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Paleontology and ichnology of the late Ediacaran Nasep–Huns transition (Nama Group, southern Namibia)

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Abstract.—The Nasep and Huns members of the Urusis Formation (Nama Group), southern Namibia, preserve some of the most diverse trace-fossil assemblages known from the latest Ediacaran worldwide, including potentially the world's oldest "complex" vertical sediment-penetrating burrows. These sediments record relatively diverse communities of bilaterian metazoans existing before the base of the Cambrian and an increase in the intensity of metazoan ecosystem engineering behaviors that could eventually produce profound changes in the character of the Phanerozoic sedimentary record (the "agronomic revolution"). Despite this, relatively little about this trace-fossil assemblage is known. We explore the Nasep–Huns transition at two localities in the Witputs sub-basin and describe the trace- and body-fossil diversity present in these horizons alongside a paleoenvironmental reconstruction. We document eight unique ichnotaxa from these localities, including well-preserved "probes" potentially left by priapulids. We also report the first occurrence of *Corumbella* from Namibia, helping to establish a biostratigraphic link between Namibia, Brazil, Paraguay, Iran, and the southwestern United States. Last, we find that several ichnotaxa, in particular small treptichnids, appear to be preferentially preserved on the bases of gutter casts, hinting at the potential existence of an unusual late Ediacaran preservational window with possible implications for timing the first appearance of key bilaterian behaviors.

Introduction

The latest Ediacaran Nama assemblage (∼550–539 Ma; Waggoner, 2003; Boag et al., 2016) records a critical interval in the history of life on Earth, marking the transition from benthic communities dominated by the soft-bodied and enigmatic Ediacara biota to communities composed of a much higher proportion of recognizable metazoans (Darroch et al., 2018a, b; Muscente et al., 2018; Wood et al., 2019; Schiffbauer et al., 2020). In addition to global-scale biotic turnover, this interval marks the appearance of several key evolutionary innovations, including the advent of metazoan biomineralization (Wood, 2011; Penny et al., 2014), gregarious benthic suspension feeding (Wood and Curtis, 2015; Gibson et al., 2019), macroscopic predation (Hua et al., 2003), and a diversification of life habits both above and below the sediment–water interface (Jensen et al., 2000; Mángano and Buatois, 2014; Buatois et al., 2018; Cribb et al., 2019; Darroch et al., 2020; Tarhan et al., 2020). The Nama Assemblage thus records ecosystems that are transitional between the older Ediacaran "White Sea" assemblage and the subsequent Cambrian (Darroch et al., 2016; Schiffbauer et al., 2016; Wood et al., 2019) and likely marks the origins of the modern, animal-dominated biosphere (Darroch et al., 2018a).

Despite intensifying research into this interval, the timing and impact of emerging metazoan behaviors is still not fully understood. The diversification of bilaterian animals in the latest Ediacaran (as represented by trace fossils) potentially had powerful ecosystem engineering impacts (Cribb et al., 2019) and may have played an outsized role in driving major shifts in Earth systems over the Ediacaran–Cambrian transition. These changes include the removal of seafloor microbial mats, leading to shifts in substrate rheology (termed the "agronomic revolution"; Seilacher, 1999; Bottjer et al., 2000; Mángano and Buatois, 2017), changes to sediment redox gradients (Rosenberg et al., 2001; Canfield and Farquhar, 2009; Tarhan et al., 2015; van de Velde and Meysman, 2016), patterns of nutrient cycling (Bertics and Ziebis, 2009), and the volume of suspended sediment in the water column (Rhoads and Young, 1970). Some studies have suggested that metazoan ecosystem engineering may have driven the extinction of the Ediacara biota (Laflamme et al., 2013; Darroch et al., 2015), although there are currently a variety of competing models seeking to explain these intervals of biotic turnover (see, e.g., Smith et al., 2016; Budd and Jensen, 2017; Zhang et al., 2018). Trace-fossil assemblages in the latest Ediacaran, therefore, not only provide insights into rates and patterns of metazoan evolution but also allow for investigations into patterns of coupling between the biosphere and geosphere, helping to establish the extent to which biological activity may have structured the

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animal-dominated ecosystems that characterize the Phanerozoic. Here, we describe the trace- and body-fossil diversity of the late Ediacaran Nasep and Huns members (Urusis Formation) from the Nama Group, southern Namibia, alongside an assessment of their paleoenvironmental context. These sections preserve the oldest reported treptichnid traces (and thus the earliest evidence for "complex" burrowing; Jensen et al., 2000) yet found within the Ediacaran. Detailed investigation of the trace- and body-fossil composition of the Nasep–Huns transition in their sedimentological and stratigraphic context thus provides a window into the composition and functioning of late Ediacaran ecosystems and offers an opportunity to study potential controls on the emergence of complex animal behaviors.

