930b, 1933) first described several forms, including the iconic *Rangea* and *Pteridinium*. In addition to his extensive work on *Ernietta*, Pflug (1966, 1970a,b, 1972a,b) was instrumental in describing many of the Namibian fronds (i.e. the "Petalonamae" *sensu stricto*); and much of this descriptive terminology is still in use to this day (e.g. Laflamme and Narbonne, 2008). Body fossils are perhaps best known from the well-documented assemblages preserved on Farms Aar, Swartpunt, and Hansburg (see e.g., Grotzinger et al., 1995; Narbonne et al., 1997; Bouougri et al., 2011; Elliott et al., 2011; Vickers-Rich et al., 2013; Meyer et al., 2014; Darroch et al., 2015; Ivantsov et al., 2016; Gibson et al., 2019), but are widely distributed throughout the Witputs Sub-basin. Ediacara biota are much rarer in the Zaris Sub-basin, although Darroch et al. (2016) did report large *Aspidella* holdfasts from several localities high in the Schwarzrand Subgroup (Nudaus Formation) in the vicinity of Zebra River, and subsequent exploration has recovered additional well-preserved specimens (Fig. 3g–k). Rangeomorph taxa in the Witputs include exquisitely preserved *Rangea* (Vickers-Rich et al., 2013), and Darroch et al. (2015) figured possible *Bradgatia* from near the top of the Spitskop Member on Farm Swartpunt. Erniettomorph taxa include *Pteridinium*, *Ernietta*, *Nasepia*, and the frondose taxon *Swartpuntia*. Bouougri et al. (2011) identified dense accumulations of *Ernietta* on Farm Hansburg as belonging to the Kanies Member (Dabis Formation), and thus the oldest Ediacaran fossils found in the Nama Basin. However, more recent chemostratigraphic work by Maloney et al. (2020) has established these horizons as belonging to the younger Kliphoek Member, and thus broadly equivalent with the fossil-bearing horizons at Farm Aar (Hall et al., 2013). The youngest Ediacara biota in the Nama were described by Grotzinger et al. (1995) and Narbonne et al. (1997) from siliciclastic horizons high in the Spitskop Member at Farm Swartpunt; these fossils are bracketed by well-dated volcanic ash horizons (Grotzinger et al., 1995; Linnemann et al., 2019), and are established as existing ~1 Myr prior to the Ediacaran–Cambrian boundary (Narbonne et al., 1997, 2012; Darroch et al., 2015).

The Nama Group is also well known for preserving the Ediacaran biomineralizing organisms *Cloudina*, *Namacalathus*, and *Namapoikia* (Wood, 2011). *Cloudina*, first described by Germs (1972c), is a genus within the broader family Cloudinidae (Hahn and Pflug, 1985), which comprises a variety of enigmatic metazoans that possessed calcified and organic-walled tubes constructed by a nested funnel-in-funnel configuration, the hallmark of the informal "cloudinomorph" form-grouping (Selly et al., 2019). Due to its high preservation potential and near-global distribution, *Cloudina* is currently accepted as a late Ediacaran index taxon (Xiao et al., 2016). *Cloudina* is widely distributed throughout carbonate units in the Nama Group; in the Witputs Sub-basin, its first occurrence is generally agreed to be in the Mara Member, and it is present throughout the stratigraphic succession all the way up into the highest Spitskop carbonates preserved on Farm Swartpunt. In the Zaris Sub-basin, *Cloudina* is distributed throughout the middle- to upper Omkyk and Hoogland members, and is an important frame-building component of extensive microbial reef complexes preserved in the upper Omkyk (Penny et al., 2014; Wood and Curtis, 2014, although also see Mehra and Maloof, 2018). *Namacalathus* is another enigmatic and calcifying metazoan commonly found associated with *Cloudina*, and was first described by Grotzinger et al. (2000) based on digital reconstructions and extensive serial sectioning. Although Grotzinger et al. (2000) tentatively proposed a cnidarian affinity for this organism, more recent work by Zhuravlev et al. (2015) has suggested that *Namacalathus* is more likely a lophophorate, on the basis of skeleton ultrastructure. Like *Cloudina*, *Namacalathus* is widely distributed throughout carbonate units in the Nama Group (although its FAD in the Witputs Sub-basin is still unknown), and is present in the uppermost Spitskop carbonates at Farm Swartpunt. Lastly, *Namapoikia* is a meter-scale calcifying metazoan first described by Wood et al. (2002), commonly found encrusting synsedimentary fissures in microbial reefs of the Omkyk Member. *Namapoikia* was interpreted by Wood and Penny (2018) as a poriferan, although recent work by Mehra et al. (2020) suggested that *Namapoikia* may in fact be microbial in origin.

In terms of non-calcified metazoans, Germs (1972b) was among the first to note the presence of unmineralized tube-like fossils in the Nasep Quartzite, which he identified as *Archaeichnium*. Although originally described by Haughton (1960) as an archaeocyathid, *Archaeichnium* was re-described as a possible trace fossil by Glaessner (1963), and then again as a body fossil by Glaessner (1978). New material of this fossil collected by our group from horizons in the Nasep-Huns transition (Fig. 4) reveals that *Archaeichnium* is annulated, has a tapered profile, and commonly exhibits current alignment on the base of beds preserving evidence for transport. The ranges of size and morphologies among non-calcified tubular fossils from the Nama (both *Buchholzbrunnichnus* from the Kliphoek Member [Germs, 1973] and *Gyrichnites* from the Vingerbreek Member [Zessin, 2010] possess characteristics suggestive of tubular metazoans) suggest that numerous taxa may be represented.

Lastly, the Nama Group preserves a distinctive assemblage of acritarchs typical of the Neoproterozoic (Germs et al., 1986), as well as carbonaceous ribbon-like fossils from the Vingerbreek and Feldschuhhorn members, the latter of which were assigned to *Vendotaenia* by Cohen et al. (2009). Interpretation of these carbonaceous tubes has been varied, commonly as algae (e.g., Gnilovskaya, 1983), but also as the sheaths of sulfur-oxidizing bacteria (Vidal, 1989). Cohen et al. (2009) noted that their carbonaceous fossils recovered from the Vingerbreek Member possess transverse annulations, suggestive of metazoans.

4. Trace fossils

4.1. Previous work

The first account of trace fossils in the Nama Group was produced by Germs (1972b), who reported a suite of ichnotaxa indicating a late Precambrian to Cambrian age. Additional trace fossil taxa (including several newly described forms) were subsequently reported by Germs (1973), Crimes and Germs (1982), and (more recently) Geyer and Uchman (1995), Jensen et al. (2000), Jensen and Runnegar (2005), Geyer (2005), Bouougri and Porada (2007), Macdonald et al. (2014), Darroch et al. (2016), and Buatois et al. (2018) (see also summaries in Germs, 1983, 1995; Pickford, 1995; Grotzinger and Miller, 2008 and Germs et al., 2010). Trace fossils from the younger, Cambrian-aged Fish River Subgroup were recorded by Geyer (2005). Combined, these studies have substantially improved our knowledge of late Ediacaran-Cambrian trace fossil diversity, and have helped to produce a tentative ichnostratigraphy for the Ediacaran portions of the Nama Group. However, the identification of several ichnotaxa representing complex behaviors and (potentially) high ecosystem engineering impacts have placed the Nama Group at odds with many other Ediacaran sections worldwide. For example, Germs (1972b) reported *Skolithos* from as low as the Kliphoek Member (Kuibis Subgroup) and thus in the oldest fossil-bearing units in Namibia, which is a trace fossil otherwise thought to appear post-Fortunian (e.g., Mángano and Buatois, 2014, 2017). Geyer and Uchman (1995) subsequently reported two forms of *Skolithos* from Ediacaran portions of the Nama Group, this time from the Nasep and

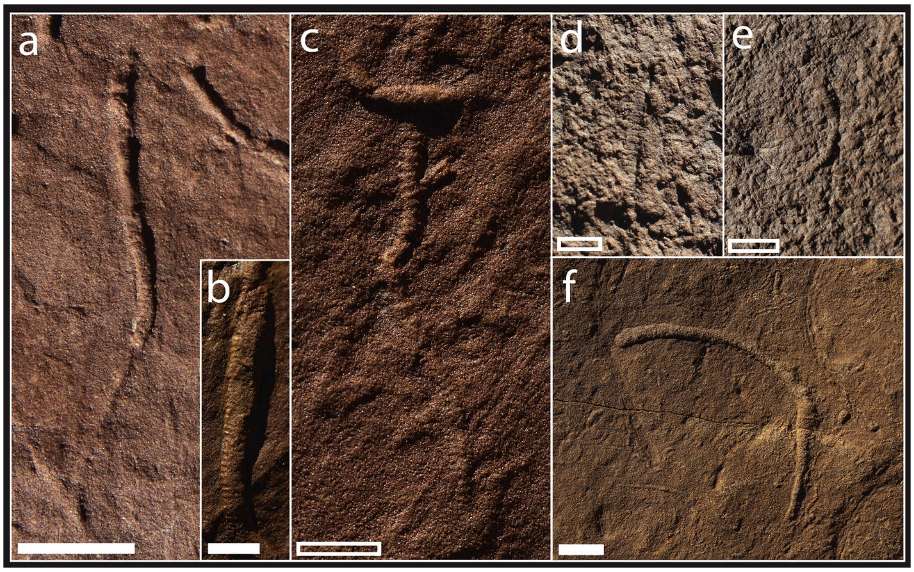

Fig. 4. Tubular and annulated body fossils from the Nasep-Huns transition (Canyon Roadhouse and Farm Arimas), illustrating a range of morphologies. Note tapered profiles in panels a and f, regular annulations in panels c-e, and potential funnel-in-funnel structure in panel c (similar to that described for *Cloudina*), hinting at the presence of multiple tubular taxa in these horizons. All slabs recovered from float, with fossils typically preserved on bed undersides. Filled scale bars 1 cm; open scale bars 5 mm.

Huns members. Likewise, Crimes and Germs (1982) reported *Diplocraterion* from the Vingerbreek Member; *Diplocraterion* is a relatively deep-tier U-shaped dwelling burrow with significant bioirrigation potential, and, like *Skolithos*, is generally thought to appear in Cambrian Stage 2 (Mángano and Buatois, 2014). Crimes and Germs (1982) also documented specimens assigned to *Nereites* and a possible occurrence of *Chondrites*, both typical Phanerozoic ichnogenera. Lastly, Macdonald et al. (2014) reported large structures that were assigned to *Zoophycos* from the Upper Omkyk Member tens of meters below ash beds dated at ~548 Ma (Grotzinger et al., 1995); *Zoophycos* represents intense exploitation of the sediment subsurface, recording a behavior not thought to appear elsewhere until the Cambrian (Jensen, 1997).

There have been, however, a number of critiques levied at the published ichnological record of the Nama Group. Crimes and Fedonkin (1996) reinterpreted many of the Ediacaran *Skolithos* from Namibia as body fossils. Jensen (2003) and Jensen et al. (2006) also deemed many of these trace fossils (and Ediacaran *Skolithos* in particular) 'doubtful' and 'problematic', suggesting that many occurrences may actually be the basal attachment of a body fossil, or the vertical portions of *Planolites*-type traces (Jensen et al., 2006; see also Jensen and Runnegar, 2005). Similar doubts were raised in more recent revisions (Mángano and Buatois, 2014; Buatois and Mángano, 2016). Despite this, many of these early trace fossil identifications are still typically included in paleontological summaries of the Nama Group (see, for example, Germs, 1995; Grotzinger and Miller, 2008; Bowyer et al., 2020). A careful reexamination of the Ediacaran trace fossil record of the Nama Group is thus crucial to establishing whether the Nama Group is genuinely unique in context of evolving metazoan ecology, behaviors, and body plans. This evaluation is essential to properly assess the level of complexity in the behaviors represented in the ichnologic record and the nature and extent of ecosystem engineering during the terminal Ediacaran. Wherever possible, the sites and Farms mentioned in these older studies were visited, and fresh material collected. In essence, we treat this historical compilation of trace fossil occurrences as a hypothesis to be tested with new field data. A brief summary of localities, along with outcrop styles and ichnotaxa recorded by our group is given in Table 1.

4.2. Diversity, disparity, and distribution of ichnotaxa

In order to capture the main innovations in terms of animal-substrate interactions, we have framed this section in terms of ichnodisparity categories. Accordingly, we list below the different ichnotaxa following previously defined categories of architectural design (Buatois et al., 2017).

4.2.1. Vertical plug-shaped burrows

We include in this category occurrences of simple, vertically oriented plug-shaped burrows, such as *Bergaueria* (Prantl, 1945) and *Conichnus* (Männil, 1966). Plug-shaped burrows are thought to represent a range of different behaviors by coelenterate-grade organisms occupying a (broadly) sessile life habit attached to, or partially buried in, the sediment substrate (e.g., Pemberton et al., 1988; Mata et al., 2012; Desai and Saklani, 2015). *Bergaueria* is defined as a hemispherical to shallow cylindrical, vertical structure with a rounded base, smooth, unlined or lined burrow walls and structureless infill commonly preserved in positive hyporelief (Alpert, 1973; Pemberton et al., 1988; Lima and Netto, 2012). *Conichnus* differs from *Bergaueria* in comprising a conical and downward-tapering, vertical structure, commonly exhibiting nested funnel-in-funnel laminae oriented convex downward, and locally possessing a thin lining marking the discontinuity between infill and the adjacent surrounding sediment, being typically preserved in full relief (Frey and Howard, 1981; Pemberton et al., 1988; Mata et al., 2012; Desai and Saklani, 2015). Mata et al. (2012) interpreted plug-shaped ichnotaxa as representing a continuum of behaviors belonging to actinian cnidarians, ranging from resting traces (*Bergaueria*), dwelling burrows (*Dolopichnus*), and escape structures (*Conichnus*) (see also Shinn, 1968; Alpert, 1973; Seilacher, 2007). However, *Dolopichnus* is now considered a junior synonym of *Laevicyclus* (Knaust, 2015). In addition, the emerging picture of the ethologic significance of the different ichnotaxa regarded as plug-shaped burrows is far more complex. For example, although escape behavior has been observed in some specimens of *Conichnus* (Desai and Saklani, 2015), dwelling and maintenance of equilibrium is involved in many others (e.g. Frey and Howard, 1981; Pemberton et al., 1988; Savrda, 2003; Desai and Saklani, 2015). The same can be said of *Bergaueria*; most of its ichnospecies are unlined and have been interpreted as resting traces, but lined ones are regarded as dwelling burrows (Pemberton et al., 1988). The ichnospecies *B. sucta* which, in contrast to the other *Bergaueria* ichnospecies, records evidence for lateral movement, has been originally described from the Cambrian (Seilacher, 1990). However, this ichnospecies has been subsequently recorded in Ediacaran units (Narbonne and Aitken, 1990; Seilacher et al., 2005; Menon et al., 2013; Buatois and Mángano, 2016). Further work on this ichnospecies is needed in order to confirm the Ediacaran occurrences. To complicate things further, distinction of plug-shaped burrows, in particular *Bergaueria,* from body fossils is commonly not straightforward in the case of Ediacaran specimens

Table 1
List of studied localities with brief descriptions of outcrop style and recorded ichnotaxa.

No.	Farm/site	Outcrop style	Ichnotaxa
1	Farm Driedoornvlatke	Canyon	None found
2	Farm Berghoek	Low exposures and scree slopes	Plug-shaped burrows, *Helminthopsis/Helminthoidichnites*
3	Farm Haruchas	Low exposures, scree slopes and riverbeds	Plug-shaped burrows, *Helminthopsis/Helminthoidichnites*, under-mat mining trace fossils, *Archaeonassa*
4	Farm Neuras	Cuesta	Plug-shaped burrows, *Helminthopsis/Helminthoidichnites*
5	Farm Hauchabfontein	Canyon	Arched structures
6	Farm Donkergange	Canyon	None found
7	Zebra River	Canyon	Rare plug-shaped burrows
8	Farm Nudaus	Low exposures and scree slopes	Under-mat mining trace fossils
9	Farm Kamkas	Low exposures and scree slopes	Plug-shaped burrows
10	Farm Urusis	Low exposures and scree slopes	Rare *Archaeonassa*
11	Farm Zuurburg	Low exposures, scree slopes and riverbeds	Plug-shaped burrows
12	Farm Hansburg	Low exposures, scree slopes and riverbeds	Plug-shaped burrows, arched structures
13	Farm Weltevrede	Low exposures and scree slopes	Plug-shaped burrows
14	Farm Tsachanabis	Plateau edge	Plug-shaped burrows, *Helminthopsis/Helminthoidichnites*
15	Farm Aar	Low exposures, scree slopes and plateau edge	None found
16	Farm Grens	Cuesta	None found
17	Farm Swartpunt	Cuesta	Plug-shaped burrows, *Helminthopsis/Helminthoidichnites*, *Streptichnus*, Treptichnids, Form A (meiofaunal burrows), Form B (meiofaunal networks)
18	Farm Arimas	Cuesta	Plug-shaped burrows, *Helminthopsis/Helminthoidichnites*, *Archaeonassa*, *Torrowangea*, *Gordia*, Treptichnids, Form A (meiofaunal burrows)
19	Farm Sontaagsbrunn	Canyon	Plug-shaped burrows, *Helminthopsis/Helminthoidichnites*, *Treptichnus pedum*
20	Koelkrans (Fish River)	Canyon	Plug-shaped burrows, *Helminthopsis/Helminthoidichnites*, *Parapsammichnites*
21	Canyon Roadhouse	Cuesta	Plug-shaped burrows, *Helminthopsis/Helminthoidichnites*, *Archaeonassa*, *Torrowangea*, *Gordia*, Treptichnids, Form A (meiofaunal burrows)

The stratigraphic thicknesses of exposures differ substantially between recorded outcrops, ranging from 3-30 m (low exposures, scree slopes and riverbeds), through 50-60 m (plateau edges), to 100+ m (canyons and cuestas). The vast majority of the recorded stratigraphy in the Nama Group is preserved in excellent vertical and lateral extent – especially in the Fish and Zebra River Canyons – with the exception of the middle Schwarzrand Subgroup in the Zaris Subbasin, where vertical relief is rarer.

(Jensen, 2003; Jensen et al., 2006; Buatois and Mángano, 2016). The association of *Aspidella* fossils with sedimentological fabrics consistent with equilibrium traces in the Fermeuse Formation of eastern Newfoundland (Menon et al., 2013) illustrates this potential confusion.

Occurrence. – Plug-shaped burrows are perhaps the most common trace fossils found in the Ediacaran of Namibia; our group came across these structures in virtually every locality visited, preserved in a wide variety of lithologies (Fig. 5). In the Witputs Sub-basin, plug-shaped burrows appear as low as the Kliphoek Member on farms Hansburg, Zuurburg, and Kuibis, and are ubiquitous throughout siliciclastic units higher in the stratigraphic column, including the Nasep, base of the Huns, Feldschuhhorn, and both the base and top of the Spitskop members. Plug-shaped burrows are also common in the Zaris Sub-basin, particularly throughout the Vingerbreek Member, as well as higher in the Urusis Formation. In cross section, these structures reveal a wide variety in internal morphology – some (in particular those in the Vingerbreek Member where it is exposed along the D850 road north and east of Zebra River; see Fig. 6) exhibit clear cone-in-cone infill (arrowed in Fig. 5h-i), and are thus likely best identified as *Conichnus*, whereas others exhibit structureless infill and closed conical/subconical morphologies, and are thus more similar to *Bergaueria* (Fig. 5j; see also Darroch et al., 2016, and Cribb et al., 2019). Both Darroch et al. (2016) and Cribb et al. (2019) also noted that plug-shaped burrows on slabs commonly appear paired (e.g., Fig. 5b-f), maintaining consistent distances with nearest neighbors (although these do vary between slabs). However, neighboring 'plugs' are never seen to be joined with spreite in the sediment subsurface (which would identify them as more complex burrows similar to *Diplocraterion*), and so the reason for this apparent pairing is still unclear. In addition, a U-shape has not been detected in cross-section, preventing assignment to *Arenicolites*. In some cases (e.g. Fig. 5b), neighboring 'plugs' seem to be aligned or alternating, suggesting affinities with treptichnids. Specimens described as *Brooksella* by Crimes and Germs (1982) may represent a preservational variant of plug-shaped burrows, although an inorganic origin cannot be easily rejected. In addition, a body fossil origin has been subsequently proposed for this form (Ciampaglio et al., 2006). The taxonomic status of *Brooksella* is therefore controversial, and an in-depth revision is needed (Munoz et al., 2019).

4.2.2. Simple horizontal trails

This category comprises horizontal trails with simple patterns, typically formed within the uppermost 10 mm of the sediment, and which reflect either non-specialized grazing strategies or, in some cases, simple locomotion (Narbonne and Aitken, 1990; Jensen, 2003; Droser et al., 2005; Buatois and Mángano, 2012a; Buatois et al., 2017). *Helminthopsis*Heer, 1877, *Helminthoidichnites* Fitch 1850, *Archaeonassa*Fenton and Fenton, 1937, and *Gordia*Emmons, 1844 are included in this category because, although they possess characteristics that allow distinction at ichnogenus level, they represent broadly similar behaviors (e.g., Jensen, 2003; Jensen et al., 2006; Buatois et al., 2017). *Helminthopsis* comprises meandering, unbranched, horizontal trails that typically do not touch or crosscut each other, and which lack self-overcrossing (Han and Pickerill, 1995; Wetzel and Bromley, 1996; Buatois et al., 1998; Uchman et al., 2005; Hanken et al., 2016). This is distinct from *Helminthoidichnites*, which consists of slightly winding (rather than meandering) horizontal trails locally showing scribbling patterns and commonly displaying overlap among specimens (Buatois et al., 1998; Pokorný et al., 2017). Both ichnotaxa are typically preserved as negative epirelief or positive hyporelief. However, negative hyporelief preservation is common in Ediacaran specimens (Gehling, 1999; see Fig. 6 for an illustration of a range of preservational styles in the Nama). Many putative *Helminthopsis* and *Helminthoidichnites* specimens in the Nama Group possess abrupt bends and terminations (in particular in the Nasep-Huns transition), indicating that many of these examples are more likely to be tubular body fossils – potentially poorly-preserved *Archaeichnium* or similar taxa (see, for example, Fig. 4). Also, some specimens may show discontinuous segments and pits, which suggest potential affinities with treptichnids rather than grazing trails *per se*.

Gordia is superficially similar to *Helminthopsis* and *Helminthoidichnites* in that it is a smooth, unlined and winding horizontal trail with massive infill, but can be differentiated by its tendency to self-cross (Fillion and Pickerill, 1990; Getty et al., 2017). Specimens exhibiting

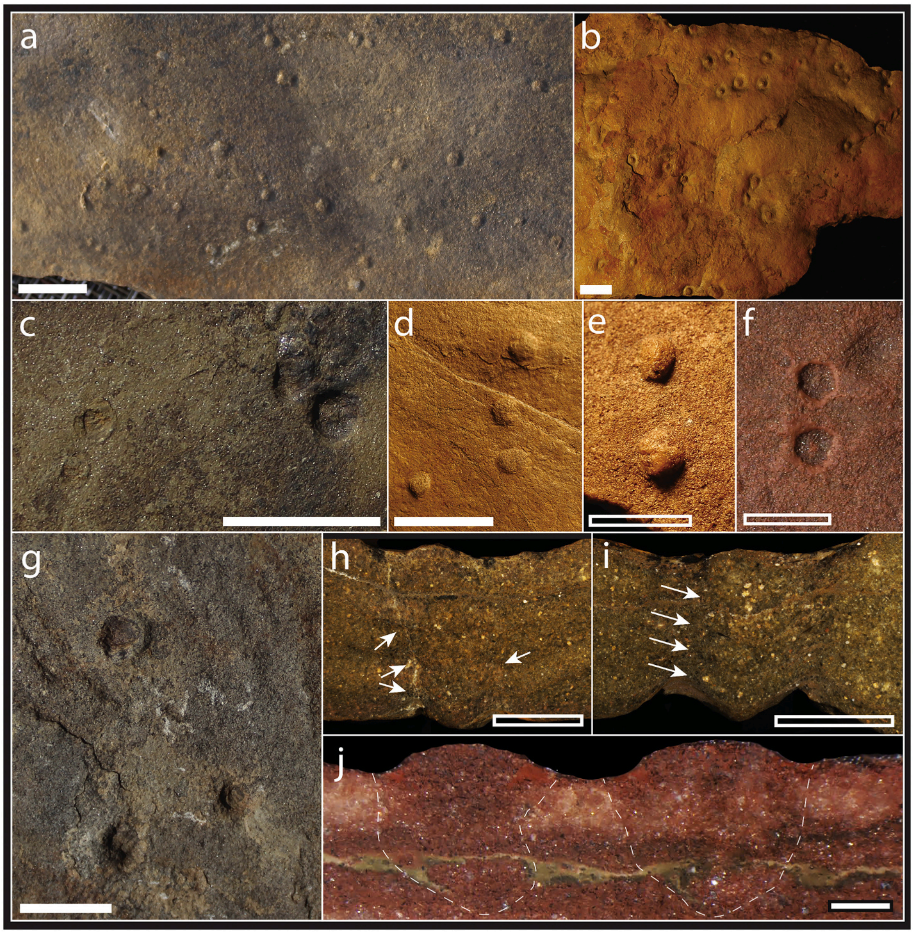

Fig. 5. a–g) Plug-shaped burrows, from: a) Farm Berghoek; b,d) Farm Nudaus; c,g) Farm Haruchas; e) Farm Kuibis; and f) Farm Tsachanabis. Burrows from a–d) and g) from the Vingerbreek Member; e–f) from the Kliphoek Member. Burrows in h–j) *Conichnus*, and the rest *Bergaueria*. Note (particularly in panels b, c, e and f) the tendency for burrows to appear paired; h–i) cross-sections of burrows from slab shown in panel b; note sharp burrow margins in panel h, and diffuse margins (and cone-in-cone sediment infill) in panel i; j) polished cross-section of burrows shown in panel f; note simple plug-shaped terminations in the sediment subsurface (outlined in white dashed lines). All fossils preserved on bed tops. Filled scale bars 1 cm; open scale bars 5 mm.

sudden burrow terminations or isolated 'nubs' are thought to indicate instances where the tracemaker probed the over- or underlying sediment, indicating that the producer of *Gordia* was capable of some limited vertical movement in the sediment subsurface, either to access food sources, or as a means of avoiding obstacles (Wang et al., 2009).