Geologic setting

The Nama Group of southern Namibia records >3,000 m of Ediacaran–Cambrian mixed carbonate–siliciclastic sediments over an area of approximately 125,000 km^2 (Saylor et al., 1995). These successions are thought to represent material derived from the Kalahari Craton and later sourced from the uplift associated with the Damara Orogen, deposited in a foreland basin formed in response to orogenic activity during the assembly of Gondwana (Germs, 1983; Stanistreet et al., 1991; Saylor et al., 1995; Grotzinger and Miller, 2008).

The Nama Group south of Windhoek is divided into two sub-basins, the Zaris (north) and Witputs (south), which are separated by the Osis Arch, interpreted as a paleotopographic high (Germs, 1983; Grotzinger and Miller, 2008; Fig. 1). The Nama exposures in both sub-basins are subdivided into three subgroups; in ascending stratigraphic order, these are the Kuibis, the Schwarzrand, and the Fish River. Sediments in both basins can broadly be split into two sedimentary successions, a siliciclastic–carbonate succession comprising the Kuibis Subgroup, and a broadly siliciclastic succession comprising the Schwarzrand Subgroup (including the Nomtsas and Vergesig formations) (Germs, 1983; Saylor et al., 1995; Grotzinger and Miller, 2008). The Schwarzrand Subgroup encompasses the Ediacaran–Cambrian boundary, with the upper Ediacaran units (Nudaus and Urusis formations) locally incised by the Nomtsas Formation, which contains abundant *Treptichnus pedum* Seilacher, 1955 and is thus identified as Cambrian (Wilson et al., 2012). As such, the Ediacaran–Cambrian boundary is generally thought to lie stratigraphically between the Urusis and the Nomtsas (Narbonne et al., 1997; Wilson et al., 2012); however, some have placed the boundary further down within the upper Spitskop Member (uppermost Urusis; see Linnemann et al., 2019). Ash beds dating from strata below the latest-known occurrence of Ediacaran macrofossils and at Farm Swartpunt have yielded ages of 540.095 ± 0.099 Ma and 538.99 ± 0.21 Ma (Linnemann et al., 2019), which suggests the Ediacaran–Cambrian boundary falls somewhere between 538 and 539 Ma. In the northern Zaris sub-basin, the Urusis Formation is thinner and consists of fluvial to shallow marine sandstone and green shale facies (Saylor, 2003). In the southern Witputs sub-basin, the Urusis Formation grades seaward into a carbonate shelf divided chronologically into the Nasep, Huns, Feldschuhhorn, and Spitskop members (Saylor, 2003; Grotzinger and Miller, 2008). The Urusis Formation varies in thickness throughout the Witputs sub-basin,

reaching a maximum thickness of 1,000 m near the Gariep Belt and thinning to less than 200 m proximal to the Osis Ridge (Saylor, 2003).

Nasep Member.—The Nasep is composed primarily of medium-grained, well-sorted sandstone (Germs, 1983; Grotzinger and Miller, 2008) and represents the base of the second depositional sequence within the Schwarzrand Subgroup (S2 of Germs, 1983; Saylor et al., 1995; Sequence A of Saylor, 2003) overlying an erosional contact incising the underlying shale. Saylor et al., (1995) recognized five facies within the Nasep Member that represent a variety of wave-dominated and delta-influenced settings, although a relative paucity of sedimentary structures in its lower sections makes precise paleoenvironmental reconstruction difficult (Saylor et al., 1995). The section begins in the basal Nasep with ∼43 m of massive- to planar-bedded medium-grained, well-sorted sandstone (Grotzinger and Miller, 2008). This transitions into 5–15 m of hummocky cross-stratified gray-green sandstone that Saylor et al. (1995) suggest marks a transition from strong current-borne sediment deposition during shoreline regression to a deeper-water, storm-dominated transgressive environment as sea level rose. The subsequent unit, a thin- to medium-bedded calcarenite with varying degrees of trough and tabular cross-bedding, indicates a shallower, shoreface environment, which is then followed by a green shale unit. The absence of major wave-generated sedimentary structures in the green shale suggests the furthest offshore deposition observed in this unit occurred at or immediately below fair-weather wave base (Grotzinger and Miller, 2008). The uppermost unit consists of thick-bedded sandstone with well-developed planar bedding, large-scale westerly directed trough and tabular cross beds, and soft sediment slumping typical of a delta slope (Grotzinger and Miller, 2008). In more landward sections, however, the Nasep Member terminates with a unit composed entirely of progradational, unidirectional cross-bedded sandstone, indicating a coastal plain depositional environment less influenced by reversing currents, possibly caused by increased fluvial or ebb-tide influence (Saylor, 2003).