Archaeonassa comprises straight to sinuous horizontal trails, possessing a median groove flanked by rounded ridges, and commonly preserved in positive epirelief (Yochelson and Fedonkin, 1997; Jensen, 2003; Mángano et al., 2005). The central furrow is typically wider than lateral ridges, which may be smooth, or ornamented with oblique to transverse striations or smaller lobes (Buckman, 1994). The lateral ridges of this ichnogenus are clear evidence of sediment displacement, and (unlike many Ediacaran trace fossils) leave little risk of confusion with body fossils (Jensen et al., 2006). The specific morphology of *Archaeonassa* is thought to depend on how deeply the animal was submerged in the sediment as well as the sediment properties; for example, sediments with high tensile strength tend to rupture, forming segmented levees (Knox and Miller, 1985; Jensen, 2003).

Ichnotaxa included under the category of simple horizontal trails are commonly interpreted as grazing traces (i.e. pascichnia) of vermiform metazoans, potentially annelid worms, arthropod larvae, or nematodes (Fillion and Pickerill, 1990; Buatois and Mángano, 1993; Getty et al., 2017). Priapulid worms have been proposed as potential producers of *Gordia* (Wang et al., 2009), but this link is less certain. In the case of *Archaeonassa*, mollusks have been suggested as potential tracemakers, but a wide variety of worm-like organisms, as well as arthropods, may produce similar structures (Buckman, 1994; Yochelson and Fedonkin, 1997).

Occurrence. – *Helminthopsis* and *Helminthoidichnites* are distributed throughout the Nama Group, and are among the most common trace fossils found in siliciclastic sediments. In the Witputs Sub-basin our group has found these ichnogenera as low as the Nasep-Huns transition in the lower Schwarzrand Subgroup where they are extremely common (Figs. 7–8), although several putative and poorly-preserved specimens have been found lower, in the Kliphoek Member on Farms Hansburg and Zuurburg (Kuibis Subgroup). They are also common in thin sandstone beds in the upper parts of the Huns limestone, at the base and top of the Feldschuhhorn Member (at Koelkrans and Farm Sonntagsbrunn, respectively), in sandstone beds at the base of the Spitskop Member, and are abundant in sandstone layers towards the top of the Spitskop at Farm Swartpunt, several meters above horizons preserving in-situ accumulations of the Ediacaran body fossils *Pteridinium* and *Swartpuntia*. In the Zaris Sub-basin, these ichnogenera are rarer, but are present in the Vingerbreek Member on farms Berghoek and Haruchas.

Gordia is rarer in Namibia than *Helminthopsis* and *Helminthoidichnites*, with the notable exception of within the Nasep-Huns transition, in particular where it is exposed at both Farm Arimas and the Canyon Roadhouse (both Witputs Sub-basin) in high densities (Fig. 7g). In these localities, *Gordia* can be extremely common, contributing substantially to relatively high (5–7%) bedding plane bioturbation indices on slabs, representing some of the most intensive trace fossil activity found anywhere in the Ediacaran portions of the Nama Group (Cribb et al., 2019). *Gordia* from these localities exhibits an approximate bimodal distribution of trail widths, with smaller trails ~1 mm in width, and rarer large trails ~3 mm. Several larger specimens collected from the base of the Huns Member at Canyon Roadhouse also exhibit abrupt terminations and discontinuous trail features on slab tops, similar to those described by Wang et al. (2009), indicating a significant degree of vertical movement (see e.g. Fig. 9a). *Gordia* is also locally present in the lowermost 10-20 m of the Feldschuhhorn Member in the Fish River

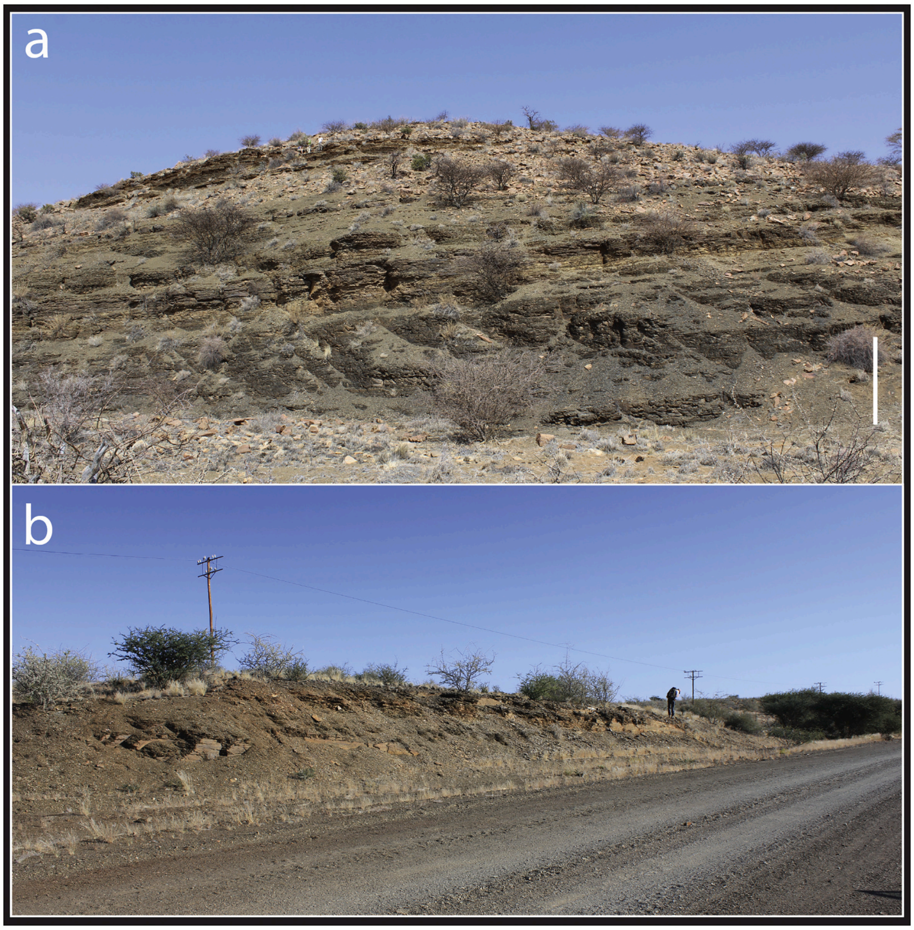

Fig. 6. Outcrops of Vingerbreek Member sediments exposed in: a) riverbed section on Farm Haruchas; and, b) next to the D850 road north and east of Zebra River (Zaris Subbasin). Vertical scale in a) 2 meters.

Canyon near Holoog. Thus far, our group has not found *Gordia* anywhere in the Zaris Sub-basin, nor has it been reported by other workers.

Archaeonassa is present in several stratigraphic horizons in the Nama Group, but is probably most common in the Zaris Sub-basin at the base of the Vingerbreek Member (lower Schwarzrand Subgroup), in particular where it is exposed on Farm Haruchas (see Bouougri and Porada, 2007). In this locality, dense *Archaeonassa* are well preserved on the top-surfaces of siltstone horizons, closely associated with beds preserving abundant evidence for microbial mats and undermat mining burrows (Bouougri and Porada, 2007; see below). Most specimens exhibit extremely well-developed levees, some of which show distinct segmentation (Fig. 9g). A specimen described as *Nereites* from these deposits (Crimes and Germs, 1982) most likely belongs in *Archaeonassa*. Our group has also found *Archaeonassa* at the base of the Huns Member at the Canyon Roadhouse, and (even rarer) in low outcrops of the Urusis shale (middle Schwarzrand Subgroup) exposed on Urusis Farm.

4.2.3. *Simple actively filled (massive) horizontal to oblique structures*

*Planolites*Nicholson, 1873 and *Torrowangea*Webby, 1970 are included in this group. *Planolites* is characterized by being unlined and having an infill different than the host rock (Pemberton and Frey, 1982). Functionally, and in contrast to the related ichnogenus *Palaeophycus*, *Planolites* records active fill. Although there are common references to the presence of *Planolites* in Ediacaran rocks, the name has been used in a very loose way, commonly referring to simple trails that are more properly assigned to *Helminthoidichnites*. Thus far, our group has not recovered convincing examples of *Planolites* from the Ediacaran portions of the Nama Group. *Torrowangea* consists of sinuous to irregularly meandering trace fossils, characterized by irregular transverse corrugations or spaced constrictions, and commonly forming overlapping burrows (Webby, 1970; Narbonne and Aitken, 1990). The constrictions in *Torrowangea* are thought to indicate peristaltic movement of the tracemaker (Narbonne and Aitken, 1990; Buatois and Mángano, 2016; Toom et al., 2019), and typically interpreted to represent locomotion and feeding (i.e. pascichnia) below the sediment-water interface (Buatois and Mángano, 2016). However, due to the abundance of annulated and tube-like organisms in many Ediacaran localities, Jensen et al. (2006) suggested that ruling out a body fossil origin for putative *Torrowangea* in every case is crucial.

Occurrence. – *Torrowangea* is present in the Nasep-Huns transition in many localities across the Witputs Sub-basin; our group identified this ichnotaxon at both Farm Arimas and the Canyon Roadhouse, whereas Geyer and Uchman (1995) figured similar material from the same horizons at Farm Holoog. Burrows are typically 3-4 mm wide, possess transverse constrictions, and are commonly found as high-density clusters on sandstone slabs (Fig. 9d-f). Although there are body fossils of *Archaeichnium* in the same sections, *Torrowangea* is readily differentiated from these by possessing irregularly (rather than regularly) spaced annulations/corrugations, meandering in a random fashion (rather than being broadly straight with one or two high-angle 'kinks'), and maintaining an approximately consistent width, rather than tapering or terminating abruptly. *Torrowangea* from the Nasep-Huns transition greatly resemble the examples figured by Carbone and Narbonne (2014) from the Blueflower Formation of northwestern Canada.

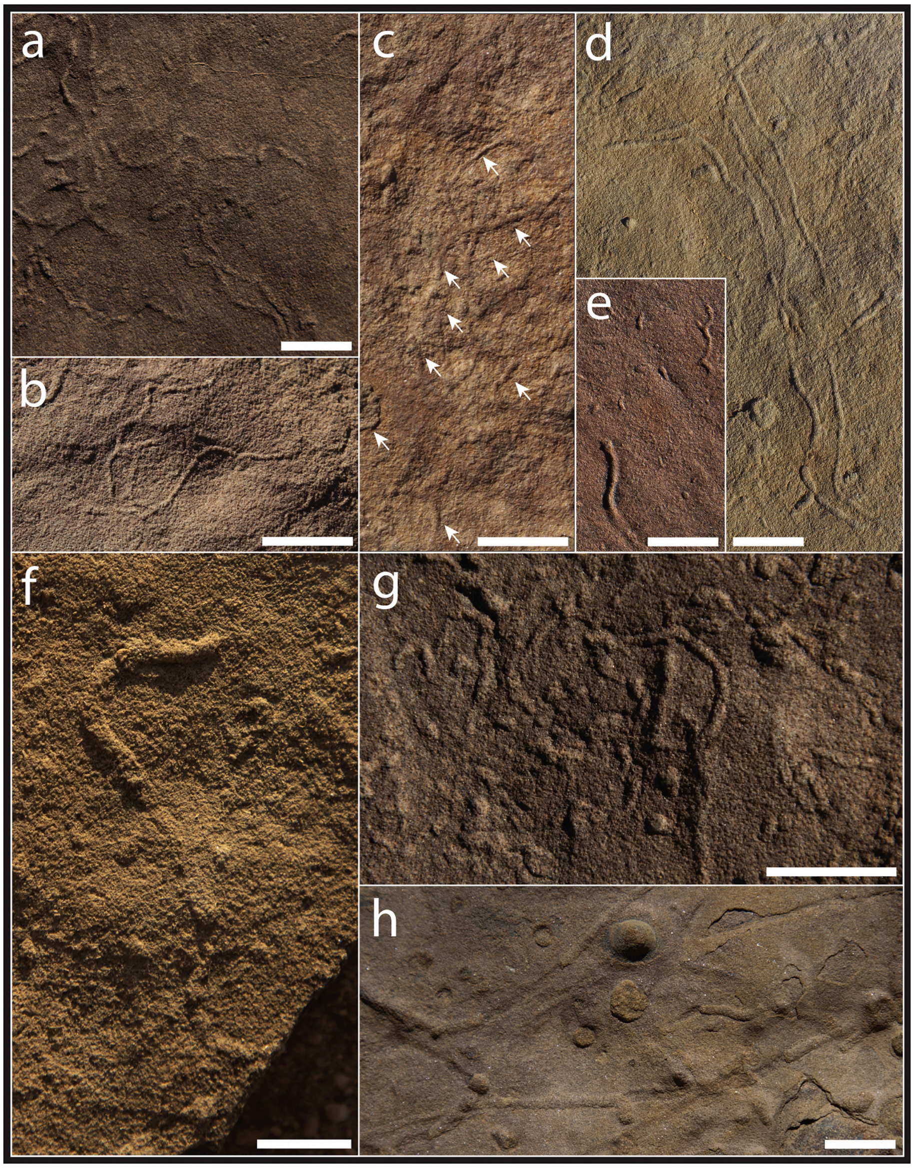

Fig. 7. Simple horizontal trails from the Ediacaran portions of the Nama Group: a–b) *Helminthopsis* (Nasep-Huns transition at Canyon Roadhouse); c–d) *Helminthoidichnites* (top of the Huns Member, Fish River Canyon, and Spitskop Member, Farm Swartpunt, respectively); e) *Helminthopsis* (Nasep-Huns transition at Canyon Roadhouse); f) unidentified simple horizontal trace (Nasep-Huns transition at Canyon Roadhouse); g) tightly meandering and self-overcrossing trail resembling *Gordia* (Nasep-Huns transition; Farm Arimas); h) *Helminthoidichnites* (basal Spitskop Formation, Fish River Canyon). Note, however, the presence of discontinuous segments and pits in a, f and g, suggesting that some of these specimens may represent partially preserved treptichnids. Trace fossils shown preserved on bed undersides, with the exception of d) and h), which are preserved on bed tops. Filled scale bars 1 cm.

4.2.4. *Complex actively filled horizontal structures*

Parapsammichnites Buatois, Almond, Mángano, Jensen, and Germs 2018 is included in this category. This ichnogenus comprises unilobate to bilobate, actively infilled, horizontal to subhorizontal and unbranched burrows describing scribbles, simple circles, spirals, and meanders (Buatois et al., 2018). Burrows are large – typically 7-10 mm in width and several 10s of cm long – and are commonly exposed in high (2-3 mm) relief on bed tops. The type (and only) ichnospecies for this ichnogenus – *Parapsammichnites pretziliformis* – was described by Buatois et al. (2018) from highly micaceous, fine-grained sandstone exposed near the boundary between the Feldschuhhorn and Spitskop members (Urusis Formation) in the Fish River Canyon, near the town of Holoog. The presence of active backfill indicates that the tracemaker was undoubtedly bilaterian, coelomate, and, moreover, was engaged in a ‘bulldozing’ behavior whereby sediment was forcibly pushed aside either using the animal’s body or with appendages (Buatois et al., 2018).

Occurrence. – Our group has recovered additional *Parapsammichnites* from throughout the Feldschuhhorn Member (as low as ~2 m above the contact with the underlying Huns limestone) and in the lowermost part of the Spitskop Member (3-4 m above the contact with the Feldschuhhorn), where they are exposed in the Fish River Canyon near Holoog. The most abundant and best-preserved specimens are exposed near Koelkrans camp, where the canyon floor meets the contact between Feldschuhhorn sandstone and Spitskop limestone (Figs. 10–11); however, this ichnotaxon is relatively widespread north and south along the main axis of the Fish River Canyon. Interestingly, while *Parapsammichnites* in the Feldschuhhorn Member are largely restricted to micaceous fine-grained sandstone, in the overlying Spitskop we have found them both in thin sandy laminae sandwiched between thin lime mudstone and in the lime mudstone themselves (Fig. 11g), suggesting that the original tracemaker was relatively unrestricted in its environmental preferences (however, no examples have yet been recorded from the Zaris Sub-basin, perhaps suggesting geographical restriction). At the base of the Spitskop in particular, *Parapsammichnites* is a component of both dense and unusually diverse trace fossil assemblages also comprising *Helminthopsis, Helminthoidichnites*, treptichnids (see below), smaller, branching horizontal burrows, and plug-shaped burrows.

4.2.5. *Horizontal burrows with horizontal to vertical branches*

This category includes *Streptichnus*Jensen and Runnegar, 2005 and the burrows informally referred to as treptichnids. *Streptichnus* is a complex trace fossil composed of clusters of horizontal, unidirectional

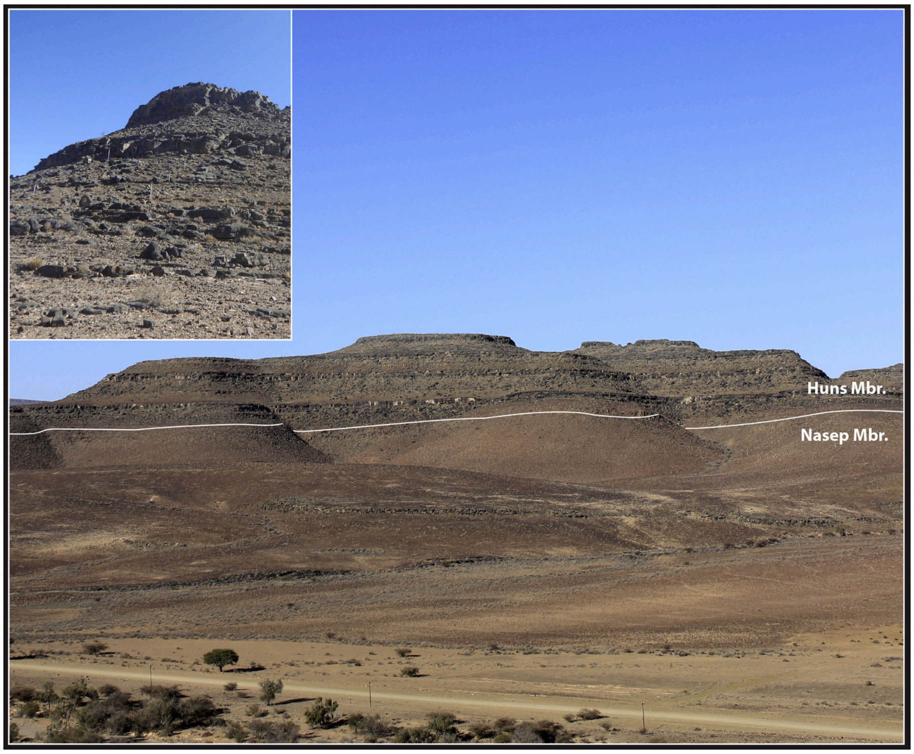

Fig. 8. Outcrop at Farm Arimas; white line marks the approximate contact between (below) sandstones belonging to the Nasep Member, and (above) carbonates belonging to the Huns Member. Inset image illustrating the view upslope from trace fossil-rich horizons at the base of the Huns Member.

and curved burrows that radiate from a central area, which themselves possess numerous probes that extend horizontally and down into the sediment (Jensen and Runnegar, 2005). This ichnogenus has many features in common with *Treptichnus*, but differs in that individual probes do not extend as far from the main burrow, and only emerge on the concave side of curved master burrows (Jensen and Runnegar, 2005). Individual radiating burrows extend up to 9 mm vertically into the sediment and appear 'twisted' suggesting a regular (and consistently dextral) spiraling movement through the sediment (Fig. 12f–h); however, the appearance of a spiral morphology may be the consequence of closely-spaced probes, in concert with vertical compression of the sediment column (Jensen and Runnegar, 2005). The type (and only) ichnospecies for this ichnogenus – *Streptichnus narbonnei* – was described by Jensen and Runnegar (2005) from sandstone high in the Spitskop Member of the Urusis Formation on Farm Swartpunt, from horizons ~10 m above beds preserving the Ediacaran organisms *Swartpuntia* and *Pteridinium*.

Treptichnids show affinities with the ichnogenus *Treptichnus*, but a current lack of understanding surrounding their three-dimensional morphology prevents establishing a firm taxonomic determination. Germs (1972b) was the first to report discontinuous burrows, ~3 mm in width, in the Nasep Member exposed on Farm Arimas (Schwarzrand Subgroup, Urusis Formation), breaching the sediment surface (underside of bed) at regular intervals, probably representing individual 'probes' possessing three parallel ridges (also mentioned in Geyer and Uchman, 1995). Jensen et al. (2000) described these in more detail (although noting that the trace fossils occur in the base of the Huns rather than at the top of the Nasep, following the modified lithostratigraphic definitions of Saylor et al., 1995), and identified them as *Treptichnus* isp., distinct from *T. pedum* in being (typically) smaller, having more strongly unidirectional probes, and a less consistent and less systematic pattern of sediment exploitation. The Huns Member treptichnids therefore represent the earliest appearance of 'complex' trace fossil behavior, but not behavior as complex as that reflected by either *Streptichnus* or *T. pedum,* the latter marking the base of the Cambrian (Narbonne et al., 1987; Landing, 1994). Although *T. pedum* is commonly interpreted as being formed by priapulid worms (Orłowski and Żylińska, 1996; Jensen et al., 2000; Vannier et al., 2010; Kesidis et al., 2019), it is unclear if the simpler treptichnid burrows were formed by similar organisms.

Occurrence. – Thus far, *Streptichnus* has not been found outside of its type locality in Spitskop Member sandstones on Farm Swartpunt (Witputs Sub-basin). Some bed-penetrative burrows found at the base of the Huns Member (along with problematic structures found in carbonates belonging to the Hoogland Member) possess an apparent (or approximate) twisted/spiral structure, but are not as organized or systematic as that seen in *S. narbonnei*, and moreover, are either preserved as single specimens, or possess highly variable morphology. Given that the Spitskop strata at Swartpunt are the youngest Ediacaran rocks preserved anywhere in Namibia (Grotzinger et al., 1995; Narbonne et al., 1997), this absence may simply reflect the fact that the *Streptichnus* tracemaker evolved in the very latest part of the Ediacaran, and erosive downcutting evidenced at the base of the Nomtsas Formation has removed *Streptichnus*–bearing strata from other parts of the basin.

Our group recovered treptichnids similar to those described by Germs (1972b) and Jensen et al. (2000) from the top of the Nasep Formation and the base of the Huns Member (Urusis Formation) on both Farm Arimas (i.e., the original locality noted in Germs, 1972b), and the Canyon Roadhouse (Fig. 13). Individual probes are oval in shape, are 1-4 mm long, and form both linear and curvilinear burrows (and more rarely, circles) several cm long (Fig. 13a-e). Those rare specimens forming circles somewhat resemble *Treptichnus coronatum* (Crimes and Anderson, 1985; MacNaughton and Narbonne, 1999; Buatois et al., 2014). In addition, our group recovered several slabs possessing treptichnids from both the base of the Feldschuhhorn Member, and the base of the Spitskop Member in the vicinity of the Fish River Canyon near Holoog. In the latter case, trepichnids are preserved in thin sandstone laminae sandwiched between lime mudstone, and commonly preserve faint traces of master burrows linking individual probes (Fig. 13f-h). Probes are slightly larger (5-6 mm), and like those of *Treptichnus* isp.

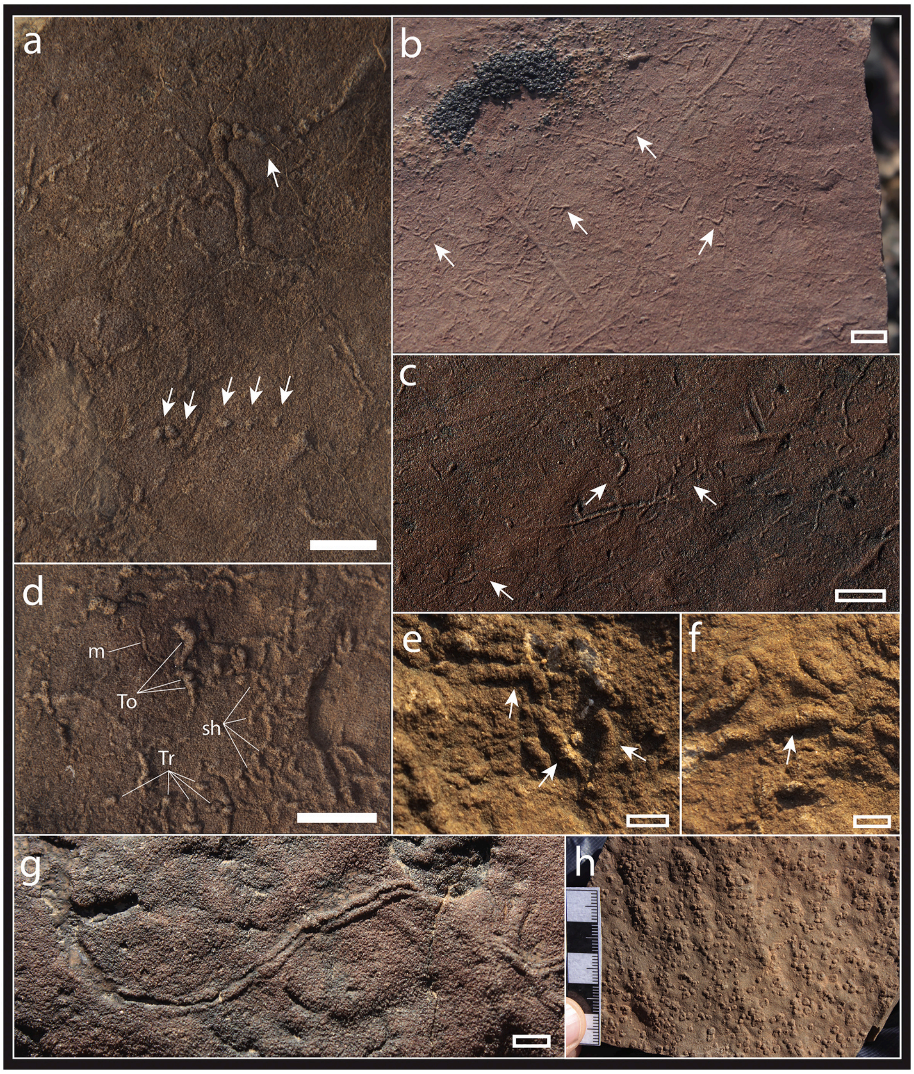

Fig. 9. Trace fossils from the Nasep-Huns transition (all Canyon Roadhouse and Farm Arimas): a) trace fossil assemblage, including *Helminthoidichnites*, a burrow similar to *Torrowangea* (arrowed top-center; note abrupt change in burrow trajectory and possible constrictions), and small treptichnids (arrowed center-bottom); b-c) sub-mm scale burrows ('Form A'), showing both branching (arrowed in b), and shallow movement in and out of the sediment plane (arrowed in c), possibly produced by meiofauna; d) diverse and densely bioturbated surface comprising several different ichnogenera, including simple horizonal trails ('sh') resembling *Helminthoidichnites*, larger traces preserving irregular constrictions (and thus evidence of peristaltic movement) similar to *Torrowangea* ('To'), sub-mm horizonal trails most likely produced by meiofauna ('m'), and oval-saped protuberances arranged in lines, suggestive of treptichnid-type behavior ('Tr'); e-f) *Torrowangea* (cf. Carbone and Narbonne, 2014; their Fig. 5), showing characteristic transverse constrictions and burrow meshworks; g) *Archaeonassa*, preserving prominent ridges of sediment either side of the central furrow; h) slab covered in dense Intrites. All trace fossils/pseudofossils shown preserved on bed undersides, with the exception of g) and h), which are preserved on bed tops. Filled scale bars 1 cm; open scale bars 5 mm.

from the Nasep-Huns transition, are largely unidirectional.

There are several trace fossils recorded in the Nama Group that do not have enough significant morphologic characteristics allowing to place them in previously known ichnotaxa. Accordingly, they cannot be confidently included in any category of architectural design. These are listed below and left in open nomenclature.

4.2.6. *Undermat mining trace fossils*

Bouougri and Porada (2007) were the first to report dendritic structures from the base of the Vingerbreek Member, resembling the undermat mining trace fossils similar to those described by Seilacher (1999) from the upper Cambrian of Oman. Burrows are typically 5–20 cm long, and form curved furrows with irregular lobe-like extensions perpendicular on either side. These structures are present in biolaminite facies preserving abundant evidence for colonization by microbial mats and episodes of subaerial exposure (including shrinkage cracks and teepee structures). Presumed burrows themselves are commonly associated with shrinkage cracks, which may have functioned as both oxygen oases and sources of moisture to trace-making organisms (Bouougri and Porada, 2007).

Occurrence. – Thus far, our group has only found these putative trace fossils at the original site described by Bouougri and Porada (2007) on Farm Haruchas (Vingerbreek Member), and from nearby Farm Nudaus (Niederhagen Member). On specific surfaces at Haruchas, these structures are abundant and well preserved on the canyon floor (Fig. 14b–e). Although they are overwhelmingly associated with shrinkage cracks (thus raising the possibility that they instead represent abiotic sedimentary structures associated with desiccation), lobe-shaped extensions off main axial structure commonly preserve clear crescentic features, suggestive of meniscate backfill (following Jensen et al., 2005). According to Bououghri and Porada (2007), the sedimentary facies and fabrics hosting the putative trace fossils suggest deposition in an extremely shallow, intertidal to lower supratidal environment characterized by periodic emergence; the relative rarity of these paleoenvironments in the succession may explain the apparent absence of these structures anywhere else in the Nama Group – essentially a function of facies restriction.

4.2.7. *Irregular networks*

Small (sub-mm-scale), horizontal, irregular networks were reported by Jensen et al. (2000) from the base of the Huns Member at Arimas Farm, and Jensen and Runnegar (2005) from the same horizons at Holoog Farm, comparable to *Olenichnus irregularis* Fedonkin 1985. *Olenichnus* was synonymized with *Multina* by Uchman and Alvaro (2000), but it has been recently regarded as valid (Marusin and Kuper, 2020). These appear superficially similar to the thread-like trace fossils figured by Germs (1972b) from the Nasep Formation on Arimas Farm (as well as from the Nomtsas Formation on Farm Swartkloofberg), and the structures referred to as *Olenichnus*-like and *Planolites*-like networks in Linnemann et al. (2019) from the Spitskop and Nomtsas formations,

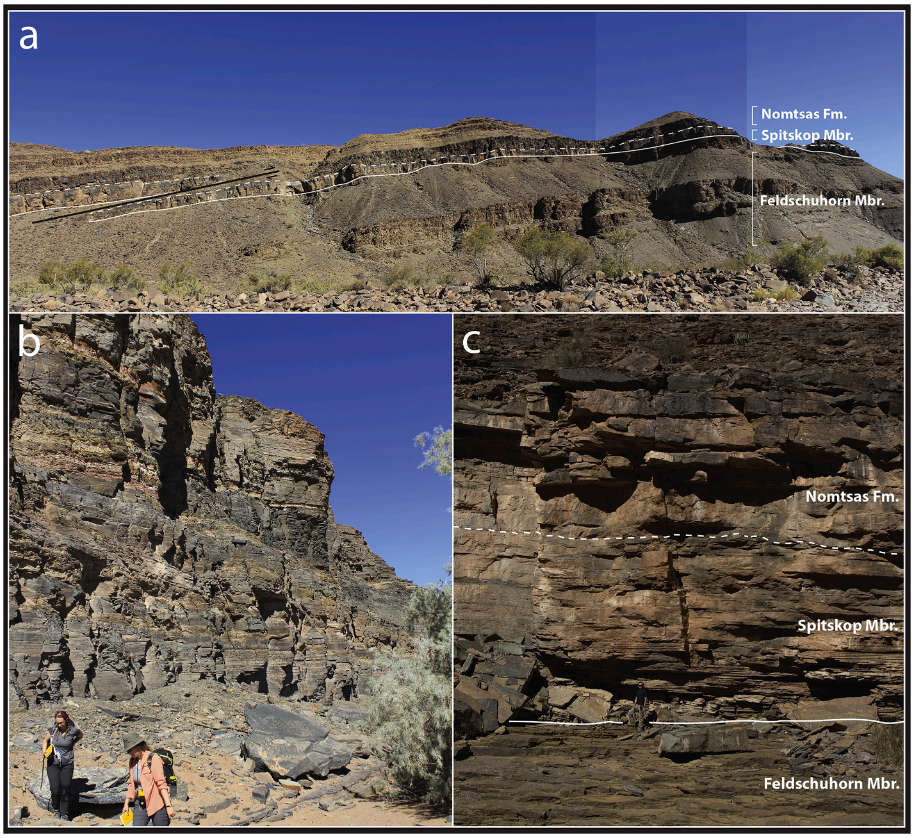

Fig. 10. Stratigraphy exposed at Koelkrans in the Fish River Canyon; a) side of the canyon visible from the campsite, with the contacts between Ediacaran-aged Feldschuhhorn and Spitskop Members, and Cambrian-aged Nomtsas Formation indicated in white. Small-scale reverse fault marked on left hand side of the image marked in black. b) Base of the Feldschuhhorn Member exposed on the eastern bank of the Fish River. c) Contacts illustrated in panel a) exposed where they meet the canyon floor eastwards of the camp; siltstones at the top of the Feldschuhhorn Member preserve dense accumulations of *Parapsammichnites pretzeliformis* (see also Buatois et al., 2018). Ribbon limestones with thin sandstone laminae at the base of the Spitskop Member preserve a moderately diverse assemblage of trace fossils, including *P. pretzeliformis*, large treptichnids, and horizonal burrows with range of sizes and morphologies (see also Figs. 11 and 19). Sandstones belonging to the Nomtsas Formation preserve rare *Treptichnus pedum*. Note both that the Spitskop member here is very thin (~6 m), and that the contact between the Spitskop Member and Nomtsas Formation in this locality is largely planar, showing little evidence for the deep incised valley-fill profiles seen elsewhere in the Witputs Subbasin, suggesting that the Koelkrans section was formed in an interfluve area that nonetheless was subjected to significant erosion (Buatois et al., 2018).

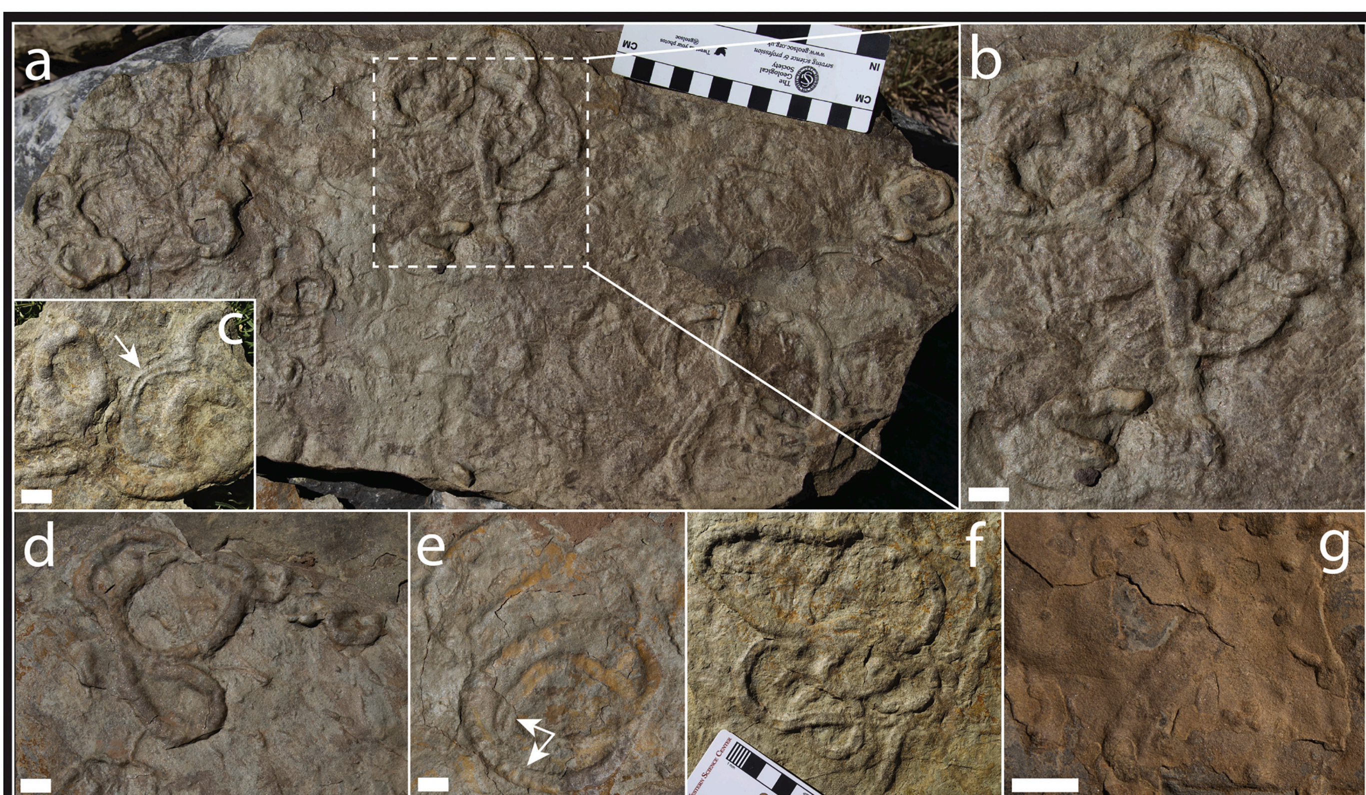

Fig. 11. *Parapsammichnites* from (a-f) the Feldschuhhorn Member, and; g) base of the Spitskop Member, in sandstone drapes overlying thin-bedded limestones (Fish River Canyon near Hologg). Note section in panel c (arrowed) where the top of the burrow has been weathered, revealing bilobed internal structure of the burrow. All fossils preserved on bed tops. Filled scale bars 1 cm.

Fig. 12. Trace fossils from the upper Spitskop Formation (Farm Swartpunt): a-d) dense networks of sub-mm scale horizontal burrows ('Form B'), showing 90 degree branching and burrow junctions (especially panel a), and regular vertical movement in and out of the sediment plane (arrowed in panels b-d); e) meshwork of indeterminate horizontal, unbranched burrows showing frequent cross-cutting and vertical avoidance; f-h) *Streptichnus narbonnei*, showing burrow radiation from central points ('c'), and characteristic corkscrew (or 'rope-like') appearance (Specimen NESM-F-626, housed at the National Earth Science Museum in Windhoek). All fossils preserved on bed undersides. Filled scale bars 1 cm; open scale bars 5 mm.

respectively. All three reports figured horizontal burrows that branch (commonly at 90-degree angles), forming diffuse networks on the tops of sandstone beds; the examples figured in Germs (1972b) from Swartkloofberg appear to show a degree of rope-like and twisted morphology, indicating that the tracemaker was capable of (or prone to) a loose spiral movement in the sediment. Similar minute forms have been interpreted as produced by meiofaunal organisms (Parry et al., 2017; Marusin and Kuper, 2020). It has been noted that the increase in trace-fossil density on bedding planes from rocks of terminal Ediacaran age has resulted in common burrow and trail overlap and, therefore, increasing the risk of misinterpreting overlap with branching; this may lead to an overestimation of the level of complexity (see discussion in Mángano and Buatois, 2020).

Occurrence. – Our group encountered small, sub-mm-scale burrows similar to those figured by Germs (1972b), Jensen and Runnegar (2005), and Linnemann et al. (2019) in several horizons from within the Witputs Sub-basin; from the top of the Nasep Member, base of the Huns Member (Farm Arimas and the Canyon Roadhouse), and from high in the Spitskop Member on Farm Swartpunt. Although all these burrows occupy a similar range of sizes (widths typically 0.3-0.5 mm), we note two distinct morphologies, hereafter termed Forms A and B. Form A (Fig. 9b-c) has been found by our group at the top of the Nasep Formation and base of the Huns Member in the Witputs Sub-basin, and comprises small, thread-like horizontal trace fossils preserved on the underside of sandstone/quartzite beds. Burrows rarely show branching, but commonly overcross, displaying a degree of vertical avoidance such that superimposed burrows go over and under one another, rather than through. Burrows are winding, and commonly show a regular sinuous pattern reminiscent of *Cochlichnus* (Fig. 9c; see also Jensen et al., 2006; their Fig. 2E). Form A does show some evidence for a small degree of movement in and out of the horizontal plane, but while it occurs in dense accumulations on single surfaces, it was not found forming networks in the localities we examined (and therefore differs from structures typically assigned to *Olenichnus*). Individual traces show bends that range from sinuous to right angles (Fig. 9b), with the sharpest bends appearing to correspond to close proximity of other traces. This form is also present at the base of the cuesta on Farm Swartpunt, likely sourced from the Spitskop Member, albeit in lower numbers.

Form B (Fig. 12a-d) was found at the top of the Spitskop Member on Farm Swartpunt (several meters both above and below beds containing *Swartpuntia* and *Pteridinium*), and comprises irregular networks of horizontal burrows preserved on bed tops. Burrows commonly branch at 90

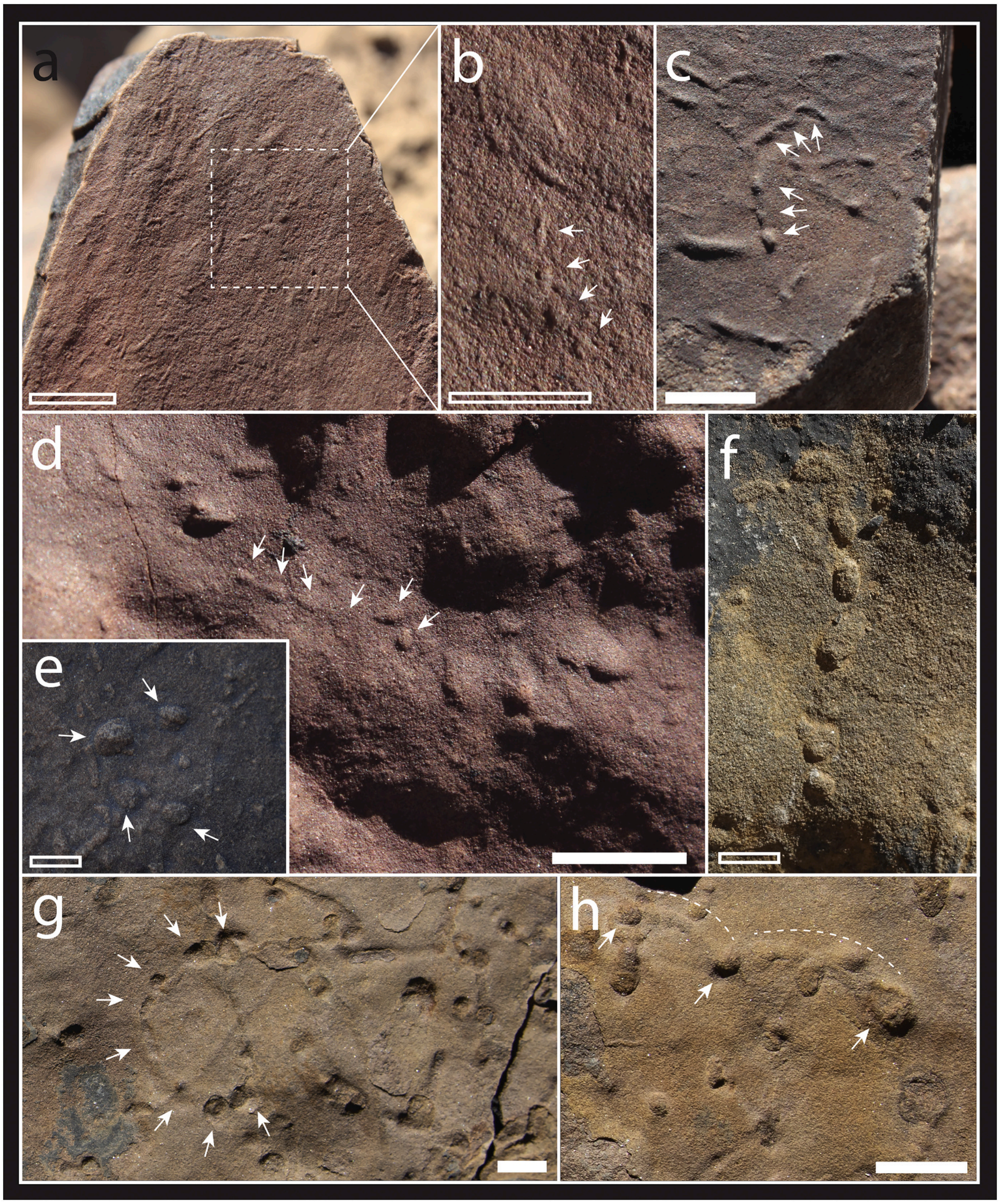

Fig. 13. Treptichnid-type traces from the Ediacaran portions of the Nama Group: a-e) small treptichnids from the Nasep-Huns transition (Canyon Roadhouse and Farm Arimas); note circular pattern of individual probes in panel e (arrowed); f-h) larger treptichnids from the basal Spitskop Member (Fish River Canyon near Holoog); note circular pattern of individual probes in panel g (arrowed), and preservation of linking burrows between steeper, vertical probes in panel h (highlighted with dashed white lines). All fossils preserved on bed undersides. Filled scale bars 1 cm; open scale bars 5 mm.

degrees, and in many places display regular vertical movement in and out of the sediment plane, creating a stitch-like pattern. Forms A and B have similar widths, but the branching and network forming of Form B are more consistent with a maintained, dwelling burrow rather than the simpler movement/feeding trace indicated by Form A.

4.3. *Pseudofossils and problematica*

Similar to many coeval sections worldwide, latest Ediacaran strata from the Nama Group preserve a wide variety of problematic structures that have been regarded as trace fossils by some authors, but considered to represent abiotic processes, microbially-induced sedimentary structures, or tubular organisms by others (see discussions in Jensen et al., 2006; Sappenfield et al., 2011 and Buatois and Mángano, 2016). This tendency for Ediacaran sediments to preserve hard-to-interpret features has been extensively noted by previous workers. For example, Paterson (1994) and Jensen et al. (2005) pointed to the role played by microbial mats in lowering the potential erodibility of thin sediment layers, which may preserve fine-scale sedimentary structures that are rare or absent in later deposits (for example, as mats become less common, see Seilacher and Pflüger, 1994, and Seilacher, 1997). Several authors have noted that the surfaces of Ediacaran microbial mats themselves can preserve features that may have been misdiagnosed as trace fossils (Gehling and Droser, 2009; Seilacher et al., 2005; Jensen et al., 2006; Buatois and Mángano, 2016; Davies et al., 2016; Tarhan et al., 2017). Hoffmann (1971) suggested that Precambrian pseudofossils and unusual sedimentary structures were likely both over-represented and over-reported (largely because of their potential evolutionary significance). However,

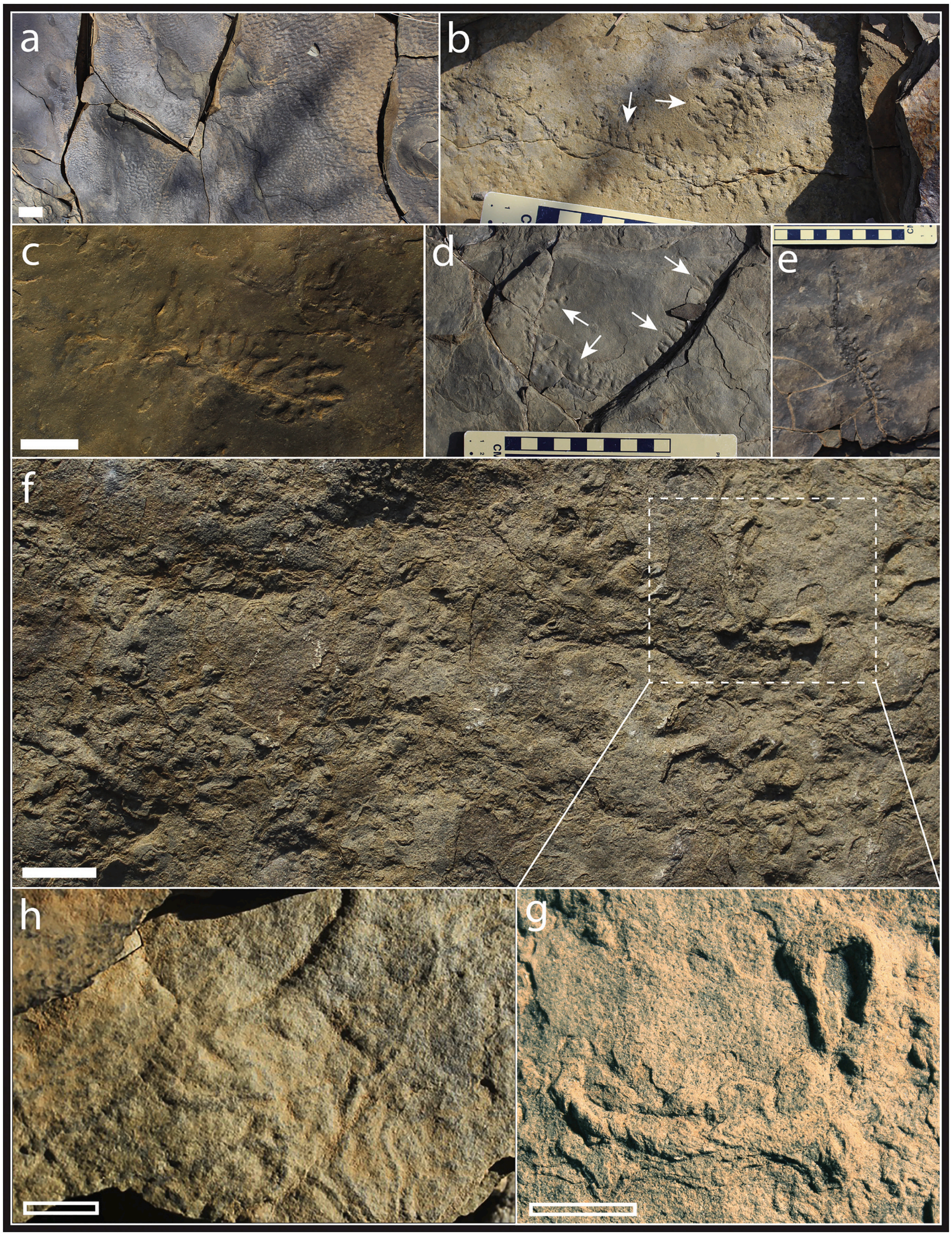

Fig. 14. Trace fossils and sedimentary structures from Farm Haruchas (Zaris Sub-basin; Vingerbreek Member): a) abundant Kinneyia-type microbial mat fabrics; b-e) dendritic undermat mining trace fossils; f) single, large *Archaeonassa*; g) close-up view of *Archaeonassa* highlighted in f), showing well-preserved sediment lobes flanking the central furrow; h) indeterminate and cross-cutting horizontal trace fossils resembling *Helminthoidichnites*. All fossils preserved on bed tops. Filled scale bars 1 cm; open scale bars 5 mm.

a majority of workers maintain that a late Ediacaran-Cambrian escalation in both depth and intensity of bioturbation would have greatly reduced the survival potential of both sedimentary and non-resistant biological structures, leading to an overall reduction in the frequency (and fidelity) of bedding-plane features (Jensen et al., 1998; McIlroy and Logan, 1999; Seilacher, 1999; Gehling et al., 2000; Buatois and Mángano, 2011, 2012a).