Huns Member.—Unconformably overlying the Nasep Member is the erosive-based Huns Member, which marks the transition into the upper Schwarzrand Subgroup (Saylor and Grotzinger, 1996) and the base of another sequence boundary (S3 of Germs, 1983; Saylor et al., 1995; Sequence B of Saylor, 2003). In the east, the Huns cuts down into the Nasep and forms an erosional boundary; however, the erosion depth decreases westward, and the western portions of the Nasep–Huns boundary present no evidence of erosion (Grotzinger and Miller, 2008). The Huns is thought to represent a storm-dominated carbonate ramp succession in the latest stages of the Ediacaran and is roughly divisible into three subsections (inner ramp, ramp crest, ramp-to-basin transition) that fall along an east-to-west transect (Saylor et al., 1995; Saylor, 2003; Grotzinger and Miller, 2008). The lower Huns (0–40 m) is marked by shale with limestone and sandstone interbedding, followed by meter-scale stromatolitic units and small patch reefs upward through the remaining ∼260 m of the section (Saylor and Grotzinger, 1996; Saylor, 2003).
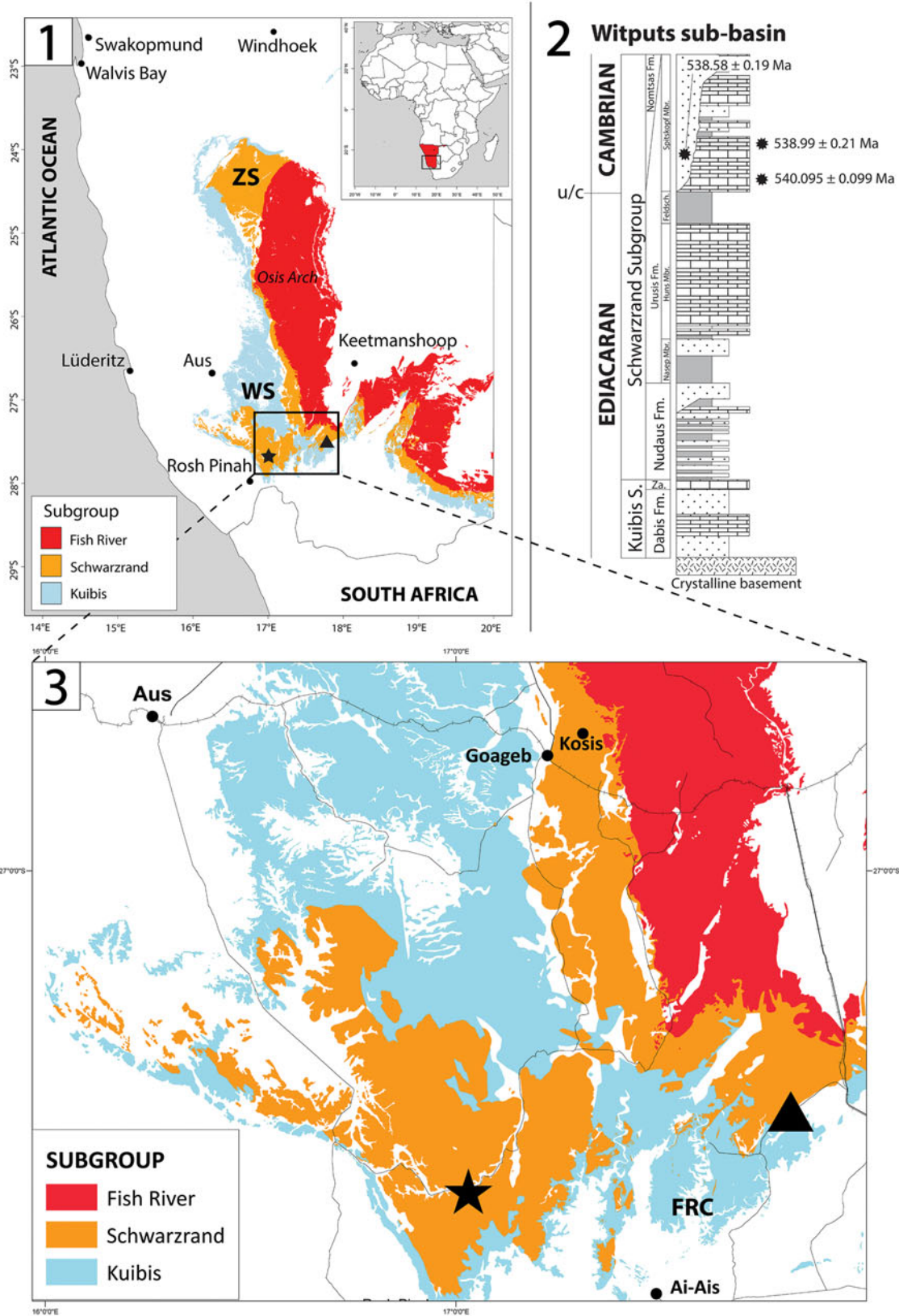
Figure 1. (**1**) Map of the Nama Group in southern Namibia, with the Zaris (ZS) and Witputs (WS) sub-basins indicated (modified from Darroch et al., 2020). (**2**) Generalized stratigraphy for the Witputs sub-basin (adapted from Darroch et al., 2020; geochronological dates follow Linnemann et al., 2019. (**3**) Higher-resolution map of study area in the Witputs sub-basin. Farm Arimas (star), Canyon Roadhouse (triangle), and Fish River Canyon (FRC) are marked.
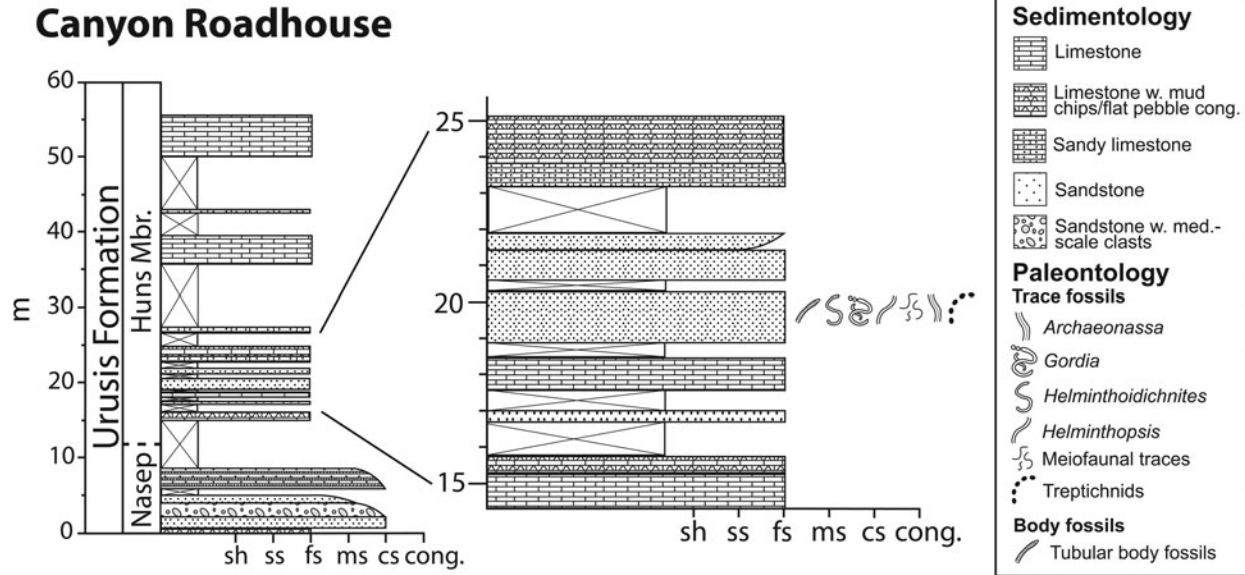
Figure 2. Stratigraphy of the Nasep–Huns exposures at Canyon Roadhouse, with (right) fossil-bearing intervals expanded. 'sh' = shale; 'ss' = siltstone; 'fs' = fine sand; 'ms' = medium sand; 'cong.' = conglomerate.

At maximum extent, the Huns can reach thicknesses of up to 500 m, although the unit-wide average is likely closer to 300 m (Saylor and Grotzinger, 1996; Grotzinger et al., 2000). The platform is capped by pinnacle reefs composed of a thrombolitic core enveloped by stromatolitic outer layers that indicate further submergence (drowning) of the carbonate platform before the deposition of the overlying Feldschuhorn shale (Saylor and Grotzinger, 1996; Grotzinger et al., 2005).

Materials and methods

Repository and institutional abbreviation.—Illustrated specimens were examined and photographed in the field; the majority were left in place. The slabs preserving the putative priapulid traces and *Corumbella* are reposited at the Geological Survey of Namibia (GSN) in Windhoek, Namibia.

Study localities and sedimentology

Two localities in the Witputs sub-basin, Canyon Roadhouse and Farm Arimas, expose the Nasep–Huns transition in wide lateral extent (Fig. 1.3). The Canyon Roadhouse exposures (27° 31′16.5″S, 17°48′43.4″E) are located approximately 25 km northeast of the Fish River Canyon (FRC) and immediately adjacent to the Gondwana Collection Canyon Roadhouse Lodge. Farm Arimas (27°41′36.1″S, 17°1′50.5″E) is approximately 55 km west of the central portion of the FRC.

At Canyon Roadhouse, the lowest Nasep exposures begin with 0.5 m of recrystallized limestone with mudstone chip inclusions (Fig. 2). This is immediately followed by 1.5 m of coarse-grained sandstone, which bears lithological and textural similarities to *Ernietta* Pflug, 1966 horizons found at localities such as Farm Hansburg (see Bouougri et al., 2011; Gibson et al., 2019; Maloney et al., 2020); however, these beds have yet to yield any
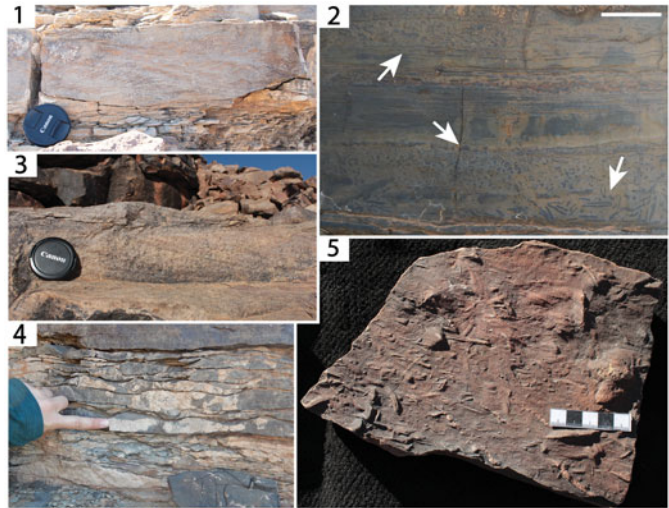

Figure 3. Sedimentary structures from Canyon Roadhouse: (**1**) climbing ripples; (**2**) mudchips (arrowed); (**3**) tabular cross bedding; (**4**) quasi-symmetrical ripples; (**5**) bioturbated slab exhibiting a number of unidirectional tool marks. Scale bar = 5 cm.