More recently, it has been suggested that the thick microbial mats that characterize much of the Neoproterozoic may not be ideal for preserving surface structures in siliciclastic sediments, as the object (or organism) typically has to penetrate the mat and disturb the sediment underneath in order for the trace to be recorded (e.g., Wray, 2015). However, this view is inconsistent with the common preservation of minute trace fossils in Ediacaran strata (Buatois and Mángano, 2016; Parry et al., 2017; Mángano and Buatois, 2020). In this context, the latest Ediacaran Nama interval may itself represent a unique preservational regime; the increase in density of very shallow-tier trace fossils as seen on bedding planes and, in particular, the local occurrence of more penetrative trace fossils may have resulted in (or from) a patchier distribution of microbially induced sedimentary structures ('MISS');

Mariotti et al. (2014) even suggested that certain types of MISS involving mat fragments may actually be the result of mat-penetrative bioturbation. Several studies (e.g., Hagadorn and Bottjer, 1997, 1999) have noted an apparent Neoproterozoic-Cambrian peak in MISS abundance. Notably, it is also true that strata in the Nama Group showing evidence of the highest intensity of bioturbation do not typically preserve microbially induced sedimentary structures (Buatois et al., 2018). In addition, although MISS (in particular Kinneyia textures and microbial wrinkle marks – see e.g., Fig. 15a-c) are abundant in the Nama Group, there are few (if any) of the 'textured organic surfaces' figured by Gehling and Droser (2009) and Tarhan et al. (2017) from the older White Sea interval. The controls on differences between interpreted mat textures in White Sea and Nama-aged sediments are as yet unknown. However, it may be that Nama-interval sedimentary environments represent a latest Neoproterozoic 'sweet spot' in the preservation of traces, where activity by motile organisms thinned microbial mats to the

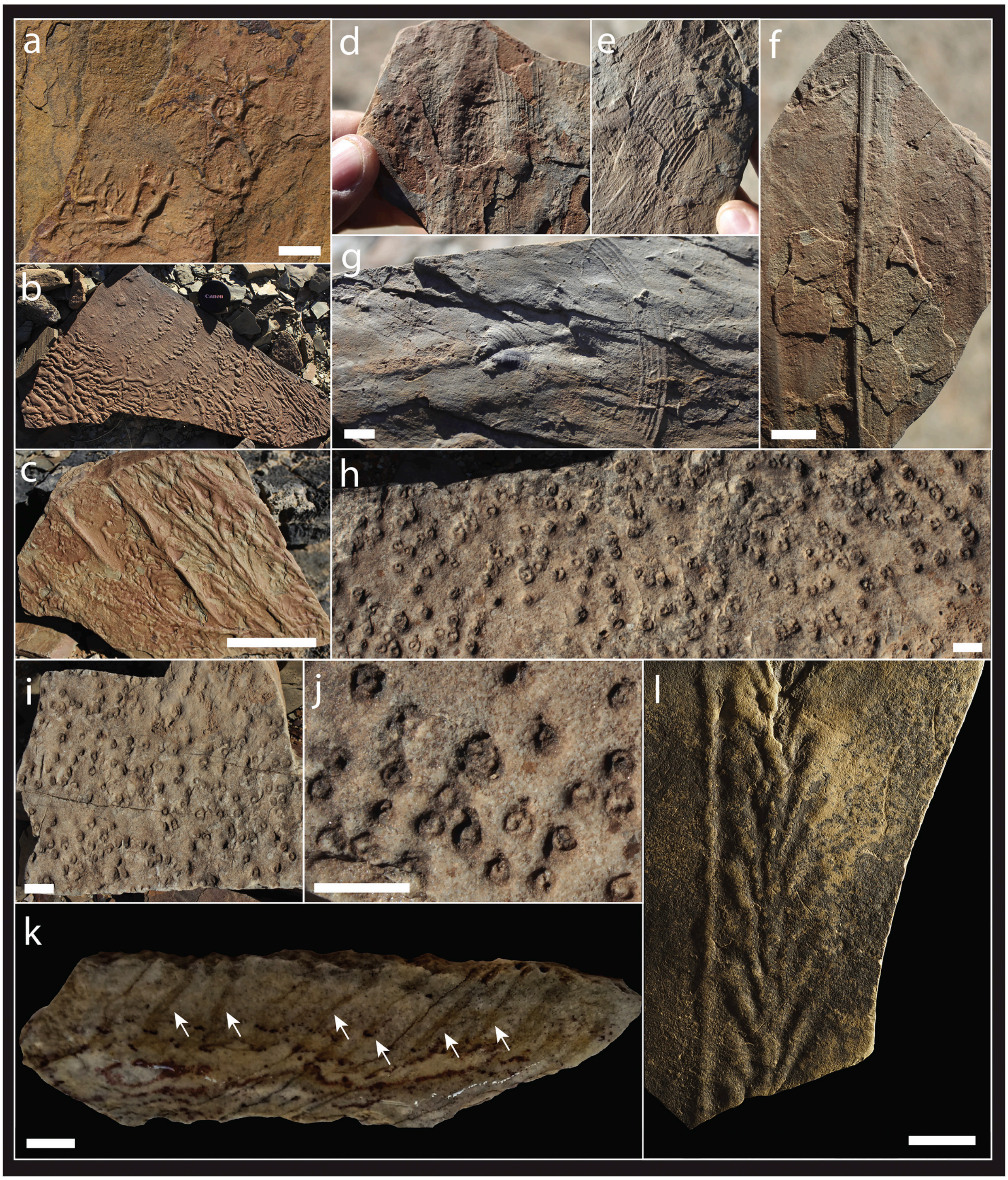

Fig. 15. Pseudofossils and problematica: a–c) dendritic pseudotraces resembling Aristophycus, potentially formed by the movement of fluid and/or gas beneath microbial mats (bed top); d–f) 'guitar strings' from near the top of the Spitskop Member on Farm Swartpunt, potentially representing sponge biofabrics (bed underside); g) Kullingia scratch circle from near the top of the Spitskop Member on Farm Swartpunt (bed underside); h–k) dense accumulations of problematic circular structures from quartzites in the Kliphoek Member on Farm Hansburg, superficially resembling *Skolithos* burrows in Cambrian 'pipe rock' (bed top); l) chevronate drag mark from the Feldschuhhorn Member, superficially resembling the Cambrian ichnotaxon *Climactichnites* (bed underside). Filled scale bars 1 cm.

extent that even the smallest disturbances were capable of deforming underlying sediment, but sediment mixing was not intense enough to weaken the sediment rheology sufficiently such that substrates become 'soupy', and small surface structures were immediately erased. Regardless, Ediacaran sediments from the Nama Group preserve an unusually large array of problematic bedding-plane structures; this may be linked to the properties of seafloor microbial mats, but is likely exacerbated by the large diversity of proximal sedimentary facies characterized by intense erosion (producing, for example, abundant tool marks, groove casts, and other features). In this section, we briefly discuss a variety of problematic structures.

4.3.1. *Arched structures*

A series of crescentic, arched structures preserved on bedding planes have been recorded from the Nama Group, and assigned to the ichnogenus *Zoophycos* (Macdonald et al., 2014). They were found in talus blocks sourced from the Upper Omkyk Member on Farm Hauchabfontein (Zaris Sub-basin), <100 m below an ash bed dated by Grotzinger et al. (1995) at 547.03 ± 0.7 Ma. These are large (5–30 cm long), but relatively shallow-penetrating (<1 cm) structures, consisting of arcuate U-shaped ridges, interpreted as thick (cm-scale) spreite that gradually increase in width (maximum ~10 cm) towards the apex (Fig. 16d). The authors also identified 2–3 mm structures that were interpreted as master burrows ('outer tube') which runs around the outside of the structure, and which would have presumably hosted the tracemaker as it systematically probed the encircled sediment for buried food particles. Several specimens were recovered from the locality, all from within thin (0.5-2 cm thick) sandstone lenses within m-scale limestone beds. The assignment of these structures is problematic, however, in that they lack several diagnostic features characteristic of *Zoophycos*, such as clear evidence of regularly spaced secondary lamellae, causative burrow, and spreite (Buatois and Mángano, 2016).

Additionally, the discovery of numerous, similar-looking structures from within the Mooifontein limestone on Farm Hansburg (Witputs Sub-basin) potentially offers an abiotic interpretation. These structures occur ~2-4 m above the contact with the underlying Kliphoek sandstones (see Maloney et al., 2020), are similarly large (10-30 cm in total length), and are characterized by arcuate U-shaped ridges that increase in diameter along the length of the structure (Fig. 16a-c). The Hansburg structures encompass a spectrum of morphologies that range from more biological-looking (i.e., elongate, directional, and with regularly-spaced arches), to more abiotic (broadly circular in aspect – see Fig. 16a-b, and comprising multiple aligned 'lobes', such as might be produced if soft sand were being forced along rheological interfaces with gradual loading of the

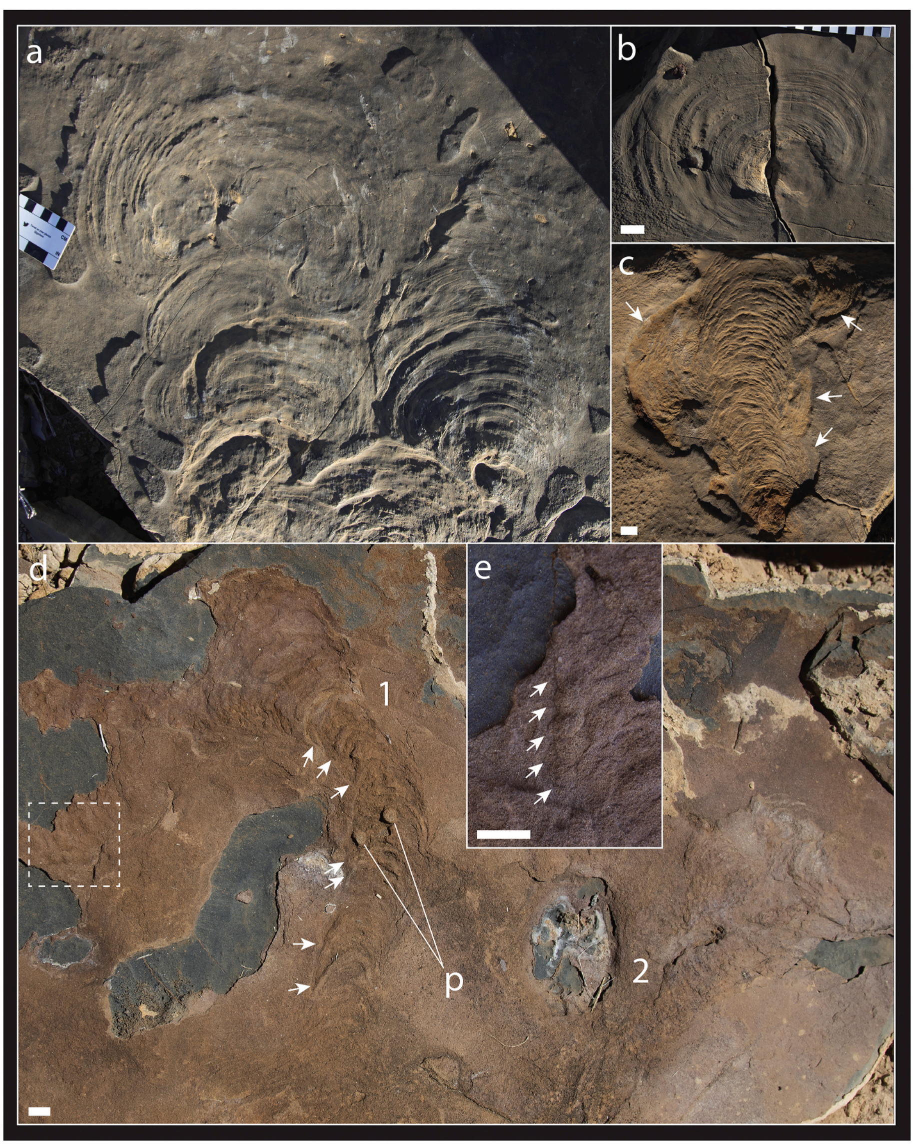

Fig. 16. Problematic arcuate structures from the Kuibis Subbgroup: a-c) repeated lobe-like structures developed in sandy horizons near the base of the Mooinfontein limestone on Farm Hansburg, illustrating sub-parallel ridges resembling spreite, and multiple 'lobes' spreading off the central structure (arrowed in c); d) arcuate structures (labelled '1' and '2') developed in sand lenses within limestones belonging to the upper Omkyk Member on Farm Hauchabfontein assigned to *?Zoophycos* isp. by Macdonald et al. (2014), illustrating parallel to sub-parallel ridges (arrowed), and paired penetrative structures ('p'); e) magnified image of area highlighted in d), showing possible coiled and rope-like horizontal trace, with numerous individual 'probes' arrowed. All fossils/pseudofossils preserved on bed tops. Filled scale bars 1 cm.

sediment pile). Crucially, the Mooifontein structures are preserved in a similar lithology to the structures from Hauchabfontein – in 1-3 cm thick sandstone lenses sandwiched within m-scale limestone beds. This lithological context (i.e., developed at the interface between sediment types with different rheological properties) offers a potential parallel with the pseudofossils figured by Knaust and Hauschke, (2004; their Fig. 3B) from the lower Triassic Buntsandstein playa deposits of Germany. These structures are commonly formed along horizontal sandstone-claystone interfaces (where claystone has different fissility along boundaries to the sandstone), and are typically of a shape and size that mimic spreiten burrows. Superficially at least, the pseudofossils figured by Knaust and Hauschke (2004) bear strong similarities with the Mooifontein structures discovered by our group, and thus may offer an abiotic interpretation for the structures discovered in the Omkyk (although this interpretation remains speculative, until more detailed petrographic analyses can be performed). We also note that the structures described by Macdonald et al. (2014) do have several unique features which are not seen in the Mooifontein structures – principally, the more regularly spaced crescentic marks (compare, for example, Fig. 16a with 16d) (S. Pruss, Pers. Comm.).

4.3.2. *V-shaped chevronate structures*

These consist of undulating, nested V-shaped chevronate structures preserved as ridges and separated by shallow furrows on the tops of micaceous, sandy siltstone (Fig. 15l). One specimen possesses a left-lateral crenulated margin ~0.3 cm in width which runs the entire length of the structure. These structures occur in the Feldschuhhorn Member, where it is exposed on Farm Sonntagsbrunn in the vicinity of the Fish River (Witputs Sub-basin). The V-shaped chevrons somewhat resemble the pattern of undulating bars and furrows of the Cambrian ichnogenus *Climactichnites* (Getty and Hagadorn, 2008). However, on closer inspection, there are a number of features which are inconsistent with interpretation of these structures as *Climactichnites* in particular and as trace fossils in general. Specifically, the tight internal angles of chevrons seen in these structures, as well as the presence of a crenulated margin on only one side of the structure (rather than both, as is seen in *Climactichnites*) are problematic. Furthermore, transverse bar morphologies characteristic of this ichnotaxon, including straight, sinusoidal, and zipper morphologies, are absent. A variety of abiotic interpretations, including chevronate tool marks or drag marks left by microbial aggregates, are therefore the most likely (cf. Peakall et al., 2020).

4.3.3. *Intrites*

In addition to the plug-shaped burrows described above, several horizons at the top of the Nasep and base of the Huns formations preserve well-developed Intrites – small, raised mounds commonly found on the top-surfaces of beds, and possessing a small central depression (Fig. 9h). The origin of Intrites is still controversial; initially it was regarded as a trace fossil (e.g., Fedonkin, 1980; Crimes, 1987), but a growing consensus has subsequently emerged considering it a body fossil (e.g., Gehling et al., 2000; McIlroy et al., 2005; Seilacher et al., 2005; Jensen et al., 2006), and affinities with paleopascichnids have been indicated for the type material (Jensen et al., 2006). Structures resembling Intrites from the Longmydian Group of England have now been interpreted as sedimentary structures resulting from interplay between microbial mats, sediment binding, and mineral precipitation on the flanks of small sediment volcanoes (Menon et al., 2016, 2017), although the potential affinities of these structures with the type material of Intrites from White Sea area deserve further exploration. The close resemblance between Intrites from the Nama and those described by Menon et al. (2017) from the Longmydian Group do, however, make a strong case that our examples from the Nasep-Huns transition represent sedimentary structures. Moreover, these occurrences suggest the strong potential influence of matgrounds in producing water and gas-escape structures in these horizons, and reinforces the notion that putative vertically-oriented trace fossils, such as *Skolithos* and *Diplocraterion*, need to be treated with caution, and ideally examined in cross-section.

4.3.4. *'Guitar strings'*

Siliciclastic deposits towards the top of the Schwarzrand Subgroup on Farm Swartpunt contain abundant straight and sub-cylindrical striations, preserved in either parallel longitudinal sets or slightly radiating groups, which are informally referred to here as 'guitar strings' (Fig. 15d–f). Striations are sub-mm in width, ranging from less than 0.1 mm up to 0.7 mm, and comprise approximately two to three size orders. Parallel striations are regularly spaced 0.1-2.0 mm apart. Sets span 3.5-188 mm in length (incomplete) and 0.6-40 mm in width, and may occur as both single- and double-parallel striation arrays. In some Swartpunt specimens, arrays are preserved in walls of higher-relief cylinders (see e.g. Fig. 15e). Smallest-scale striations average 0.075 mm in width, are preserved as densely packed thatch or in isolation, and possibly taper at termini. Thatch orientation varies but may lie transverse to larger striation arrays. "Vein"-like ridges, 0.5-7.5 mm-wide, co-occur with striation sets in Swartpunt fossils, either bounding parallel arrays or lying obliquely over/under smaller-scale structure. Veins are rectilinear to sub-cylindrical, and unlike striation arrays, cylindrical veins may show gentle curvature or deformation. Commonly, veins bounding parallel arrays form 2-4 cm-wide and up to 28 cm-long rectangular tracts. Some veins are themselves striated, indicating that they are constructed of bundles of the smaller cylindrical units.

Although the generation of subparallel, rectilinear ridges and grooves on bed surfaces by erosional flow has been demonstrated experimentally (e.g. Allen, 1969), several factors argue against a mechanical interpretation for these structures. First, overlapping arrays of parallel striations comprise multiple size orders and orientations, and exhibit no destruction that would be expected if directional shift in flow resulted in cross-cutting grooves. Second, striations do not bifurcate or re-join, as would be expected from erosional features (Allen, 1969). These factors, alongside the scale and regularity in striation spacings, suggest a biological, rather than mechanical origin. Savazzi (2015) illustrated a wide variety of Eophyton-type tool marks with broadly similar patterns of grooves, although these are overwhelmingly preserved in obvious furrows and commonly exhibit cross-cutting relationships (unlike the vast majority of 'guitar string' structures preserved in the Spitskop). Given that a number of Cambrian sponges possess parallel longitudinal spicule arrays (see e.g., Finks and Rigby, 2004), we tentatively interpret the <0.1 mm striations and parallel-arrayed sub-cylindrical striations as sponge monaxon spicules and larger spicule rods, respectively. Further, the regular sub-mm spacing of striations indicates binding by organic tissue, and we thus suggest that the longitudinal parallel arrays may represent sponge wall fragments. As such, the 'guitar strings' preserved in the Spitskop Member and in late Ediacaran deposits elsewhere may represent sponge biofabrics. An interpretation for these structures as tool marks is, however, still plausible, and thus further work will be required to establish the biogenicity of these structures beyond reasonable doubt.

4.3.5. *Circular bumps*

Among the most problematic structures found by our team in the Nama Group are medium-sized (3-5 mm in diameter) circular impressions that are commonly densely packed on bed tops (Fig. 15h-k). These possess a raised rim around a central depression, in the center of which is a raised 'bump', which itself can possess a small central depression ~0.5-1 mm in diameter. Similar structures have been occasionally referred to as *Skolithos* (e.g. Crimes and Germs, 1982). When found in large numbers, these structures can commonly appear paired (much like the *Bergaueria* and *Conichnus* described above). However, the structures here are distinguished from such ichnogenera in having a much more consistent size and appearance (for example, never preserved as epirelief 'bumps'). These circular bumps are also typically much bigger than the Intrites that are common in the Nasep-Huns transition, which also do not sit in a central depression.

Thus far, our group has almost exclusively found these structures in white quartzite units belonging the Kuibis Subgroup where it is exposed on Farm Hansburg (which on the basis of recent chemostratigraphic work, likely belong to the Kliphoek Member; Maloney et al., 2020), although similar (but less well-preserved) examples were also found in Kuibis quartzites on farms Kuibis and Tsachanabis. The circular structures occur towards the top of the quartzite units (2-3 m below beds containing *in-situ Ernietta* – see Gibson et al., 2019; Maloney et al., 2020), in thinner beds that also possess reddish and pitted areas that may indicate the influence of microbial mats. Due to extensive recrystallization, few specimens retain any trace of vertical structure; however, in the original material collected by Crimes and Germs (1982), a series of vertical pipe-like structures can be seen joining surface depressions with features several centimeters into the subsurface (Fig. 15l). The consistent width and angle of these 'pipes' along their length make identification as either water-/gas-escape structures unlikely, and thus these structures remain perhaps the strongest candidates for vertically-oriented burrows in the Ediacaran portions of the Nama. However, the possibility that these structures represent the rooting structures of body fossils that were originally anchored in the sediment requires thorough testing before comparisons with *Skolithos* and other bioirrigative structures can be made.

4.3.6. *Kullingia*

Several localities in the Nama Group, most notably the Vingerbreek Member (Zaris Sub-basin), and siliciclastic horizons near the top of the Spitskop Member of the Urusis Formation (Witputs Sub-basin), preserve bed-parallel 'scratch circles' consisting of multiple, concentrically-arranged impressions in the sediment (see Fig. 15g). Although they bear some resemblance to the holdfast structures of frondose Ediacara biota (e.g., *Aspidella*), scratch circles can usually be distinguished on the basis of sharp, deeply-impressed ridges arranged around a raised central boss (Jensen et al., 2018). Rather than body fossils or trace fossils, they represent the wind- or current-induced rotation of a fixed organism where some portion of the organism is in contact with the sediment (Jensen et al., 2002, 2018).

4.3.7. *Aristophycus*

Aristophycus refers to bed-parallel dendritic structures where variable filaments are distally bifurcated and cross cut one another (Knaust and Hauschke, 2004; Davies et al., 2016; McMahon et al., 2017). Problematic dendritic structures are found through the Nama Group (see Fig. 15a–c), although most commonly in shallow-water facies that also preserve evidence for subaerial exposure, in particular parts of the Vingerbreek and Niederhagen members (Nudaus Formation; Zaris Sub-basin). McMahon et al. (2017) reviewed the potential interpretations of this structure, which fall within three major groups: (1) expulsion of interstitial water through burrows (Seilacher, 1982), (2) dewatering of unconsolidated sands beneath a clay seal (Knaust and Hauschke, 2004), and (3) movement of gas or water through sediment capped by microbial mats (Seilacher, 2007; Kumar and Ahmad, 2014). The absence of any associated vertical burrow allows ruling out the first interpretation in the case of the Nama structures. As in the case of the structures described by McMahon et al. (2017), a dewatering origin in connection to a microbial mat seal is inferred for the structures in the Nudaus Formation. A similar origin may be tentatively put forward for structures referred to as ?*Chondrites* from the Vingerbreek Member by Crimes and Germs (1982).

4.3.8. *Meandering tubes*

Darroch et al. (2016) described accumulations of tubular structures with closely-spaced transverse annulations from the Vingerbreek Member (Schwarzrand Subgroup) north of Zebra River which they tentatively identified as the body fossil *Shaanxilithes ningqiangensis*, broadly based on a comparison of tube widths (Fig. 17). However, these fossils also bear passing resemblances to *Palaeopascichnus minimus*, a likely protozoan (Seilacher et al., 2005; Antcliffe et al., 2011).

Shaanxilithes, represented by a sole species, *S. ningqiangensis*, is a ribbon-like body fossil, ranging in width from sub-mm-scale up to nearly 15 mm, composed of closely spaced, potentially stacked, discoidal, lensoidal, or crescentic segments (Meyer et al., 2012; Tarhan et al., 2014; Darroch et al., 2016). Taphonomically, *Shaanxilithes* is preserved either as carbonaceous compressions (Tarhan et al., 2014) or via aluminosilicate templating (Meyer et al., 2012). In either taphonomic style, *Shaanxilithes* can be densely aggregated on bedding surfaces, appearing as long, winding ribbons that can overlap and/or disarticulated clusters of discs (Meyer et al., 2012), although it rarely exhibits significant three dimensionality. The winding or meandering appearance of the transversely annulated fossils from the Vingerbreek Member might be grossly comparable to *Shaanxilithes*, but the thin, repeating, discoidal structures typical of *Shaanxilithes* differ from what is observed in the Vingerbreek specimens, which instead have evenly-spaced straight ridges along a ribbon-like trough. The common disarticulated discs associated with *Shaanxilithes* are also absent from these Vingerbreek samples.

While it may have the appearance of a trace fossil, *Palaeopascichnus* is an Ediacaran body fossil consisting of a series of latitudinal segments preserved as flattened and curved-to-crescent shaped chambers (Jensen, 2003; Shen et al., 2007; Antcliffe et al., 2011). *Palaeopascichnus* is represented by four species, *P. delicatus*, *P. linearis* (inc. *P. sinuosus*), *P. meniscatus*, and *P. minimus* (Shen et al., 2007; Antcliffe et al., 2011; Kolesnikov et al., 2018), and likely grew through accretion of individual segments or chambers (Kolesnikov et al., 2018), although the arrangement of these chambers may be inconsistent throughout growth of the organism. Of the four described species, *P. minimus* is the smallest, is non-branching, maintains a fairly constant chamber width, and has the simplest overall morphology (Shen et al., 2007) – which may be most comparable of the genus to the Vingerbreek meandering tubes. Tubes of *P. minimus* are less than 0.7 mm in width and have total lengths of less than 10 mm, with individual chambers being up to 0.2 mm in thickness (Shen et al., 2007). As with *Shaanxilithes*, similarities between the Vingerbreek tubes and *Palaeopascichnus* dominantly lie within the gross ribbon-like morphology of the fossils. Unlike all species of *Palaeopascichnus*, the "chambers" of the Vingerbreek tubes are instead a series of straight ridges, with the major ridge axis perpendicular to the ribbon length, and the ridges maintaining separation (terminating at the fossil edge) instead of joining to form walls of individual chambers. Some of these apparent disparities, however, may come from differences in preservation (i.e., flattened impressions of chamber walls in White Sea-aged examples, as opposed to the three-dimensional preservation, potentially 'chamber-fill', seen here), and so further investigation is warranted.

In summary, the tubular fossils described by Darroch et al. (2016) from the Vingerbreek Member bear superficial similarities to *Palaeopascichnus*, but possess key characteristics that preclude identification as such. At present, these fossils can be best interpreted as body fossils belonging to tubular and annulated organisms. This interpretation is supported by the presence of overlapping (rather than crosscutting) relationships, and rare instances where ridges are oriented at an oblique angle to the tube margin, suggesting that individual annuli may have 'slipped' in the process of decay and disarticulation (Fig. 17c), similar to that described by Cai et al. (2013). However, these fossils also bear some notable dissimilarities with *Shaanxilithes*, and so it seems likely that they represent a new taxon, requiring more in-depth investigation.

5. Discussion

5.1. *Ediacaran ichnodiversity and ichnodisparity in the Nama Group*

In both sub-basins, the Ediacaran trace fossil record of the Nama

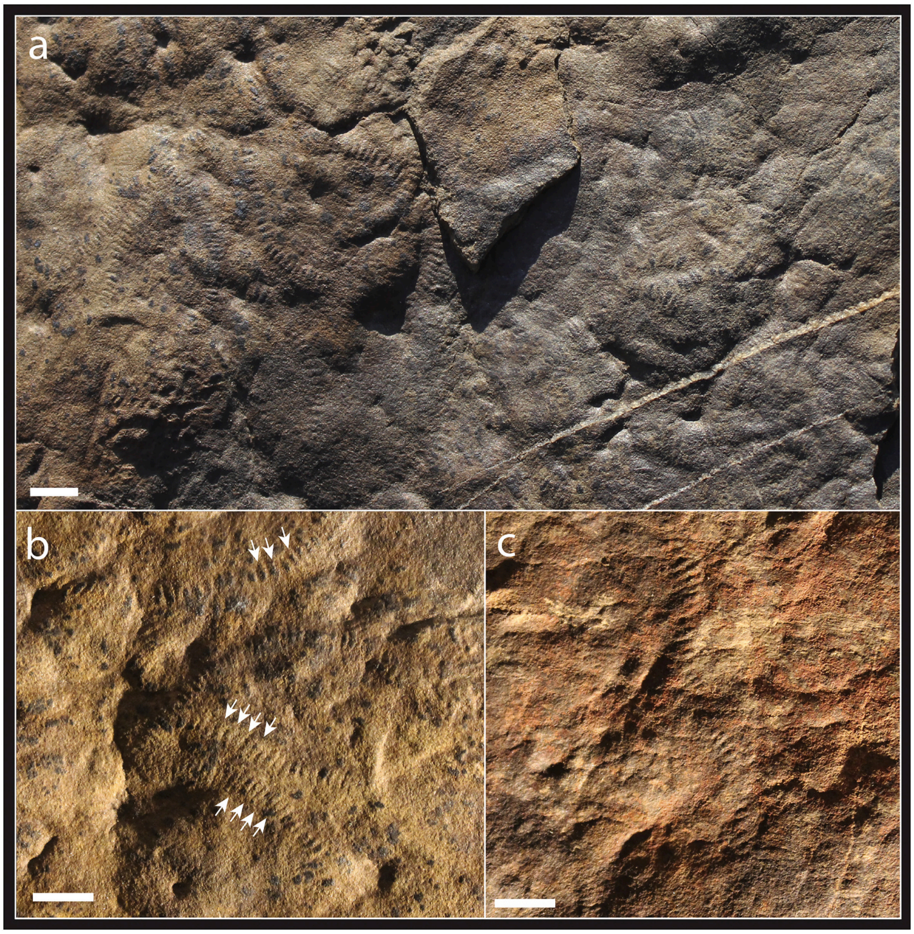

Fig. 17. a–c) Meandering and annulated tubes from the Vingerbreek Member, Zaris Sub-basin. Although these fossils bear passing resemblance to the likely protozoan body fossil *Palaeopascichnus*, they possess features that are incompatible with this taxon; note in particular the straight ridges defining annuli (arrowed in b) that maintaining separation rather joining to form walls of individual chambers, and overlapping, but not crosscutting relationships (typical of body fossils). In c), note where annuli are oriented at an oblique angle to the tube margin, suggesting that individual annuli may have 'slipped' in the process of decay and disarticulation, similar to that described by Cai et al. (2013). All fossils preserved on bed underside. Scale bars 1 cm.

Group preserves a progression from simple plug-shaped burrows with a variety of internal fabrics (potentially representing actinian cnidarians – see Mata et al., 2012; Darroch et al., 2016), into simple horizontal burrows produced by bilaterians within ~1 cm of the sediment-water interface (including undermat mining), and finally more complex burrows preserving evidence of systematic feeding behaviors, and/or vertical disruption of the sediment-water interface (see also Cribb et al., 2019). As yet, our group has found no unequivocal evidence for mid- to deep-tier domichnia (for example, *Skolithos* and *Diplocraterion*) below the Cambrian-aged Nomtsas Formation, and previous reports of these ichnotaxa from the Ediacaran portions of the Nama Group seem likely to represent either paired *Conichnus/Bergaueria* (see e.g., Fig. 5), individual treptichnid probes (e.g., Fig. 13), or potentially even the attachment sites of tubular body fossils, supporting suggestions made by Crimes and Fedonkin (1996), Jensen (2003), and Jensen et al. (2006) (although we also note that several problematic structures, in particular the 'circular bumps' found in the Kliphoek Member, deserve more in-depth analysis). This revised ichnostratigraphy brings the Nama Group into line with many other late Ediacaran to Cambrian-aged successions worldwide (e.g., Jensen, 2003; Mángano and Buatois, 2017), including those recorded from Newfoundland (Crimes and Anderson, 1985; Narbonne et al., 1987; Buatois et al., 2014; Herringshaw et al., 2017; Gougeon et al., 2018; Laing et al., 2019), NW Canada (Carbone and Narbonne, 2014), Argentina (Buatois and Mángano, 2004, 2012b) and Norway (Banks, 1970; Högström et al., 2013; McIlroy and Brasier, 2017; Jensen et al., 2018). More importantly, the succession of behavioral complexity is similar to what has been reported from NW Canada (Carbone and Narbonne, 2014), with a variety of horizontal to oblique grazing and deposit-feeding trace fossils (including both 2D and 3D avoidance) appearing in the late Ediacaran prior to the FAD of *T. pedum*. The principal differences between the Ediacaran succession observed in the Nama Group and coeval sections worldwide are: 1) the early appearance, size, and abundance of treptichnids (see in particular those from the Nasep-Huns transition, and the base of the Spitskop Member – Figs. 9 and 13); and 2) the presence of irregular 'network' traces (see Section 4.2.7 above). Even if the existence of Ediacaran *Skolithos* and *Diplocraterion* is not supported, this revised ichnostratigraphy of the Nama Group thus extends the ranges of some key metazoan behaviors and ichnotaxa below the Ediacaran-Cambrian boundary (Fig. 18).

The Zaris and Witputs Sub-basins contain markedly different trace fossil assemblages; whereas trace fossils are abundant and diverse throughout the Witputs succession (specifically, above the Kliphoek Member), they are comparatively rare in the Zaris Sub-basin, with many of the localities that our group examined possessing none at all. In particular, many of the more energetically costly and complex traces (for example, treptichnid-type burrows) are apparently absent in the Zaris. This discrepancy mirrors the distribution of soft-bodied Ediacara biota in the region, which are also comparatively rare in the Zaris (although not entirely absent – see Fig. 3g-k). This disparity can potentially be explained in terms of the redox conditions inferred to have been operating in each basin. Although iron speciation data suggest that redox conditions were highly dynamic in both the Zaris and Witputs (with persistent oxygenation mostly present in mid-ramp settings during transgressive systems tracts – see Wood et al., 2015), the Zaris Sub-basin is thought to have been less persistently oxygenated, possibly driven by upwelling anoxic ferruginous deep water (Wood et al., 2015; Bowyer et al., 2017). Both Wood et al. (2015) and Tostevin et al. (2016) also noted a general trend of increasing oxygenation throughout the stratigraphic columns of both sub-basins, which may represent an overriding control on biological activity in the region. Therefore, although

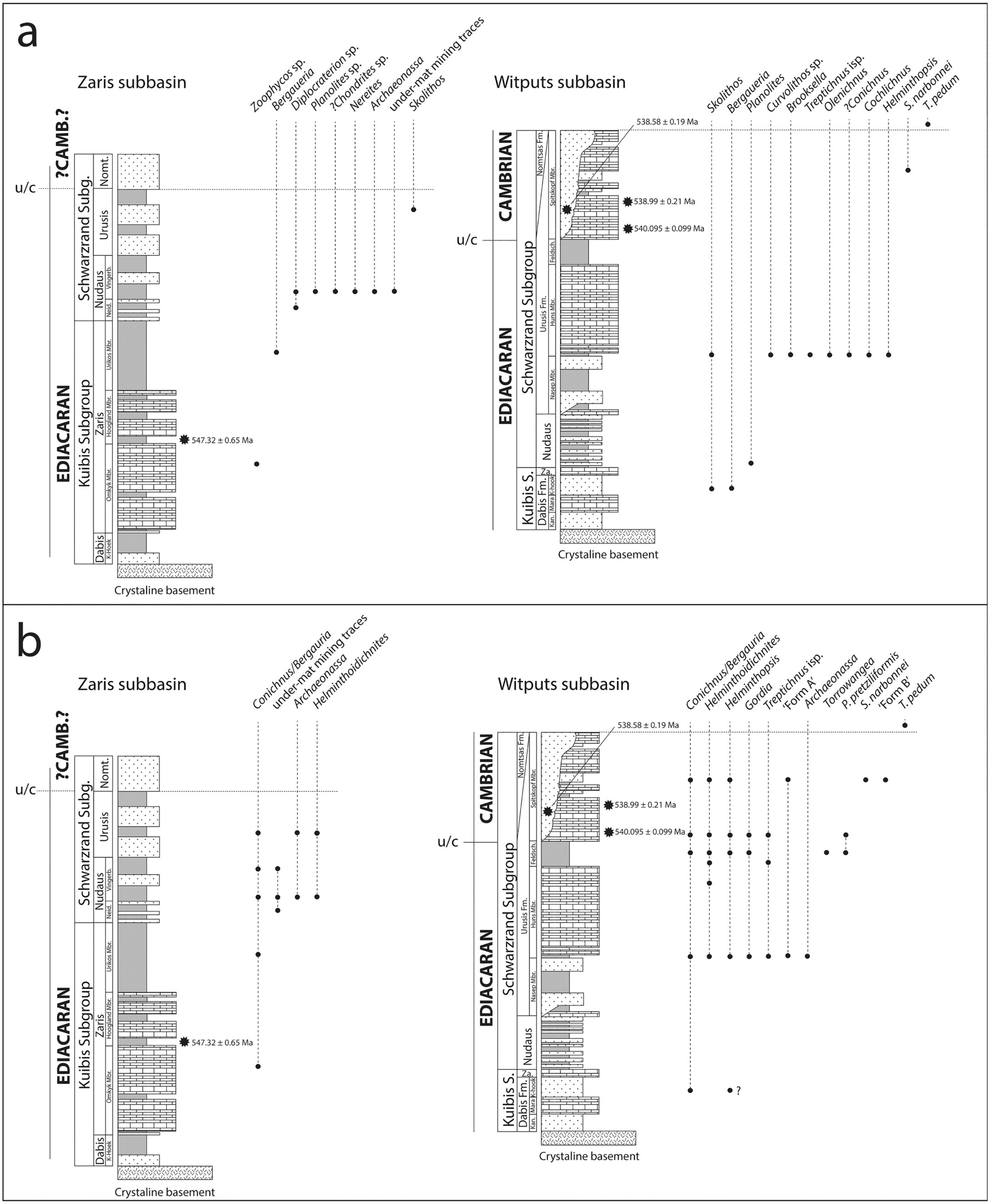

Fig. 18. Top panel: a) ichnostratigraphy of the Nama Group as compiled from Crimes and Germs (1982), Germs (1972b, 1995), Jensen et al. (2000), Jensen and Runnegar (2005); Bouougri and Porada (2007), and Macdonald et al. (2014). Bottom panel: b) revised ichnostratigraphy of the Ediacaran portions of the Nama Group, based on both a critical appraisal of the literature, and our own field investigations. 'u/c' = unconformity.

stratigraphic trends in trace fossil diversity, complexity, and bioturbation intensity plausibly represents a genuine evolutionary signal (e.g., Cribb et al., 2019), the differences in paleontological content between sub-basins illustrate that this signal may be modulated by spatial and temporal trends in ocean redox conditions. However, we also note that alternative explanations involving (for example) different paleoenvironments and associated taphonomic potentials also require testing.

5.2. Proximal-distal trends

The diversity of paleoenvironments preserved in the Nama Group allows for a preliminary description of proximal-distal trends, and an opportunity to address the question of precisely *where* complex burrowing behaviors were appearing in the terminal Neoproterozoic, and thus whether there were paleoenvironmental and/or -ecological influences on bilaterian evolution.

Trace fossil assemblages in the Nama Group are unusual in context of the late Ediacaran, not just for the diversity and complexity of traces that have been described, but also in that multiple ichnotaxa can often be found in close association on the same slab. Two horizons in the Witputs Sub-basin where this is particularly true are the Nasep-Huns transition, and the base of the Spitskop Member. Both these stratigraphic horizons host unusually dense and diverse trace fossil communities (in places with 3+ different bilaterian behaviors represented – see Fig. 19), and mark pronounced increases in alpha ichnodiversity. Interestingly, both localities record relatively shallow and high-energy environments. In the vicinity of the Fish River, the Nasep Member is 8-20 m thick and divided into distinct units – well-sorted, massive to planar-bedded sandstone at the base (suggesting deposition by strong, sediment-laden currents), and which are overlain by grey-green siltstone with local hummocky cross-bedding and symmetric and quasi-symmetric ripples, representing alternation of storms and suspension fallout below fair-weather base during a transgressive event (Grotzinger and Miller, 2008). The overall paleoenvironment for this sequence is interpreted as fluvial to wave-dominated shallow-marine (Germs, 1983; Grotzinger and Miller, 2008). High-energy transport is consistent with the presence of abundant tool marks, current-aligned tubular body fossils, and gutter casts. Oscillatory flows are indicated by hummocky cross-stratification, and the symmetric and quasi-symmetric ripples, which are suggestive of waves and combined flows, respectively. The base of the Huns Member is marked by 10-40 cm of pebbly, very coarse- to coarse-grained sandstone with large-scale ripples, which are subsequently overlain by ~260 m of interbedded platform limestone and shale (Grotzinger and Miller, 2008). Similarly, the base of the Spitskop Member at Koelkrans Camp is composed of current-ripple cross-laminated, micaceous, siltstone and very fine- to fine-grained sandstone that preserve abundant tool marks and primary current lineation, and pass upwards to cross-bedded very fine- to medium-grained sandstone with reactivation surfaces and superimposed ripples that are interpreted as representing subtidal dunes formed by strong tidal currents (Buatois et al., 2018), and also record part of a transgressive systems tract and relative deepening (Grotzinger and Miller, 2008). These clastic horizons are then overlain by >100 m of alternating siliciclastics and ramp limestone, the uppermost of which are preserved on Farm Swartpunt.

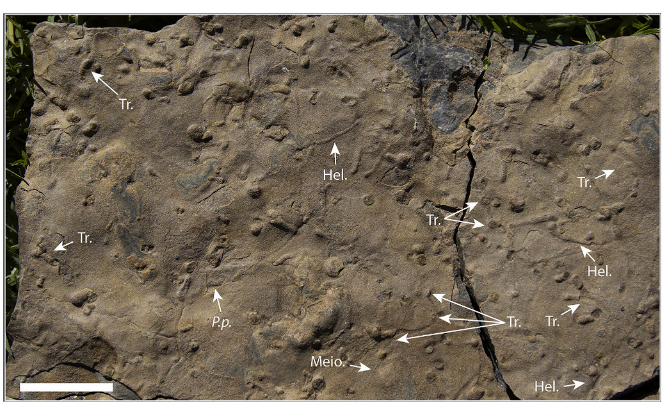

Fig. 19. Slab preserving a moderately diverse assemblage of trace fossils from the base of the Spitskop Member (Urusis Formation) collected from the vicinity of the Fish River. View is of slab underside, broken along the plane of a thin (sub-cm scale) sand drape separating 2-3 cm-thick limestone beds. '*Hel.*' – *Helminthoidichnites*; 'Meio.' – meiofaunal traces resembling 'Form A' found lower in the stratigraphy; '*P.p.*' – *Parapsammichnites pretzeliformis* briefly exposed between sandstone laminae, showing characteristic bilobate structure; 'Tr.' – abundant treptichnid-type traces preserved in a variety of styles, including as a characteristic semicircle of probes (far right; see also Fig. 13g), and as individual probes (top left), in places showing branching off a central master burrow (e.g., lower right, far left). Remnants of the central burrow between individual probes can be clearly seen. View is of bed underside. Scale bar 5 cm.

The two most diverse trace fossil assemblages (and also those that record the most complex behaviors and among the largest trace widths) in the Nama Group occur in transgressive settings below fair-weather wave base (but above storm wave base), characterized by the alternation of high-energy episodes (e.g. during storms) and low-energy background conditions. This could certainly be coincidence (or represent a preservational bias), but could also hint at paleoenvironmental and ecological controls, and support a general evolutionary proximal-distal trend in the appearance of new bilaterian behaviors and intensity of infaunal activity (see e.g., Buatois et al., 2020). For example, Wood et al. (2015) noted that persistent oxygenation in the Nama basin is primarily associated with transgressive systems tracts, suggesting that ventilation of the water column took place during relative sea-level rises, whereas limited accommodation during highstand systems tracts resulted in episodic oxygenation. In this light, pulses of oxygenation into the Witputs basin could have facilitated the evolution of more diverse and energy-intensive behaviors, which would then have spread into deeper water later in the Phanerozoic (e.g. Crimes and Fedonkin, 1994). A general proximal-innovation, distal-archaic pattern in Paleozoic benthic ecosystems was first noted by Jablonski et al. (1983), and potentially explained either in terms of shallow-marine clades being more extinction resistant (increasing the probability that innovations persist long enough to diversify and spread into distal environments), or shallow-marine environments being more temporally and spatially variable, and thus more conducive to the development of evolutionary novelties (Jablonski et al., 1983; Bottjer et al., 1996; Mata et al., 2012). Alternatively, shallow water environments would also be subject to a much higher degree of mechanical mixing with the atmosphere due to wave action, and would therefore be more highly oxygenated. Lastly, there would also be more organic carbon in offshore settings, and increased food availability likely would have allowed for more energy-intensive complex bioturbation behaviors, particularly for deposit feeding tracemakers (Dunne et al., 2007; Sperling and Stockey, 2018). Regardless of the driving mechanism, several studies have since noted that both new behaviors and increases in the intensity of bioturbation typically moved from proximal to distal settings through the Paleozoic, indicating that the evolutionary innovations responsible first appeared in relatively shallow water, before expanding into deeper water settings (Droser, 1987; Droser and Bottjer, 1989, 1993; Crimes and Fedonkin, 1994, 1996; Mángano and Buatois, 2014; Buatois et al., 2009, Buatois et al., 2020).

Viewed in this light, the first appearance of diverse tracemaking communities (and key new behaviors, such as treptichnid-type burrowing) in shallow-marine settings may represent the Ediacaran origins of a key Phanerozoic macroevolutionary and macroecological trend. Lastly, given that complex, multicellular (if not necessarily metazoan) communities first flourished in deepwater environments before moving into the nearshore (Boag et al., 2018), the emergence and proximal-distal migration of more complex bilaterian behaviors would illustrate that modern marine benthic ecosystems owe their existence to two separate evolutionary cradles (although we note that the degree to which Avalon-aged Ediacara biota are related to Metazoa is still debated).

5.3. Ecosystem engineering, and implications for drivers of the Ediacaran-Cambrian transition

In context of the Ediacaran-Cambrian transition and a putative 'biotic replacement' model for the extinction of soft-bodied Ediacara biota, a key question is: to what extent might the trace fossils and metazoan behaviors preserved in the Nama Group represent agents of geobiological change, and/or a source of ecological stress for Ediacaran organisms? Application of the 'Ecosystem Engineering Impact' values ('EEIs' of Herringshaw et al., 2017) to the Nama Group showed relatively high values in the Witputs Sub-basin for the Nasep-Huns transition (Fig. 15b; see also Cribb et al., 2019). However, this approach has been criticized based on the fact that overlap of functional group (e.g. epifaunal bioturbators, surficial modifiers) with tiering position may lead to distortions in the final estimation of ecosystem engineering effects (Mángano and Buatois, 2020; Buatois et al., 2020). The problem of redundancy may be particularly serious in the case of Ediacaran ichnofaunas, which are dominated by epifaunal and very shallow infaunal organisms, leading to overestimations of the actual impact of ecosystem engineers. Regardless of these metrics, how these activities may have impacted communities of Ediacara biota is an under-explored topic in studies discussing putative mechanisms of biotic replacement (Darroch et al., 2018a).

As mentioned above, bioturbation is a crucial ecosystem process that can have profound geobiological effects, including in oxygenating the water column, altering pore water redox chemistry, reducing sediment stability, and in the cycling of marine nutrients. Many of these effects are associated with strong positive feedbacks – for example, the advent of vertical sediment penetration would have led to the mixing of both oxygen and labile organic matter into the subsurface, creating new ecospace and encouraging deeper and more intense bioturbation (McIlroy and Logan, 1999). As a result, although the treptichnid-type traces present in the Nasep-Huns transition (for example) are small and relatively shallow, they may represent the trigger for runaway ecological feedbacks encouraging deeper and more systematic exploitation of the sediment, and limited only by organism physiology, and the rate at which adaptations for more efficient feeding and burrowing can evolve. It may thus be the case that the first appearance of new burrowing behaviors (and their associated ecosystem engineering impacts) is as, if not more, important than their initial size, depth, or abundance. Additionally, the recognition of meiofaunal trace fossils which, at least locally, occur in higher densities has significant implications for our understanding of evolution of the sediment mixed layer. Meiofauna are important ecosystem components in modern oceans, significantly modifying the chemical, physical and biological properties of the sediment even when macrofauna are absent (e.g. Schratzberger and Ingels, 2018). The extent to which they may have aided colonization of the sediment by macroinfauna, or have influenced environmental conditions affecting the life or preservation of the soft-bodied Ediacara biota, requires more in-depth investigation.

In terms of the specific ichnotaxa recorded here, trace fossils in the Nama Group predominantly represent an increase in biomixing intensity, rather than an increase in bioirrigation intensity. In the Zaris Sub-basin, for example, most trace fossils represent horizontal sediment mixing behaviors, such as *Archaeonassa, Helminthoidichnites,* and undermat mining traces, which tend to be present in bedding planes with relatively high density of trace fossils (Cribb et al., 2019). Such trace fossils represent behaviors that are effective at mixing solid sediment particles but are less effective at solute mixing. Critically, these biomixing behaviors results in the downward transport of reactive organic matter, stimulating anaerobic pathways such as denitrification, manganese-reduction, iron-reduction, and sulfate-reduction (Aller, 1977), thereby increasing the production of N_2, Mn^{2+}, Fe^{2+}, and H_2S in the sediment above the methanogenesis zone (e.g., Thamdrup et al., 1994). However, the extent to which biomixing behaviors increase the depth of organic matter remineralization is dependent on the depth of bioturbation, and horizontal trace fossils in the Zaris Sub-basin do not represent deep sediment mixing. Nevertheless, even very shallow biomixing without contemporaneous and nearby bioirrigation behaviors to re-supply microbially-consumed oxygen in the sediment could have actually led to a shallowing of oxygenated sediment layers. Plug-shaped burrows, such as *Conichnus*, may in fact represent the earliest bioirrigation behaviors in this basin. Following the interpretation that *Conichnus* and other plug-shaped burrows represent dwelling, resting, and escape traces of actinia (Pemberton et al., 1988; Mata et al., 2012), these trace fossils likely represent suspension feeders, which typically need to ventilate their burrows while feeding in order to keep up with physiological food demand (Christensen et al., 2000; Kristensen et al., 2012). The *Conichnus/Bergaueria* tracemakers may thus have contributed to the flushing out of any reduced compounds (such as sulfide and ammonium) in the sediment via advective forcing across the burrow wall-water interface, and up through the porous coarse sediment (Kristensen et al., 2012). However, we note that these trace makers were quite small, so their physiological demands for food were likely low and thus their feeding behaviors would not have resulted in nearly the same level of bioirrigation as observed for modern suspension feeders. In this regard, it is worth noting that Cambrian representatives of plug-shaped burrows are typically much larger and deeper than their Ediacaran counterparts (e.g. Pemberton and Magwood, 1990; Mata et al., 2012), suggesting an increase in irrigation levels.

A similar pattern occurs in the Witputs Sub-basin. Horizontal trace fossils like *Helminthoidichnites, Helminthopsis, Gordia, Cochlichnus, Archaeonassa,* and *Parapsammichnites* represent biomixing behaviors with little to no solute mixing component. The presence of *Parapsammichnites pretzliliformis* in the Spitskop Member is significant for the Witputs Sub-basin benthic ecosystems, though, as coelomic-grade sediment bulldozing behaviors (Buatois et al., 2018), record a much more intense biomixing behavior than those represented by the smaller horizontal trace fossils. *P. pretziliformis* tracemakers could have therefore mixed more organic matter deeper into the sediment, increasing oxygen consumption even more intensely than smaller tracemakers earlier in the Witputs and Zaris sub-basins. However, the Witputs Sub-basin is also unique in the early appearance and size of treptichnids, as well as the early appearance and widespread occurrences of plug-shaped burrows such as *Conichnus*. Bioirrigation behaviors, therefore, are more widely represented and occur earlier in the Witputs Sub-basin, and thus seafloor sediments are more likely to have been oxygenated to a deeper depth than in coeval Zaris Sub-basin sediments. The eventual appearance of *T. pedum* in the Witputs Sub-basin represents styles of animal-sediment interaction that, despite being dominantly horizontal biomixing behaviors, would have resulted in at least minor solute mixing between sediment porewaters and the overlying water by consequence of moving between the sediment-water interface and the deeper sediment. In either of these behaviors, increased solute mixing between the sediment and oxygenated overlying waters could have both increased the depth of oxygen penetration into the sediment, stimulating aerobic respiration, and flushing out reduced species, such as hydrogen sulfide (Banta et al., 1999; van de Velde and Meysman, 2016). This in turn could have facilitated colonization of the sediment by organisms more sensitive to pore-water oxygenation.

This escalation in both the diversity and intensity of bioturbation could plausibly have a number of downstream impacts on benthic marine organisms (see also Buatois et al., 2018, and Cribb et al., 2019). First, increasing bioturbation intensity and depth of burrow penetration would have led to at least partial removal of microbial matgrounds, altering the rheological properties of the sediment–water interface and leading to the formation of less firm substrates. This could potentially represent a severe source of ecological stress for Ediacaran organisms that require matgrounds for either attachment (e.g., frondose Ediacaran taxa possessing holdfasts) or a source of nutrients (e.g., *Dickinsonia*). Second, the presence of infaunal deposit-feeders, particularly represented by large trace fossils, such as *Parapsammichnites*, can have detrimental effects on benthic suspension feeders. Disrupting the sediment–water interface can inhibit the settlement of larvae and re-suspend sediment in a way that can 'clog' the feeding apparatus of suspension-feeding organisms positioned in the water column ('trophic group amensalism', see Rhoads and Young, 1970; Buatois et al., 2018). Third, it is possible that some of the bilaterian trace fossils preserved in the Nama Group represent the movement of predators (priapulid worms, which are frequently claimed as the producers of treptichnids, are overwhelmingly predatory), representing a new ecological pressure on soft-bodied Ediacara biota. Lastly, the evolution of bioturbation has long been linked to state shifts in global biogeochemical cycles. Perhaps most critically, bioturbation is shown to increase phosphorus relative to carbon in organic matter (Aller, 1994). Because phosphorus is generally the limiting nutrient for oxygen production in organic matter degradation, increased bioturbation has been shown to have potentially driven global anoxia (Boyle et al., 2014; van de Velde et al., 2018). Although the Nama Group trace fossil record represents the work of small and shallow bioturbators, van de Velde and Meysman (2016) showed through diagenesis modeling that shallow bioturbation can result in significant biogeochemical impacts. Thus, bioturbation itself could have resulted in dynamic redox conditions on the Ediacaran seafloor, stimulating evolutionary innovation in early bioturbating Metazoa (Wood and Erwin, 2017). Moreover, if the onset of bioturbation during the Ediacaran did contribute to anoxia, even on a local scale, the resulting reduction in size of benthic habitable ecosystem (van de Velde et al., 2018) may have potentially led to (enhanced) competition between the Ediacara biota and (more motile) Metazoa.

These hypothetical ecological and biogeochemical drivers of biotic replacement bring with them predictions, which can be subjected to (albeit rudimentary) testing through looking at the identity of latest Ediacaran 'survivors' (see also Darroch et al., 2018a). The first model – removal of microbial matgrounds – would perhaps predict that mobile taxa such as the dickinsonimorphs and bilateromorphs would persist at the expense of sessile and frondose taxa, as (all other conditions being equal) they would be able to move up- or downslope following the distribution of unexploited substrate. Perhaps surprisingly the opposite seems to be true, with the latest Ediacaran Nama interval comprising an assemblage of exclusively sessile rangeomorphs, erniettomorphs and arboreomorphs, many of which (e.g., *Rangea*, *Swartpuntia*) possess holdfast structures thought to represent sophisticated adaptations to a matground lifestyle. One difficulty is the small amount of fossiliferous rock preserved from the latest Ediacaran – we may not be sampling all communities that were present at this time, exacerbated by the potential reduction in habitable environment.

The second model – re-suspension of sediment – might predict the survival of osmotrophs at the expense of low-tier suspension feeders. This prediction receives at least weak support from apparent late Ediacaran extinction patterns; the Nama interval is dominated by rangeomorphs, which are widely thought to have fed osmotrophically on the basis of modeled surface area-to-volume ratios (Sperling et al., 2007; Laflamme et al., 2009; Hoyal-Cuthill and Conway Morris, 2016), and erniettomorphs, whose tubular construction may have allowed for osmotrophy if the units were hollow or fluid-filled. Concurrently, two taxa that have been recently reconstructed as possible low-tier suspension feeders (*Tribrachidium*, *Parvancorina*; see Rahman et al., 2015; Darroch et al., 2017) are among those that apparently disappear during the first pulse of Ediacaran extinction (Darroch et al., 2018a). The early biomineralizing metazoan *Cloudina* is another potential low-tier suspension feeder that was prolific in the latest Ediacaran, but was apparently largely restricted to reef-top environments (Penny et al., 2014), and so perhaps less likely to be affected by increased turbidity – especially given the lower documented incidence of bioturbation in carbonate environments. We note, however, that the common late Ediacaran fossil *Ernietta* has also been reconstructed as a suspension feeder (Gibson et al., 2019), and so this may be inconsistent with this model. However, this taxon's growth and development was highly unusual (apparently collecting sediment within the body cavity as it grew – see Ivantsov et al., 2016), and may not have possessed the specialized feeding structures typical of many metazoan suspension feeders.

The third model – predation – is much harder to test; the appearance of mobile bilaterian bioturbators and predators would perhaps predict the survival of mobile over sessile Ediacaran taxa (which, as we note above, is inconsistent with current data); however, it is unknown to what extent soft-bodied Ediacara biota may have possessed defensive mechanisms against emerging bilaterian predators. Added to which, although predation as a feeding strategy is thought to have been present in the latest Ediacaran (Bengston and Yue, 1992; Hua et al., 2003; Schiffbauer et al., 2016), there is as yet no fossil evidence for bilaterian metazoan bioturbators preying upon soft-bodied Ediacara biota. Darroch et al. (2016) suggested that, if many of the *Conichnus/Bergaueria* which are widespread through the Ediacaran portions of the Nama Group do represent resting- or escape-traces of actinian cnidarians (e.g., Mata et al., 2012), then this might represent a proliferation in passive predation, and a severe ecological pressure on water-borne Ediacaran larvae or propagules. However, the methods by which many Ediacaran groups were reproducing and dispersing are still unclear, and so predation as a mechanism of biotic replacement remains speculative. Lastly, several authors (Crimes and Fedonkin, 1996; Darroch et al., 2016) have noted that, in the latest Ediacaran at least, trace fossils are rare or absent in most horizons containing soft-bodied Ediacara biota (although see Budd and Jensen, 2017; Tarhan et al., 2018; and Gehling and Droser, 2018, for a competing picture from the older White Sea interval), suggesting that these two broad community types may have engaged in a form of niche or environmental partitioning. If this observation is borne out by more targeted studies, then it may offer some valuable clues as to how the soft-bodied Ediacara biota and emerging Cambrian-type metazoan fauna interacted.

The final model – anoxia leading to increased competition – is similar to the predation model in that it does not carry predictions that can be easily tested. Although several studies (Wood et al., 2015; Tostevin et al., 2017) have helped to produce a basin-scale reconstruction of redox conditions through the Nama Group, and shown that the oxygenation state of the water column was likely highly variable, few studies have been done at the extreme local scale required to link bioturbation with localized anoxia. Enhanced competition may imply that a greater proportion of soft-bodied Ediacara biota and metazoan trace-makers should be found co-occurring within communities; however (and as noted above), evidence for this is equivocal, and a more detailed investigation of co-occurrence metrics is required. Lastly, the idea that metazoans may have outcompeted soft-bodied Ediacara biota for resources is interesting and (in theory) perhaps the easiest tenet of this model to test. However, extremely little is currently known about how a majority of Ediacaran groups fed and obtained nutrients. Recent work – principally involving computational fluid dynamics – has helped elucidate the feeding modes of several taxa (Rahman et al., 2015; Darroch et al., 2017; Gibson et al., 2019), and suggests that several Ediacaran groups that did not survive the first pulse of extinction may have principally functioned as low-tier passive suspension feeders. The hypothesis that a diversification and intensification in bioturbating behaviors fundamentally altered the hydrodynamic landscape of the sediment-water interface (changing the character or availability of transported organic matter at specific tiers in the water column) is thus certainly one that deserves further exploration.

Lastly, we note that there is no *a priori* reason to assume a single driver of Ediacaran extinction, especially given the now widely-held understanding that they contain multiple unrelated clades (e.g. Xiao and Laflamme, 2009) possessing different biologies and ecologies, and which would have likely responded in different ways to sources of ecological and/or environmental change. It is entirely possible that the four models here acted in concert, combined with the advent of ecological innovations through the latest Neoproterozoic (see e.g., Darroch et al., 2018a; Wood et al., 2019), resulting in a protracted transition from Ediacaran to Cambrian biotas.

6. Final considerations

The trace fossil record of the Nama Group from the Kuibis through Schwarzrand subgroups illustrates a pronounced increase in the diversity, intensity, behavioral complexity, and ecosystem engineering impact of metazoan bioturbation (Buatois et al., 2018; Cribb et al., 2019). On the basis of our field investigations, we produce a revised ichnostratigraphy for the Nama Group that describes the distribution of recently-discovered forms, removes occurrences of Ediacaran-aged deep-tier burrows such as *Skolithos* and *Diplocraterion*, and brings the trace fossil record of the Nama into much closer alignment with what is known from other Ediacaran sections worldwide. The activity represented by these trace fossils would have had a variety of geobiological effects, many of which could have had downstream impacts on communities of soft-bodied Ediacara biota. However, observed patterns of extinction and survival over the first pulse of late Ediacaran extinction are hard to ally with any one specific source of ecological stress associated with bioturbation (although this picture may obviously change, as we gain a better idea of how many soft-bodied Ediacaran taxa fed, reproduced, and interacted within communities). Consequently, although many (or all) of these mechanisms may have been in operation, a putative biotic replacement model is more likely to have been driven by some combination of these factors, rather than any single one. We also note that bioturbation is far from the only facet of metazoan ecosystem engineering likely to have been operating over the Ediacaran-Cambrian transition; filter feeders (in particular sponges) would have likely helped to oxygenate the water column (Butterfield, 2009), newly-evolved metazoans possessing guts (e.g., Schiffbauer et al., 2020) would have altered the character and particle size of bioavailable carbon, and the burgeoning Cambrian-style metazoan fauna may have competed with soft-bodied Ediacarans for a variety of resources (summarized in Erwin and Tweedt, 2012, Laflamme et al., 2013). A robust test of 'biotic replacement' may therefore require sophisticated modeling techniques, incorporating substrate stability, nutrient cycling, seawater chemistry, and a better understanding of the ecological and physiological requirements of Ediacaran organisms.

Credit author contributions

SAFD and ML designed the research ('Conceptualization'). SAFD, ATC, LAB, GJBG, JA, CGK, KMM, THB, RAR, KAT, BMG, BK, SMT and ML performed fieldwork ('Investigation'). GRO and JDS performed in-depth analysis of key specimens, while GJBG and JA provided the locations of key fossil sites ('Resources'). SAFD, JDS, EFS, HM, and ML acquired the financial support required for fieldwork ('Funding acquisition'). SAFD, ATC, LAB, ML and GJBG wrote the original draft, with CGK, KMM, BMG, HM, EFS and JDS providing reviews and edits.

Declaration of Competing Interest

The authors declare no conflicts of interest.

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References

Allen, J.R.L., 1969. Erosional current marks of weakly cohesive mud beds. J. Sediment. Petrol. 39, 607–623.

Aller, R.C., 1977. The Influence of Macrobenthos on Chemical Diagenesis of Marine Sediments. PhD thesis. Yale University, New Haven, Connecticut.

Aller, R.C., 1982. The effects of macrobenthos on the chemical properties of marine sediments and overlying water. In: McCall, P.L., Tevesz, M.J.S. (Eds.), Animal-sediment Relations: The Biogenic Alterations of Sediments. Springer, Berlin, pp. 53–102.

Aller, R.C., 1994. Bioturbation and remineralization of sedimentary organic matter: effects of redox oscillation. Chem. Geol. 114, 331–345.

Alpert, S.P., 1973. *Bergaueria* Prantl (Cambrian and Ordovician), a probable actinian trace fossil. J. Paleontol. 47, 919–924.

Amthor, J.E., Grotzinger, J.P., Shröder, S., Bowring, S.A., Ramezani, J., Martin, M.W., Matter, A., 2003. Extinction of *Cloudina* and *Namacalathus* at the Precambrian–Cambrian boundary in Oman. Geology 31, 431–434.

Antcliffe, J.B., Gooday, A.J., Brasier, M.D., 2011. Testing the protozoan hypothesis for Ediacaran fossils: a developmental analysis of Palaeopaschichnus. Palaeontology 54, 1157–1175.

Banks, N.L., 1970. Trace fossils from the late Precambrian and Lower Cambrian of Finnmark, Norway. In: Crimes, T.P., Harper, J.C. (Eds.), Trace fossils. Geological Journal Special Issue, pp. 19–34.

Banta, G.T., Holmer, M., Jensen, M.H., Kristensen, E., 1999. Effects of two polychaete worms, *Nereis diversicolor* and *Arenicola marina*, on aerobic and anaerobic decomposition in a sandy marine sediment. Aquat. Microb. Ecol. 19, 189–204.

Bengston, S., Yue, Z., 1992. Predatorial borings in late Precambrian mineralized skeletons. Science 257, 367–369.

Bertics, V.J., Ziebis, W., 2009. Biodiversity of benthic microbial communities in bioturbated coastal sediments is controlled by geochemical microniches. ISME J. 3, 1269–1285.

Boag, T.H., Darroch, S.A.F., Laflamme, M., 2016. Ediacaran distributions in space and time: testing assemblage concepts of earliest macroscopic body fossils. Paleobiology 39, 591–608.

Boag, T.H., Stockey, R.G., Elder, L.E., Hull, P.M., Sperling, E.A., 2018. Oxygen, temperature and the deep-marine stenothermal cradle of Ediacaran evolution. Proc. R. Soc. B 285. https://doi.org/10.1098/rspb.2018.1724.

Bottjer, D.J., Schubert, J.K., Droser, M.L., 1996. Comparative evolutionary palaeoecology; assessing the changing ecology of the past. In: Hart, M.B. (Ed.), Biotic Recovery from Mass Extinction Events. Geological Society of London, pp. 1–13.

Bottjer, D.J., Hagadorn, J.W., Dornbos, S.Q., 2000. The Cambrian substrate revolution. GSA Today 10, 1–7.

Bouougri, E.H., Porada, H., 2007. Siliciclastic biolaminites indicative of widespread microbial mats in the Neoproterozoic Nama Group of Namibia. J. Afr. Earth Sci. 48, 38–48.

Bouougri, E.H., Porada, H., Weber, K., Reitner, J., 2011. Sedimentology and palaeoecology of Ernietta-bearing Ediacaran deposits in southern Namibia: implications for infaunal vendobiont communities. Adv. Stromat. Geobiol. 313, 473–506.

Bowyer, F., Wood, R.A., Poulton, S.W., 2017. Controls on the evolution of Ediacaran metazoan ecosystems: a redox perspective. Geobiology 15, 516–551.

Bowyer, F.T., Shore, A.J., Wood, R.A., Alcott, L.J., Thomas, A.L., Butler, I.B., Curtis, A., Hainanan, S., Curtis-Walcott, S., Penny, A.M., Poulton, S.W., 2020. Regional nutrient decrease drove redox stabilisation and metazoan diversification in the late Ediacaran Nama Group, Namibia. Sci. Rep. 10, 2240. https://doi.org/10.1038/s41598-020-59335-2.

Boyle, R.A., Dahl, T.W., Dale, A.W., Shields-Zhou, G.A., Zhu, M., Brasier, M.D., Canfield, D.E., Lenton, T.M., 2014. Stabilization of the coupled oxygen and

phosphorus cycles by the evolution of bioturbation. Nat. Geosci. 7, 671–676. https://doi.org/10.1038/ngeo2213.
Buatois, L.A., Mángano, M.G., 1993. Trace fossils from a Carboniferous turbiditic lake: implications for the recognition of additional nonmarine ichnofacies. Ichnos 2, 237–258.
Buatois, L.A., Mángano, M.G., Buatois, L.A., 2004. Terminal Proterozoic–Early Cambrian ecosystems: ichnology of the Puncoviscana Formation, Northwest Argentina. In: Webby, B.D., Mángano, M.G. (Eds.), Trace Fossils in Evolutionary Palaeoecology. Fossils and Strata, 51, pp. 1–16.
Buatois, L.A., Mángano, M.G., 2011. The Déjà vu effect: recurrent patterns in the exploitation of ecospace, the establishment of the mixed layer, and the distribution of matgrounds. Geology 39, 1163–1166.
Buatois, L.A., Mángano, M.G., 2012a. The trace-fossil record of organism-matground interactions in space and time. In: Noffke, N., Chafetz, H. (Eds.), Microbial Mats in Siliciclastic Sediments, 101. SEPM Special Publication, pp. 15–28.
Buatois, L.A., Mángano, M.G., 2012b. Ichnology of the Ediacaran-Cambrian Puncoviscana Formation of northwest Argentina: recent progress in understanding its potential in paleoecology and macroevolution. In: Netto, R.G., Carmona, N.B., Tognoli, F.M.W. (Eds.), Ichnology of Latin America, Selected Papers. Monografias da Sociedade Brasileira de Paleontologia, 2, pp. 27–36.
Buatois, L.A., Mángano, M.G., 2016. Ediacaran ecosystems and the dawn of animals. In: Mángano, M.G., Buatois, L.A. (Eds.), The Trace-fossil Record of Major Evolutionary Events, Topics in Geobiology, 39. https://doi.org/10.1007/978-94-017-9600-2_2.
Buatois, L.A., Mángano, M.G., Maples, C.G., Lanier, W.P., 1998. Ichnology of an Upper Carboniferous fluvio-estuarine paleovalley: the Tonganoxie Sandstone, Buildex Quarry, eastern Kansas, USA. J. Paleontol. 72, 152–180.
Buatois, L.B., Mángano, M.G., Brussa, E.D., Benedetto, J.L., Pompei, J.L., 2009. The changing face of the deep: Colonization of the Early Ordovician deep-sea floor, Puna, northwest Argentina. Palaeogeogr. Palaeoclimatol. Palaeoecol. 280, 291–299.
Buatois, L.A., Narbonne, G.M., Mángano, M.G., Carmona, N.B., Myrow, P., 2014. Relict ecosystems at the dawn of the Phanerozoic revolution. Nat. Commun. 5, 3544–3549.
Buatois, L.A., Wisshak, M., Wilson, M.A., Mángano, M.G., 2017. Categories of architectural designs in trace fossils: A measure of ichnodisparity. Earth-Sci. Rev. 164, 102–181.
Buatois, L.A., Almond, J., Mángano, M.G., Jensen, S., Germs, G.J.B., 2018. Sediment disturbance by Ediacaran bulldozers and the roots of the Cambrian explosion. Sci. Rep. 8, 4514. https://doi.org/10.1038/s41598-018-22859-9.
Buatois, L.A., Mángano, M.G., Minter, N.J., Zhou, K., Wisshak, M., Wilson, M.A., Olea, R. A., 2020. Quantifying ecospace utilization and ecosystem engineering during the early Phanerozoic – the role of bioturbation and bioerosion. Sci. Adv. 6, eabb0618.
Buckman, J.O., 1994. *Archaeonassa* Fenton and Fenton 1937 reviewed. Ichnos 3, 185–192. https://doi.org/10.1080/10420949409386387.
Budd, G.E., Jackson, I.S.C., 2016. Ecological innovations in the Cambrian and the origins of the crown group phyla. Proc. R. Soc. B 371. https://doi.org/10.1098/rstb.2015.0287.
Budd, G.E., Jensen, S., 2017. The origin of the animals and a 'savannah' hypothesis for early bilaterian evolution. Biol. Rev. 92, 446–473. https://doi.org/10.1111/brv.12239.
Butterfield, N.J., 2009. Oxygen, animals and oceanic ventilation: an alternative view. Geobiology 7, 1–7.
Butterfield, N.J., 2011. Animals and the invention of the Phanerozoic earth system. Trends Ecol. Evol. 26, 81–87.
Cai, Y., Hua, H., Zhang, X., 2013. Tube construction and life mode of the late Ediacaran tubular fossil *Gaojiashania cyclus* from the Gaojiashan Lagerstätte. Precambrian Res. 224, 255–267.
Canfield, D.E., Farquhar, J., 2009. Animal evolution, bioturbation, and the sulfate concentration of the oceans. Proc. Natl. Acad. Sci. USA 106 (p), 8123–8127. https://doi.org/10.1073/pnas.0902037106.
Carbone, C., Narbonne, G.M., 2014. When life got smart: the evolution of behavioral complexity through the Ediacaran and early Cambrian of NW Canada. J. Paleontol. 88, 309–330.
Christensen, B., Vedel, A., Kristensen, E., 2000. Carbon and nitrogen fluxes in sediment inhabited by suspension-feeding (*Nereis diversicolor*) and non-suspension-feeding (*N. virens*) polychaetes. Mar. Ecol. Prog. Ser. 192, 203–217.
Ciampaglio, C.N., Babcock, L.E., Wellman, C.L., York, A.R., Brunswick, H.K., 2006. Phylogenetic affinities and taphonomy of *Brooksella* from the Cambrian of Georgia and Alabama, USA. Palaeoworld 15, 256–265.
Cohen, P.A., Bradley, A., Knoll, A.H., Grotzinger, J.P., Jensen, S., Abelson, J., Hand, K., Love, G., Metz, J., McLoughlin, N., Meister, P., Shepard, R., Tice, M., Wilson, J.P., 2009. Tubular compression fossils from the Ediacaran Nama Group, Namibia. J. Paleontol. 83, 110–122.
Cribb, A.T., Kenchington, C.G., Koester, B., Gibson, B.M., Boag, T.H., Racicot, R.A., Mocke, H., Laflamme, M., Darroch, S.A.F., 2019. Increase in metazoan ecosystem engineering prior to the Ediacaran-Cambrian boundary in the Nama Group, Namibia. R. Soc. Open Sci. 6, 190548.
Crimes, T.P., 1987. Trace fossils and correlation of late Precambrian and early Cambrian strata. Geol. Mag. 124, 97–119.
Crimes, T.P., Anderson, M.M., 1985. Trace fossils from Late Precambrian-Early Cambrian strata of southeastern Newfoundland (Canada): temporal and environmental implications. J. Paleontol. 59, 310–343.
Crimes, T.P., Fedonkin, M.A., 1994. Evolution and dispersal of deepsea traces. Palaios 9, 74–83.
Crimes, T.P., Fedonkin, M.A., 1996. Biotic changes in platform communities across the Precambrian Phanerozoic boundary. Riv. Ital. Paleontol. Stratigr. 102, 317–332.
Crimes, T.P., Germs, G.J.B., 1982. Trace fossils from the Nama Group (Precambrian-Cambrian) of Southwest Africa (Namibia). J. Paleontol. 56, 890–907.
Dahms, H.-U., Dobretsov, S., Qian, P.-Y., 2004. The effect of bacterial and diatom biofilms on the settlement of the bryozoan *Bugula neritina*. J. Exp. Mar. Biol. Ecol. 313, 191–209.
Darroch, S.A.F., Sperling, E.A., Boag, T., Racicot, R.A., Mason, S.J., Morgan, A.S., Tweedt, S., Myrow, P., Erwin, D.H., Laflamme, M., 2015. Biotic replacement and mass extinction of the Ediacara biota. Proc. R. Soc. B 282. https://doi.org/10.1098/rspb.2015.1003.
Darroch, S.A.F., Boag, T., Racicot, R.A., Tweedt, S., Mason, S.J., Erwin, D.H., Laflamme, M., 2016. A mixed Ediacaran-metazoan assemblage from the Zaris Sub-basin, Namibia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 459, 198–208.
Darroch, S.A.F., Rahman, I., Gibson, B., Racicot, R.A., Laflamme, M., 2017. Inference of facultative mobility in the enigmatic Ediacaran organism *Parvancorina*. Biol. Lett. 13. https://doi.org/10.1098/rsbl.2017.0033.
Darroch, S.A.F., Smith, E., Laflamme, M., Erwin, D.H., 2018a. Ediacaran extinction and Cambrian Explosion 2018. Trends Ecol. Evol. 33, 653–663.
Darroch, S.A.F., Laflamme, M., Wagner, P.J., 2018b. High ecological complexity in benthic Ediacaran ecosystems. Nat. Ecol. Evol. 2, 1541–1547.
Davies, N.S., Liu, A.G., Gibling, M.R., Miller, R.F., 2016. Resolving MISS conceptions and misconceptions: a geological approach to sedimentary surface textures generated by microbial and abiotic processes. Earth-Sci. Rev. 154, 210–246.
de Deckere, E.M.G.T., Tolhurst, T.J., de Brouwer, J.F.C., 2001. Destabilization of cohesive intertidal sediments by infauna. Estuar. Coast. Shelf Sci. 53, 665–669.
Desai, B.G., Saklani, R.D., 2015. Palaeocommunity dynamics and behavioral analysis of *Conichnus*: Bhuj Formation (Lower Creatceous), Kachchh-India. Ichnos 22, 43–55.
Dibenedetto, S., Grotzinger, J.P., 2005. Geomorphic evolution of a storm-dominated carbonate ramp (c. 549 Ma), Nama Group, Namibia. Geol. Mag. 142, 583–604. https://doi.org/10.1017/S0016756805000890.
Droser, M.L., 1987. Trends in extent and depth of bioturbation in Great Basin Precambrian-Ordovician strata, California, Nevada and Utah. Unpublished PhD dissertation. University of Southern California, Los Angeles, California (365 pp.).
Droser, M.L., Bottjer, D.J., 1989. Ordovician increase in extent and depth of bioturbation: implications for understanding early Paleozoic ecospace utilization. Geology 17, 850–852.
Droser, M.L., Bottjer, D.J., 1993. Trends and patterns of Phanerozoic ichnofabrics. Annu. Rev. Earth Planet. Sci. 21, 205–225.
Droser, M.L., Gehling, J.G., Jensen, S., Briggs, D.E.G., 2005. Ediacaran trace fossils: true or false. In: Evolving Form and Function: Fossils and Development. Peabody Museum of Natural History.
Droser, M.L., Tarhan, L.G., Gehling, J.G., 2017. The rise of animals in a changing environment: global ecological innovation in the Late Ediacaran. Annu. Rev. Earth Planet. Sci. 45, 593–617.
Dunn, F.S., Liu, A.G., Donoghue, P.C.J., 2018. Ediacaran developmental biology. Biol. Rev. 93, 914–932.
Dunne, J.P., Sarmiento, J.L., Gnanadesikan, A., 2007. A synthesis of global particle export from the surface ocean and cycling through the ocean interior and on the seafloor. Glob. Biogeochem. Cycles 21. https://doi.org/10.1029/2006GB002907.
Elliott, D.A., Vickers-Rich, P., Trusler, P., Hall, M., 2011. New evidence on the taphonomic context of the Ediacaran *Pteridinium*. Acta Palaeontol. Pol. 56, 641–650.
Emmons, E., 1844. The Taconic System: Based on Observations in New York. Albany, Caroll and Cook, Massachusetts, Maine, Vermont and Rhode Island (68 pp.).
Erwin, D.H., Tweedt, S.M., 2012. Ecological drivers of the Ediacaran-Cambrian diversification of Metazoa. Evol. Ecol. 26, 417–433.
Erwin, D.H., Valentine, J.W., 2013. The Cambrian Explosion: the Construction of Animal Biodiversity. Roberts Publishers.
Erwin, D.H., Laflamme, M., Tweedt, S.M., Sperling, E.A., Pisani, D., Peterson, K.J., 2011. The Cambrian conundrum: early divergence and later ecological success in the early history of animals. Science 334, 1091–1097.
Fedonkin, M.A., 1980. Iskopaemye sledy dokembrijskikh metazoan, 1. Izvestia Akademiya Nauk SSSR, Seriya Geologicheskaya, pp. 39–46.
Fenton, C.L., Fenton, M.A., 1937. *Archaeonassa*, Cambrian snail trails and burrows. Am. Midl. Nat. 18, 454–456.
Fike, D.A., Grotzinger, J.P., Pratt, L.M., Summons, R.E., 2006. Oxidation of the Ediacaran ocean. Nature 444, 744–747.
Fillion, D., Pickerill, R.K., 1990. Ichnology of the Upper Cambrian to Lower Ordovician Bell Islands and Wabana groups of eastern Newfoundland, Canada. Palaeontogr. Can. 7, 119 (Ottawa).
Finks, R.M., Rigby, J.K., 2004. Palaeozoic Demosponges. In: Finks, R.M., Reid, R.E.H., Rigby, J.K. (Eds.), Treatise on Invertebrate Paleontology, Part E, Porifera, Revised, 3. Geological Society of America, University of Kansas Press, Boulder, CO, Lawrence, KS, pp. 9–171.
Frey, R.W., Howard, J.D., 1981. *Conichnus* and *Schaubcylindrichnus*: redefined trace fossils from the Upper Cretaceous of the Western Interior. J. Paleontol. 55, 800–804.
Gehling, J.G., 1999. Microbial mats in terminal Proterozoic siliciclastics: Ediacarn death masks. Palaios 14, 40–57.
Gehling, J.G., Droser, M.L., 2009. Textured organic surfaces associated with the Ediacara biota in South Australia. Earth-Sci. Rev. 96, 196–206.
Gehling, J.G., Droser, M.L., 2018. Ediacaran scavenging as a prelude to predation. Emerg. Topics Life Sci. 2, 213–222.
Gehling, J.G., Narbonne, G.M., Anderson, M.M., 2000. The first named Ediacaran body fossil, *Aspidella terranovica*. Palaeontology 43, 427–456.
Germs, G.J.B., 1972a. The Stratigraphy and Paleontology of the Lower Nama Group, South West Africa, 12. Bulletin – Chamber of Mines Precambrian Research Unit, Univeristy of Cape Town, pp. 1–250.
Germs, G.J.B., 1972b. Trace fossils from the Nama Group, South West Africa. J. Paleontol. 46, 864–870.

Germs, G.J.B., 1972c. New shelly fossils from the Nama Group, South West Africa. Am. J. Sci. 272, 752–761.
Germs, G.J.B., 1973. Possible sprigginid worm and a new trace fossil from the Nama Group, South West Africa. Geology 1, 69–70.
Germs, G.J.B., 1983. Implications of a sedimentary facies and depositional environmental analysis of the Nama Group in South West Africa/Namibia. Spec. Publ. Geol. Soc. S. Afr. 11, 89–114.
Germs, G.J.B., 1995. The Neoproterozoic of southwestern Africa, with emphasis on stratigraphy and paleontology. Precambrian Res. 73, 137–151.
Germs, G.J.B., Gaucher, C., 2012. Nature and extent of a late Ediacaran (ca.547 Ma) glacigenic erosion surface in southern Africa. S. Afr. J. Geol. 115, 91–102.
Germs, G.J.B., Gresse, P.G., 1991. The foreland basin of the Damara and Gariep orogens in Namaqualand in southern Namibia: stratigraphic correlations and basin dynamics. S. Afr. J. Geol. 94, 159–169.
Germs, G.J.B., Knoll, A.H., Vidal, G., 1986. Latest Proterozoic microfossils from the Nama Group, Namibia (south west Africa). Precambrian Res. 32, 45–62. https://doi.org/10.1016/0301-9268(86)90029-X.
Germs, G.J.B., Miller, R.M., Frimmel, H.E., Gaucher, C., 2010. Syn- to late-orogenic sedimentary basins of southwestern Africa. In: Gaucher, C., Sial, A.N., Halverson, G. P., Frimmel, H.E. (Eds.), Neoproterozoic-Cambrian Tectonics, Global Change and Evolution: A Focus on Southwestern Gondwana. Developments in Precambrian Geology, 16. Elsevier, pp. 183–203.
Getty, P.R., Hagadorn, J.W., 2008. Reinterpretation of *Climactichnites* Logan 1860 to include subsurface burrows, and erection of *Musculopodus* for resting traces of the trailmaker. J. Paleontol. 82, 1162–1171.
Getty, P.R., Sproule, R., Stimson, M., Lyons, P.C., 2017. Invertebrate trace fossils from the Pennsylvanian-aged Rhode Island Formation of Massachusetts. Atl. Geol. 53, 43–65.
Geyer, G., 2005. The Fish River Subgroup in Namibia: stratigraphy, depositional environments, and the Proterozoic-Cambrian boundary problem revisited. Geol. Mag. 14, 465–498. https://doi.org/10.1017/S0016756805000956.
Geyer, G., Uchman, A., 1995. Ichnofossil assemblages from the Nama Group (Neoproterozoic-Lower Cambrian) in Namibia and the Proterozoic-Cambrian boundary problem revisited. In: Geyer, G., Landing, E. (Eds.), Morocco 95, the Lower-Middle Cambrian Standard of Western Gondwana, 2. Beringeria, pp. 175–202.
Gibson, B.M., Rahman, I., Maloney, K., Racicot, R., Mocke, H., Laflamme, M., Darroch, S. A.F., 2019. Gregarious suspension fee,ding in a modular Ediacaran organism. Sci. Adv. 5, eaaw0260.
Glaessner, M.F., 1963. Zur Kenntnis der Nama-Fossilien Südwest-Afrikas. Annalen des Naturhistorischen Museums in Wien A 66, 113–120.
Glaessner, M.F., 1978. Re-examination of *Archaeichnium*, a fossil from the Nama Group. Ann. S. Afr. Museum 74, 335–342.
Glass, J.B., Chen, S., Dawson, K.S., Horton, D.R., Vogt, S., Ingall, E.D., Twining, B.S., Orphan, V.J., 2018. Trace metal imaging of sulfate-reducing bacteria and methanogenic archaea at single-cell resolution by synchrotron X-ray fluorescence imaging. Geomicrobiol J. 35, 81–89.
Gnilovskaya, M.B., Rozanov, A.Yu., 1983. Vendotaenides. In: Urbanek, A. (Ed.), Upper Precambrian and Cambrian Paleontology of the East European Platform. Publishing House Wydawnictwa Geologiczne, Warsaw, Poland, pp. 46–56.
Godfrey, L.V., Glass, J.B., 2011. The geochemical record of the ancient nitrogen cycle, nitrogen isotopes, and metal cofactors. Methods Enzymol. 486, 483–506. https://doi.org/10.1016/S0076-6879(11)86022-2.
Gougeon, R.C., Mángano, M.G., Buatois, L.A., Narbonne, G.M., Laing, B.A., 2018. Early Cambrian origin of the shelf sediment mixed layer. Nat. Commun. 9, 1909. https://doi.org/10.1038/s41467-018-04311-8.
Grotzinger, J.P., Miller, R., 2008. The nama group. In: Miller, R. (Ed.), The Geology of Namibia, 2. Geological Society of Namibia Special Publication, 13-229–13-272.
Grotzinger, J.P., Bowring, S.A., Saylor, B.Z., Kaufman, A.J., 1995. Biostratigraphic and geochronologic constraints on early animal evolution. Science 270, 598–604.
Grotzinger, J.P., Watters, W.A., Knoll, A.H., 2000. Calcified metazoans in thrombolite–stromatolite reefs of the terminal Proterozoic Nama Group, Namibia. Paleobiology 26, 334–359.
Grotzinger, J.P., Adams, E.W., Schröder, S., 2005. Microbial – metazoan reefs of the terminal Proterozoic Nama Group (c. 550 – 543 Ma), Namibia. Geol. Mag. 142, 499–517.
Gürich, G., 1929. Die ältesten Fossilien Südafrikas. Zeitschrift praktische Geologie mit besonderer Berücksichtigung der Lagerstättenkunde 37, 85.
Gürich, G., 1930a. Die bislang ältesten Spuren von Organismen in Südafrika. In: C.R. 15. International Geological Congress, South Africa, 1929, pp. 670–680.
Gürich, G., 1930b. Über den Kuibisquarzit in Südwestafrika. Z. Dtsch. Geol. Ges. 82, 637.
Gürich, G., 1933. Die Kuibis-Fossilien der Nama-Formation von Südwestafrika. Nachträge und Zusätze. Paläontol. Z. 15, 137–154.
Hagadorn, J.W., Bottjer, D.J., 1997. Wrinkle structures: microbially-induced sedimentary structures common in subtidal siliciclastic settings at the Proterozoic-Phanerozoic transition. Geology 25, 1047–1050.
Hagadorn, J.W., Bottjer, D.J., 1999. Restriction of a late Neoproterozoic biotope: suspect-microbial structures and trace fossils at the Vendian-Cambrian transition. Palaios 14, 73–85.
Hahn, G., Pflug, H.D., 1985. Die Cloudinidae n. fam., Kalk-Röhren aus dem Vendium und Unter-Kambrium. Senckenb. Lethaea 65, 413–431.
Hall, M., Kaufman, A.J., Vickers-Rich, P., Ivantsov, A., Trusler, T., Linnemann, U., Hofmann, M., Elliott, D., Cui, C., Fedonkin, M., Hoffmann, K.-H., Wilson, S.A., Schneider, G., Smith, J., 2013. Stratigraphy, palaeontology and geochemistry of the late Neoproterozoic Aar Member, southwest Namibia: reflecting environmental controls on Ediacara fossil preservation during the terminal Proterozoic in African Gondwana. Precambrian Res. 238, 214–232.
Han, Y., Pickerill, R.K., 1995. Taxonomic review of the ichnogenus *Helminthopsis* Heer 1877 with a statistical analysis of selected ichnospecies. Ichnos 4, 83–118.
Hanken, N.-M., Uchman, A., Nielsen, J.K., Olaussen, S., Eggebø, T., Steinsland, R., 2016. Late Ordovician trace fossils from offshore to shallow water mixed siliciclastic and carbonate facies in the Ringerike Area, Oslo Region, Norway. Ichnos 23, 189–221. https://doi.org/10.1080/10420940.2016.1199427.
Hastings, A., Byers, J.E., Crooks, J.A., Cuddington, K., Jones, C.G., Lambrinos, J.G., Talley, T.S., Wilson, W.G., 2007. Ecosystem engineering in space and time. Ecol. Lett. 10, 153–164.
Haughton, S.H., 1960. An archaeocyathid from the Nama System. Trans. R. Soc. S. Afr. 36, 57–59.
Heer, O., 1877. Florafossilis Helvetias. In: Die vorweltische flora der Schweiz. J. Wurster and Co., Zurich (182 pp.).
Herringshaw, L.G., Callow, R.T., McIlroy, D., 2017. Engineering the Cambrian explosion: the earliest bioturbators as ecosystem engineers. Geol. Soc. Lond. Spec. Publ. 448 https://doi.org/10.1144/SP448.18.
Hoffmann, H.J., 1971. Precambrian fossils, pseudofossils and problematica in Canada. Geol. Surv. Can. Bull. 189, 1–146.
Högström, A.E.S., Jensen, S., Palacios, T., Ebbestad, J.O.R., 2013. Information on the Ediacaran-Cambrian transition in the Vestertana Group, Finnmark, northern Norway, from trace fossils and organic-walled microfossils. Nor. Geol. Tidsskr. 93, 95–106.
Hoyal-Cuthill, J.F., Conway Morris, S., 2016. Fractal branching organizations of Ediacaran rangeomorph fronds reveal a lost Proterozoic body plan. Proc. Natl. Acad. Sci. 111 (p), 13122–13126.
Hua, H., Pratt, B.R., Zhang, L.Y., 2003. Borings in *Cloudina* shells: complex predator-prey dynamics in the terminal neoproterozoic. Palaios 18, 454–459.
Ivantsov, A.Y., Narbonne, G.M., Trusler, P.W., Greentree, C., Vickers-Rich, P., 2016. Elucidating *Ernietta*: new insights from exceptional specimens in the Ediacaran of Namibia. Lethaia 49, 540–554.
Jablonski, D., Sepkoski Jr., J.J., Bottjer, D.J., Sheehan, P.M., 1983. Onshore-offshore patterns in the evolution of Phanerozoic shelf communities. Science 222, 1123–1125.
Jensen, S., 1997. Trace fossils from the Lower Cambrian Mickwitzia sandstone, south-central Sweden. Fossils Strata 42, 1–111.
Jensen, S., 2003. The Proterozoic and earliest trace fossil record; patterns, problems and perspectives. Integr. Comp. Biol. 43, 219–228.
Jensen, S., Runnegar, B.N., 2005. A Complex Trace Fossil From the Spitskopf Member (terminal Ediacaran-Lower Cambrian) of Southern Namibia, 142. Geological Magazine, pp. 561–569.
Jensen, S., Gehling, J.G., Droser, M.L., 1998. Ediacara-type fossils in Cambrian sediments. Nature 393, 567–569.
Jensen, S., Saylor, B.Z., Gehling, J.G., Germs, G.J.B., 2000. Complex trace fossils from the terminal Proterozoic of Namibia. Geology 28, 143–146.
Jensen, S., Gehling, J.G., Droser, M.L., Grant, S.W.F., 2002. A scratch circle origin for the medusoid fossil *Kullingia*. Lethaia 35, 291–299.
Jensen, S., Droser, M.L., Gehling, J.G., 2005. Trace fossil preservation and the early evolution of animals. Palaeogeogr. Palaeoclimatol. Palaeoecol. 220, 19–29.
Jensen, S., Droser, M.L., Gehling, J.G., 2006. A critical look at the Ediacaran trace fossil record. In: Kaufman, J., Xiao, S. (Eds.), Neoproterozoic Geobiology and Paleobiology. Topics in Geobiology, 27, pp. 115–157.
Jensen, S., Hogstrom, A.E.S., Almond, J., Taylor, W.L., Meinhold, G., Hoyberget, M., Ebbestad, J.O.R., Agic, H., Palacios, T., 2018. Scratch circles from the Ediacaran and Cambrian of Arctic Norway and southern Africa, with a review of scratch circle occurrences. Bull. Geosci. 93, 287–304.
Johnston, D.T., Poulton, S.W., Goldberg, T., Sergeev, V.N., Podkovyrov, V., Vorob'Eva, N.G., Bekker, A., Knoll, A.H., 2012. Late Ediacaran redox stability and metazoan evolution. Earth Planet. Sci. Lett. 335, 25–35.
Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386.
Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78, 1946–1957.
Kesidis, G., Slater, B.J., Jensen, S., Budd, G.E., 2019. Caught in the act: priapulid burrowers in early Cambrian substrates. Proc. R. Soc. B 286, 20182505. https://doi.org/10.1098/rspb.2018.2505.
Kimura, H., Watanabe, Y., 2001. Oceanic anoxia at the Precambrian-Cambrian boundary. Geology 29, 995–998.
Kirchman, D., Graham, S., Reish, D., Mitchell, R., 1982. Bacteria induce settlement and metamorphosis of *Janua (Dexiospira) brasiliensis* Grube (Polychaeta: Spirorbidae). J. Exp. Mar. Biol. Ecol. 56, 153–163.
Knaust, D., 2015. Siphonichnidae (new ichnofamily) attributed to the burrowing activity of bivalves: Ichnotaxonomy, behaviour and palaeoenvironmental implications. Earth-Sci. Rev. 150, 497–519.
Knaust, D., Hauschke, N., 2004. Trace fossils versus pseudofossils in Lower Triassic playa deposits, Germany. Palaeogeogr. Palaeoclimatol. Palaeoecol. 215, 87–97.
Knox, L.W., Miller, M.F., 1985. Environmental control of trace fossil morphology. In: Curran, H.A. (Ed.), Biogenic Structures: Their Use in Interpreting Depositional Environments, 35. Society of Economic Paleontologists and Mineralogists, Special Publications, pp. 167–176.
Kolesnikov, A., Rogov, V.I., Bykova, N., Danelian, T., Clausen, S., Maslov, A., Grazhdankin, D.V., 2018. The oldest skeletal macroscopic organism *Palaeopascichnus linearis*. Precambrian Res. 316, 24–37.

Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C.O., Banta, G. T., 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Mar. Ecol. Prog. Ser. 446, 285–302.

Kumar, S., Ahmad, S., 2014. Microbially-induced sedimentary structures (MISS) from the Ediacaran Jodhpur Sandstone, Marwar Supergroup, Western Rajasthan. J. Asian Earth Sci. 91, 352–361.

Laflamme, M., Narbonne, G.M., 2008. Competition in a Precambrian world: palaeoecology of Ediacaran fronds. Geol. Today 25, 182–187.

Laflamme, M., Xiao, S., Kowalewski, M., 2009. Osmotrophy in modular Ediacara organisms. Proc. Natl. Acad. Sci. 106 (p), 14438–14443.

Laflamme, M., Darroch, S.A.F., Tweedt, S.M., Peterson, K.J., Erwin, D.H., 2013. The end of the Ediacara biota: extinction, biotic replacement, or Cheshire Cat? Gondwana Res. 23, 558–573.

Laing, B.A., Mángano, M.G., Buatois, L.A., Narbonne, G.M., Gougeon, R.C., 2019. A protracted Ediacaran-Cambrian transition: an ichnologic ecospace analysis of the Fortunian in Newfoundland, Canada. Geol. Mag. 156, 1623–1630.

Lambshead, P.J.D., Tietjen, J., Glover, A., Ferrero, T., Thistle, D., Gooday, A.J., 2001. Impact of large-scale natural physical disturbance on the diversity of deep-sea North Atlantic nematodes. Mar. Ecol. Prog. Ser. 214, 121–126.

Landing, E., 1994. Precambrian-Cambrian boundary global stratotype ratified and a new perspective of Cambrian time. Geology 22, 179–182.

Laverock, B., Gilbert, J.A., Tait, K., Osborn, A.M., Widdicombe, S., 2011. Bioturbation: impact on the marine nitrogen cycle. Biochem. Soc. Trans. 39, 315–320. https://doi.org/10.1042/BST0390315.

Lima, J.H.D., Netto, R.G., 2012. Trace fossils from the Permian Teresina Formation at Cerro Caveiras (S Brazil). Rev. Brasil. Paleontol. 15, 5–22.

Linnemann, U., Ovtcharova, M., Schaltegger, U., Gartner, A., Hautmann, M., Geyer, G., Vickers-Rich, P., Rich, T., Plessen, B., Hofmann, M., Zieger, J., Krause, R., Kriesfield, L., Smith, J., 2019. New high-resolution age data from the Ediacaran–Cambrian boundary indicate rapid, ecologically driven onset of the Cambrian explosion. Terra Nova 31, 49–58.

Macdonald, F.A., Pruss, S.B., Strauss, J.V., 2014. Trace fossil with spreiten from the late Ediacaran Nama Group, Namibia: complex feeding patterns five million years before the Precambrian-Cambrian boundary. J. Paleontol. 88, 299–308.

MacNaughton, R.B., Narbonne, G.M., 1999. Evolution and ecology of Neoproterozoic-Lower Cambrian trace fossils, NW Canada. Palaios 14, 97–115.

Maloney, K.M., Boag, T., Facciol, A., Gibson, B., Cribb, A., Koester, B., Kenchington, C., Racicot, R.A., Darroch, S.A.F., Laflamme, M., 2020. Facies analysis of fossiliferous Ediacaran deposits in southern Namibia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 556 https://doi.org/10.1016/j.palaeo.2020.109884.

Mángano, M.G., Buatois, L.A., 2014. Decoupling of body-plan diversification and ecological structuring during the Ediacaran-Cambrian transition: evolutionary and geobiological feedbacks. Proc. R. Soc. B 281. https://doi.org/10.1098/rspb.2014.0038.

Mángano, M.G., Buatois, L.A., 2016. The trace-fossil record of major evolutionary events. Top. Geobiol. 39 https://doi.org/10.1007/978-94-017-9600-2_1.

Mángano, M.G., Buatois, L.A., 2017. The Cambrian revolutions: trace-fossil record, timing, links and geobiological impact. Earth-Sci. Rev. 173, 96–108.

Mángano, M.G., Buatois, L.A., 2020. The rise and early evolution of animals: where do we stand from a trace-fossil perspective? Interface Focus 10, 20190103.

Mángano, M.G., Buatois, L.A., Muniz Guinea, F., 2005. Ichnology of the Alfarcito Member (Santa Rosita Formation) of northwestern Argentina: animal-substrate interactions in a lower Paleozoic wave-dominated shallow sea. Ameghiniana 42, 641–668.

Männil, R., 1966. In: Hecker, R.F. (Ed.), Vertical Burrows in Ordovician Limestones of the Baltic. The Organism and Environment in the Geological Past, pp. 200–207.

Marenco, K.N., Bottjer, D.J., 2007. Ecosystem engineering in the fossil record: early examples from the Cambrian Period. In: Cuddington, K., Byers, J.E., Wilson, W.G., Hastings, A. (Eds.), Ecosystem Engineers: Plants to Protists, pp. 163–183.

Marenco, K.N., Bottjer, D.J., 2011. Quantifying bioturbation in Ediacaran and Cambrian rocks. In: Laflamme, M., Schiffbauer, J.D., Dornbos, S.Q. (Eds.), Quantifying the Evolution of Early Life. Springer, Dordrecht, The Netherlands, pp. 135–160.

Mariotti, G., Pruss, S.B., Perron, J.T., Bosak, T., 2014. Microbial shaping of sedimentary wrinkle structures. Nat. Geosci. 7, 736–740.

Marusin, V.V., Kuper, K.E., 2020. Complex tunnel systems of early Fortunian macroscopic endobenthos in the Ediacaran-Cambrian transitional strata of the Olenek Uplift (NE Siberian Platform). Precambrian Res. 340, 105627.

Mata, S.A., Corsetti, C.L., Corsetti, F.A., Awramik, S.M., Bottjer, D.J., 2012. Lower Cambrian anemone burrows from the upper member of the Wood Canyon Formation, Death Valley region, United States: paleoecological and paleoenvironmental significance. Palaios 27, 594–606. https://doi.org/10.2110/palo.2012.p12-016r.

McFadden, K.A., Huang, J., Chu, X., Jiang, G., Kaufman, A.J., Zhou, C., Yuan, X., Xiao, S., 2008. Pulsed oxidation and biological evolution in the Ediacaran Doushantuo Formation. Proc. Natl. Acad. Sci. USA 105 (p), 3197–3202. https://doi.org/10.1073/pnas.0708336105.

McIlroy, D., Brasier, M.D., 2017. Ichnological evidence for the Cambrian explosion in the Ediacaran Cambrian succession of Tanafjord, Finnmark, northern Norway. In: Brasier, A.T., McIlroy, D., McLoughlin, N. (Eds.), Earth System Evolution and Early Life: A Celebration of the Work of Martin Brasier, Geological Society, London, Special Publications, 448, pp. 351–368.

McIlroy, D., Logan, C.A., 1999. The impact of bioturbation on infaunal ecology and evolution during the Proterozoic-Cambrian transition. Palaios 14, 59–72. https://doi.org/10.2307/3515361.

McIlroy, D., Crimes, T.P., Pauley, J.C., 2005. Fossils and matgrounds from the Neoproterozoic Longmyndian Supergroup, Shropshire, UK. Geol. Mag. 142, 441–455.

McMahon, W.J., Davies, N.S., Went, D.J., 2017. Negligible microbial matground influence on pre-vegetation river functioning: evidence from the Ediacaran-Lower Cambrian Series Rouge, France. Precambrian Res. 292, 13–34.

Mehra, A., Maloof, A.C., 2018. Multiscale approach reveals that *Cloudina* aggregates are detritus and not in situ reef constructions. Proc. Natl. Acad. Sci. USA 115, E2519–E2527. https://doi.org/10.1073/pnas.1719911115.

Mehra, A., Watters, W.A., Grotzinger, J.P., Maloof, A.C., 2020. Three-dimensional reconstructions of the putative metazoan Namapoikia show that it was a microbial construction. Proceedings of the National Academy of Sciences USA. https://doi.org/10.1073/pnas.2009129117.

Menon, L.R., McIlroy, D., Brasier, M.D., 2013. Evidence for Cnidaria-like behaviour in ca. 560 Ma Ediacaran *Aspidella*. Geology 41, 895–898. https://doi.org/10.1130/G34424.1.

Menon, L.R., McIlroy, D., Liu, A., Brasier, M.D., 2016. The dynamic influence of microbial mats on sediments: fluid escape and pseudofossil formation in the Ediacaran Longmyndian Supergroup, UK. J. Geol. Soc. 173, 177–185.

Menon, L.R., McIlroy, D., Brasier, M.D., 2017. '*Intrites*' from the Ediacaran Longmyndian Supergroup, UK: a new form of microbially-induced sedimentary structure (MISS). In: Brasier, A.T., McIlroy, D., McLoughlin, N. (Eds.), Earth System Evolution and Early Life: A Celebration of the Work of Martin Brasier, Geological Society, London, Special Publications, 448, pp. 271–283.

Meyer, M., Schiffbauer, J.D., Xiao, S., Cai, Y., Hua, H., 2012. Taphonomy of the upper Ediacaran enigmatic ribbonlike fossil *Shaanxilithes*. Palaios 27, 354–372.

Meyer, M., Xiao, S., Gill, B.C., Schiffbauer, J.D., Chen, Z., Zhou, C., Yuan, X., 2014. Interactions between Ediacaran animals and microbial mats: Insights from *Lamonte trevallis*, a new trace fossil from the Dengying Formation of South China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 396, 62–74.

Meysman, F.J.R., Middelburg, J.J., Heip, C.H.R., 2006. Bioturbation: a fresh look at Darwin's last idea. Trends Ecol. Evol. 21, 688–695.

Munoz, D.F., Mangano, M.G., Buatois, L.A., 2019. Unravelling Phanerozoic evolution of radial to rosette trace fossils. Lethaia 52, 350–369.

Muscente, A.D., Boag, T.H., Bykova, N., Schiffbauer, J.D., 2018. Environmental disturbance, resource availability, and biologic turnover at the dawn of animal life. Earth Sci. Rev. 177, 248–264.

Muscente, A.D., Bykova, N., Boah, T.H., Buatois, L.A., Mángano, G.M., Eleish, A., Prabhu, A., Pan, F., Meyer, M.B., Schiffbauer, J.D., Fox, P., Hazen, R.M., Knoll, A.H., 2019. Ediacaran biozones identified with network analysis provide evidence for pulsed extinctions of early complex life. Nat. Commun. 10, 911. https://doi.org/10.1038/s41467-019-08837-3.

Narbonne, G.M., Aitken, J.D., 1990. Ediacaran fossils from the Sekwi Brook area, Mackenzie Mountains, northwestern Canada. Palaeontology 33, 945–980.

Narbonne, G.M., Myrow, P., Landing, E., Anderson, M.M., 1987. A candidate Stratotype for the Precambrian-Cambrian boundary, Fortune Head, Burin Peninsula, southeastern Newfoundland. Can. J. Earth Sci. 24, 1277–1293. https://doi.org/10.1139/e87-124.

Narbonne, G.M., Saylor, B.Z., Grotzinger, J.P., 1997. The youngest Ediacaran fossils from Southern Africa. J. Paleontol. 71, 953–967.

Narbonne, G.M., Xiao, S., Shields, G., 2012. The Ediacaran Period. In: Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.), Geologic Timescale. Elsevier, Amsterdam, pp. 413–435.

Nicholson, H.A., 1873. Contributions to the study of the errant Annelids of the older Paleozoic rocks. Proc. R. Soc. Lond. 21 (p), 288–290.

Orłowski, S., Żylińska, A., 1996. Non-arthropod burrows from the Middle and Late Cambrian of the Holy Cross Mountains, Poland. Acta Palaeontol. Pol. 41, 385–409.

Parry, L.A., Boggiani, P.C., Condon, D.J., Garwood, R.J., Leme, J.D.-M., McIlroy, D., Brasier, M.D., Trindade, R., Campanha, G.A.C., Pacheco, M.L.A.F., Diniz, C.Q.C., Liu, A.G., 2017. Ichnological evidence for meiofaunal bilaterians from the terminal Ediacaran and earliest Cambrian of Brazil. Nat. Ecol. Evol. 10. https://doi.org/10.1038/s41559-017-0301-9.

Paterson, D.M., 1994. Microbiological mediation of sediment structure and behaviour. In: Stal, L.J., Caumette, P. (Eds.), Microbial Mats. NATO ASI Series (Series G: Ecological Sciences), vol 35. Springer, Berlin, Heidelberg.

Peakall, J., Best, J., Baas, J.H., Hodgson, D.M., Clare, M.A., Talling, P.J., Dorrell, R.M., Lee, D.R., 2020. An integrated process-based model of flutes and tool marks in deep-water environments: implications for palaeohydraulics, the Bouma sequence and hybrid event beds. Sedimentology 67, 1601–1666.

Pemberton, S.G., Frey, R.W., 1982. Trace fossil nomenclature and the *Planolites Palaeophycus* dilemma. J. Paleontol. 56 (v), 843–881.

Pemberton, S.G., Magwood, J.P.A., 1990. A unique occurrence of *Bergaueria* in the Lower Cambrian Gog Group near Lake Louise, Alberta. J. Paleontol. 64, 436–440.

Pemberton, S.G., Frey, R.W., R.W. and R.G. Bromley, R.G., 1988. The ichnotaxonomy of *Conostichus* and other plug-shaped ichnofossils. Can. J. Earth Sci. 25, 866–892.

Penny, A.M., Wood, R.A., Curtis, A., Bowyer, F.T., Tostevin, R., Hoffman, K.-H., 2014. Ediacaran metazoan reefs from the Nama Group, Namibia. Science 344, 1504–1506. https://doi.org/10.1126/science.1253393.

Pflug, H.D., 1966. Neue Fossilreste aus den Nama-Schichten in Suedwest-Afrika. Paleontol. Zh. 40, 14–24.

Pflug, H.D., 1970a. Zur Fauna der Nama-Schichten in Südwest Afrika I. Pteridinia, Bau und Systematische Zugehörigkeit. Palaeontographica A134, 226–262.

Pflug, H.D., 1970b. Zur Fauna der Nama-Schichten in Südwest-Afrika. II. Rangeidae, Bau und Systematische Zugehörigkeit. Palaeontographica A135, 198–231.

Pflug, H.D., 1972a. Zur Fauna der Nama-Schichten in Südwest-Afrika. III. Erniettomorpha, Bau und Systematik. Palaeontographica A139, 134–170.

Pflug, H.D., 1972b. Systematik der jung-praekambrischen Petalonamae Pflug 1970. Palaeontol. Z. 46, 56–67.
Pickford, M.H.L., 1995. Review of the Riphean, Vendian and early Cambrian palaeontology of the Otavi and Nama Groups, Namibia. Commun. Geol. Surv. Namibia 10, 57–81.
Pokorný, R., Krmíček, L., Sudo, M., 2017. An endemic ichnoassemblage from a late Miocene paleolake in SE Iceland. Palaeogeogr. Palaeoclimatol. Palaeoecol. 485, 761–773. https://doi.org/10.1016/j.palaeo.2017.07.033.
Prantl, F., 1945. Dve zahadne Zklameneliny (stopy). z vrstev chrustenickch - d82, Rozpravy II. Tridy Ceske Akademie 55, 3–8.
Rahman, I., Darroch, S.A.F., Racicot, R.A., Laflamme, M., 2015. Suspension feeding in the enigmatic Ediacaran organism *Tribrachidium* demonstrates complexity of Neoproterozoic ecosystems. Sci. Adv. 1, e1500800 https://doi.org/10.1126/sciadv.1500800.
Rhoads, D.C., Young, D.K., 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structures. J. Mar. Res. 28, 150–187.
Rhoads, D.C., Yingst, J.Y., Ullman, W.J., 1978. Seafloor stability in central Long Island Sound: Part I. Temporal changes in erodibility of fine-grained sediment. In: Wiley, M.L. (Ed.), Estuarine Interactions, pp. 221–244. https://doi.org/10.1016/C2013-0-11712-6.
Ries, J.B., Fike, D.A., Pratt, L.M., Lyons, T.W., Grotzinger, J.P., 2009. Superheavy pyrite (δ34Spyr > δ34SCAS) in the terminal Proterozoic Nama Group, southern Namibia: a consequence of low seawater sulfate at the dawn of animal life. Geology 37, 743–746.
Rosenberg, R., Nilsson, H.C., Diaz, R.J., 2001. Response of benthic fauna and changing sediment redox profiles over a hypoxic gradient. Estuar. Coast. Shelf Sci. 53, 343–350.
Sahoo, S., Planavsky, N., Jiang, G., Kendall, B., Owens, J., Wang, X., Shi, X., Anbar, A., Lyons, T., 2016. Oceanic oxygenation events in the anoxic Ediacaran ocean. Geobiology 14, 457–468.
Sappenfield, A., Droser, M.L., Gehling, J.G., 2011. Problematica, Trace Fossils, and Tubes within the Ediacara Member (South Australia): redefining the Ediacaran Trace Fossil Record One Tube at a Time. J. Paleontol. 85, 256–265.
Savazzi, E., 2015. The early Cambrian Eophyton toolmark and its producer. Paleontol. Res. 19, 61–75.
Savrda, C., 2003. Equilibrium responses reflected in a large *Conichnus* (Upper Cretaceous Eutaw Formation, Alabama, USA). Ichnos 9, 33–40.
Saylor, B.Z., 2003. Sequence stratigraphy and carbonate–siliciclastic mixing in a terminal Proterozoic foreland basin, Urusis Formation, Nama Group, Namibia. J. Sediment. Res. 73, 264–279.
Saylor, B.Z., Grotzinger, J.P., 1996. Reconstruction of important Proterozoic-Cambrian boundary exposures through the recognition of thrust deformation in the Nama Group of southern Namibia. Commun. Geol. Surv. Namibia 11, 1–12.
Saylor, B.Z., Grotzinger, J.P., Germs, G.J.B., 1995. Sequence stratigraphy and sedimentology of the Neoproterozoic Kuibis and Schwarzrand Subgroups (Nama Group), southwestern Namibia. Precambrian Res. 73, 153–171.
Saylor, B.Z., Kaufman, A.J., Grotzinger, J.P., Urban, F., 1998. A composite reference section for the terminal Proterozoic strata of southern Namibia. J. Sediment. Res. 68, 1223–1235.
Schiffbauer, J.D., Huntley, J.W., O'Neil, G.R., Darroch, S.A.F., Laflamme, M., Cai, Y., 2016. The Latest Ediacaran Wormworld Fauna: setting the Ecological Stage for the Cambrian Explosion. GSA Today 26, 4–11.
Schiffbauer, J.D., Selly, T., Jacquet, S.M., Merz, R.A., Nelson, L.L., Strange, M.A., Cai, Y., Smith, E.F., 2020. Discovery of bilaterian-type through-guts in cloudinomorphs from the terminal Ediacaran Period. Nat. Commun. 11, 205. https://doi.org/10.1038/s41467-019-13882-z.
Schmitz, M.D., 2012. Radiometric ages used in GTS2012. In: Gradstein, F., Ogg, J., Ogg, G. (Eds.), The Geologic Time Scale. Elsevier, Boston, MA, pp. 427–449.
Schratzberger, M., Ingels, J., 2018. Meiofauna matters: the roles of meiofauna in benthic ecosystems. J. Exp. Mar. Biol. Ecol. 502, 12–25. https://doi.org/10.1016/j.jembe.2017.01.007.
Seilacher, A., 1982. Distinctive features of sandy tempestites. In: Einsele, G., Seilacher, A. (Eds.), Cyclic and Event Stratification. Springer, Berlin, pp. 333–349.
Seilacher, A., 1990. Paleozoic trace fossils. In: Said, R. (Ed.), The Geology of Egypt. A.A. Balkema, Rotterdam, Brookfield, pp. 649–722.
Seilacher, A., Pflüger, F., 1994. From biomats to benthic agriculture: a biohistoric revolution. In: Krumbein, W.E., Peterson, D.M., Stal, L.J. (Eds.), Biostabilization of sediments. Bibliotheks und Informationssystem der Carl von Ossietzky Universität Odenburg, pp. 97–105.
Seilacher, A., 1997. Fossil Art. The Royal Tyrrell Museum of Paleontology, Drumheller.
Seilacher, A., 1999. Biomat-related lifestyles in the Precambrian. Palaios 14, 86–93.
Seilacher, A., 2007. Trace Fossil Analysis. Springer, Heidelberg.
Seilacher, A., Buatois, L.A., Mángano, M.G., 2005. Trace fossils in the Ediacaran-Cambrian transition: behavioural diversification, ecological turnover and environmental shift. Palaeogeogr. Palaeoclimatol. Palaeoecol. 227, 323–356.
Selly, T., Schiffbauer, J.D., Jacquet, S.M., Smith, E.F., Nelson, L.L., Andreasen, B.D., Huntley, J.W., Strange, M.A., O'Neil, G.R., Thater, C.A., Bykova, N., Steiner, M., Yang, B., Cai, Y., 2019. A new cloudinid fossil assemblage from the terminal Ediacaran of Nevada, USA. J. Syst. Palaeontol. 18, 357–379.
Shen, B., Xiao, S., Dong, L., Chuanming, Z., Liu, J., 2007. Problematic macrofossils from Ediacaran successions in the North China and Chaidam blocks: implications for their evolutionary roots and biostratigraphic significance. J. Paleontol. 81, 1396–1411.
Shinn, E.A., 1968. Burrowing in recent lime sediments of Florida and the Bahamas. J. Paleontol. 42, 879–894.
Smit, M.G.D., Holthaus, K.I.E., Trannum, H.C., Neff, J.M., Kjeilen-Eilertsen, G., Jak, R.G., Singsaas, I., Huijbregts, M.A.J., Hendriks, A.J., 2008. Species sensitivity distributions for suspended clays, sediment burial, and grain size change in the marine environment. Environ. Toxicol. Chem. 27, 1006–1012.
Smith, E.F., Nelson, L.L., Strange, M.A., Eyster, A.E., Rowland, S.M., Schrag, D.P., Macdonald, F.A., 2016. The end of the Ediacaran: two exceptionally preserved body fossil assemblages from Mt. Dunfee, Nevada. Geology 44, 911–914.
Sperling, E.A., Stockey, R.G., 2018. The temporal and environmental context of early animal evolution: considering all the ingredients of an "Explosion". Integr. Comp. Biol. 48, 605–622.
Sperling, E.A., Pisani, D., Peterson, K.J., 2007. Poriferan paraphyly and its implications for Precambrian palaeobiology. In: Vickers-Rich, P., Komarower, P. (Eds.), The Rise and Fall of the Ediacaran Biota, Special Publications, 286. Geological Society, London, pp. 355–368.
Stanistreet, I.G., Kukla, P.A., Henry, G., 1991. Sedimentary basinal responses to a Late Precambrian Wilson cycle: the Damara Orogen and Nama Foreland, Namibia. J. Afr. Earth Sci. 13, 141–156.
Tarhan, L.G., Hughes, N.C., Myrow, P.M., Bhargava, O.N., Ahluwalla, A.D., Kudryavtsev, A.B., 2014. Precambrian-Cambrian boundary interval occurrence and form of the enigmatic tubular body fossil *Shaanxilithes ningqiangensis* from the Lesser Himalaya of India. Palaeontology 57, 283–298.
Tarhan, L.G., Droser, M.L., Planavsky, N.J., Johnston, D.T., 2015. Protracted development of bioturbation through the early Palaeozoic Era. Nat. Geosci. 8, 865–869.
Tarhan, L.G., Droser, M.L., Gehling, J.G., Dzaugis, M.P., 2017. Microbial mat sandwiches and other anactualistic sedimentary features of the Ediacara Member (Rawnsley Quartzite, South Australia): implications for interpretation of the Ediacaran sedimentary record. Palaios 32, 181–194.
Tarhan, L.G., Droser, M.L., Cole, D.B., Gehling, J.G., 2018. Ecological expansion and extinction in the Late Ediacaran: weighing the evidence for environmental and biotic drivers. Integr. Comp. Biol. 58, 688–702. https://doi.org/10.1093/icb/icy020.
Thamdrup, B., Fossing, H., Jorgensen, B.B., 1994. Mangenes, iron, and sulfur cycling in a coastal marine sediment, Aarhus Bay, Denmark. GCA 58, 5115–5129.
Toom, U., Vinn, O., Hints, O., 2019. Ordovician and Silurian ichnofossils from carbonate facies in Estonia: a collection-based review. Palaeoworld 28, 123–144.
Tostevin, R., Wood, R.A., Shields, G.A., Poulton, S.W., Guilbaud, R., Bowyer, F., Penny, A.M., He, T., Curtis, A., Hoffmann, K.-H., Clarkson, M.O., 2016. Low-oxygen waters limited habitable space for early animals. Nat. Commun. 7, 12818. https://doi.org/10.1038/ncomms12818.
Tostevin, R., Clarkson, M.O., Gangl, S., Shields, G.A., Wood, R.A., Bowyer, F., Penny, A.M., Stirling, C.H., 2019. Uranium isotope evidence for an expansion of anoxia in terminal Ediacaran oceans. Earth Planet. Sci. Lett. 506, 104–112.
Uchman, A., Alvaro, J.-J., 2000. Non-marine invertebrate trace fossils from the Tertiary Calatayud-Teruel Basin, NE Spain. Rev. Espan. Paleontol. 15, 203–218.
Uchman, A., Hanken, N.-M., Binns, R., 2005. Ordovician bathyal trace fossils from metasiliciclastics in central Norway and their sedimentological and paleogeographical implications. Ichnos 2, 105–133.
van de Velde, S., Meysman, F.J.R., 2016. The influence of bioturbation on iron and Sulphur cycling in marine sediments: a model analysis. Aquat. Geochem. 22, 469–504. https://doi.org/10.1007/s10498-016-9301-7.
van de Velde, S., Mills, B.J.W., Meysman, F.J.R., Lenton, T.M., Poulton, S.W., 2018. Early Palaeozoic ocean anoxia and global warming driven by the evolution of shallow burrowing. Nat. Commun. 9, 2554.
Vannier, J., Calandra, I., Gaillard, C., Żylińska, A., 2010. Priapulid worms: pioneer horizontal burrowers at the Precambrian-Cambrian boundary. Geology 38, 711–714. https://doi.org/10.1130/G30829.1.
Vickers-Rich, P., Ivantsov, A.-Y., Trusler, P.W., Narbonne, G.M., Hall, M., Wilson, S.A., Greentree, C., Fedonkin, M.A., Elliott, D.A., Hoffmann, K.H., Schneider, G.I.C., 2013. Reconstructing *Rangea*: new discoveries from the Ediacaran of Southern Namibia. J. Palaeontol. 87, 1–15.
Vidal, G., 1989. Are late Proterozoic carbonaceous megafossils metaphytic algae or bacteria? Lethaia 22, 375–379.
Waggoner, B., 2003. The Ediacaran biotas in space and time. Integr. Comp. Biol. 43, 104–113.
Wang, Y., Lin, J.-P., Zhao, Y.-L., Orr, P.J., 2009. Palaeoecology of the trace fossil *Gordia* and its interaction with nonmineralizing taxa from the early Middle Cambrian Kaili Biota, Guizhou Province, South China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 277, 141–148. https://doi.org/10.1016/j.palaeo.2009.02.017.
Webby, B.D., 1970. Late Precambrian trace fossils from New South Wales. Lethaia 3, 79–109.
Wei, G., Planavsky, N.J., Tarhan, L.G., Chen, X., Wei, W., Li, D., Ling, H., 2018. Marine redox fluctuations as a potential trigger for the Cambrian explosion. Geology 46, 587–590. https://doi.org/10.1130/G40150.1.
Wetzel, A., Bromley, R.G., 1996. Re-evaluation of the ichnogenus *Helminthopsis* – a new look at the type material. Palaeontology 39, 1–19.
Wilson, J.P., Grotzinger, J.P., Fischer, W.W., Hand, K.P., Jensen, S., Knoll, A.H., Abelson, J., Metz, J.M., McLoughlin, N., Cohen, P., Tice, M.M., 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., 2011. Paleoecology of the earliest skeletal metazoans: implications for early biomineralization. Earth-Sci. Rev. 106, 184–190.
Wood, R., Curtis, A., 2014. Extensive metazoan reefs from the Ediacaran Nama Group, Namibia: the rise of benthic suspension feeding. Geobiology 13, 112–122. https://doi.org/10.1111/gbi.12122.
Wood, R., Erwin, D.H., 2017. Innovation not recovery: dynamic redox promotes metazoan radiations. Biol. Rev. 93, 863–873. https://doi.org/10.1111/brv.12375.

Wood, R.A., Penny, A.M., 2018. Substrate growth dynamics and biomineralization of an Ediacaran encrusting poriferan. Proc. R. Soc. B 285. https://doi.org/10.1098/rspb.2017.1938.
Wood, R.A., Grotzinger, J.P., Dickson, J.A.D., 2002. Proterozoic modular biomineralized metazoan from the Nama Group, Namibia. Science 296, 2383–2386.
Wood, R.A., Poulton, S.W., Prave, A.R., Hoffmann, K.-H., Clarkson, M.O., Guilbaud, R., Lyne, J.W., Tostevin, R., Bowyer, F., Penny, A.M., Curtis, A., Kasemann, S.A., 2015. Dynamic redox conditions control late Ediacaran metazoan ecosystems in the Nama Group, Namibia. Precambrian Res. 261, 252–271. https://doi.org/10.1016/j.precamres.2015.02.004.
Wood, R., Liu, A.G., Bowyer, F., Wilby, P.R., Dunn, F.S., Kenchington, C.G., Hoyal Cuthill, J.F., Mitchell, E.G., Penny, A., 2019. Integrated records of environmental change and evolution challenge the Cambrian explosion. Nat. Ecol. Evol. 3, 528–538. https://doi.org/10.1038/s41559-019-0821-6.
Wood, R., Donoghue, P.C.J., Lenton, T.M., Liu, A.G., Poulton, S.W., 2020. The origin and rise of complex life: progress requires interdisciplinary integration and hypothesis testing. Interface Focus 10, 20200024.
Wray, G.A., 2015. Molecular clocks and the early evolution of metazoan nervous systems. Proc. R. Soc. B 370, 1684. https://doi.org/10.1098/rstb.2015.0046.
Wright, J.P., Jones, C.G., Flecker, A.S., 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecología 132, 96–101.
Xiao, S., Laflamme, M., 2009. On the eve of animal radiation: phylogeny, ecology and evolution of the Ediacara biota. Trends Ecol. Evol. 24, 31–40.
Xiao, S., Narbonne, G.M., Zhou, C., Laflamme, M., Grazhdankin, D.V., Moczylowska-Visal, M., Cui, H., 2016. Towards an Ediacaran time scale: problems, protocols, and prospects. Episodes 39, 540–555.
Yochelson, E.L., Fedonkin, M.A., 1997. The type specimens (Middle Cambrian) of the trace fossil *Archaeonassa* Fenton and Fenton. Can. J. Earth Sci. 34, 1210–1219.
Zessin, W., 2010. Ein neues Spurenfossil aus der Nama-Formation Südwestafrikas (Namibia). Ursus, Mitteilungsblatt des Zoovereins und des Zoos Schwerin 16, 63–72.
Zhang, L.-J., Qi, Y.-A., Buatois, L.A., Mángano, M.G., Meng, Y., Li, D., 2017. The impact of deep-tier burrow systems in sediment mixing and ecosystem engineering in early Cambrian carbonate settings. Sci. Rep. 7, 45773.
Zhang, F., Xiao, S., Kendell, B., Romaniello, S.J., Cui, H., Meyer, M., Gilleaudeau, G.J., Kaufman, A.J., Anbar, A.D., 2018. Extensive marine anoxia during the terminal Ediacaran Period. Sci. Adv. 4, eeaan8983 https://doi.org/10.1126/sciadv.aan8983.
Zhuravlev, A.Y., Wood, R.A., Penny, A.M., 2015. Ediacaran skeletal metazoan interpreted as a lophophorate. Proc. R. Soc. B Biol. Sci. 282, 20151860.