Ediacaran body fossils. These successions fine upward over 2 m into a medium-grained sandstone with small pebble-sized clasts and are capped with a thin layer of fine-grained sand. Another fining-upward interval occurs from 6 to 9 m, recording 20 cm beds of thick, coarse-grained sandstone interbedded with ~30 cm layers of fine-grained sandstone with oscillation ripples (Fig. 3.4). The Nasep–Huns boundary likely falls somewhere in the intermediate ~6 m of nonexposure as the next outcrops appear at ~15 m and consist of >2 m layers of interbedded mudchip-dominated limestone and micaceous fine-grained, silty sandstone, some containing coarser-grained sand. There is no exposure from 27 to 35 m, where ~4 m of weathered
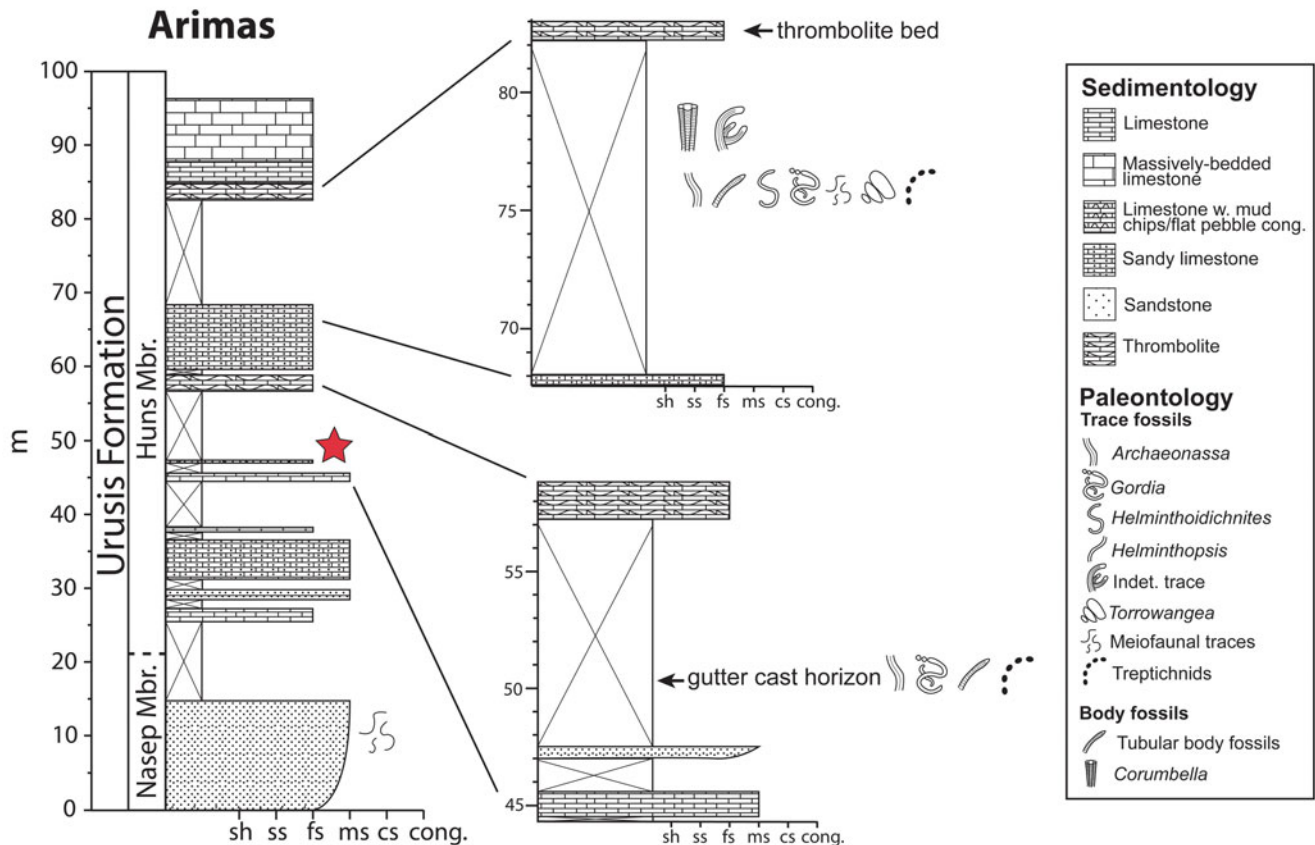
Figure 4. Stratigraphy of the Nasep–Huns exposures at Farm Arimas, with (right) fossil-bearing intervals expanded. Star indicates approximate location of the treptichnid-bearing horizons described by Jensen et al. (2000) and Buatois and Mángano (2016). 'sh' = shale; 'ss' = siltstone; 'fs' = fine sand; 'ms' = medium sand; 'cong.' = conglomerate.

black limestone outcrops. After a thin >1 m interval of the same carbonate material with sandy inclusions at 43 m, the section resumes at 50 m with the characteristic weathered Huns carbonate before ceasing at approximately 56 m.

The Nasep–Huns transition at Farm Arimas is more extensive than its counterpart at Canyon Roadhouse, with approximately 96 m of vertical exposure (Fig. 4). The uppermost Nasep constitutes the lower 15 m of the section and is composed of reddish-brown medium-grained sandstone with intermittent oscillation ripples and channelization, as well as meiofaunal traces. The Nasep–Huns boundary is presumed to fall within the successive 10 m of nonexposure as the next exposure (at approximately 25 m) indicates a transition into the characteristic Huns limestone. The next 30 m alternate between <2 m thick exposures of Nasep-type sandstone and more extensive 3–5 m exposures of weathered, sandy, black limestone with ~25 cm thick beds and small-scale laminations. A thrombolite horizon within the bedded limestone appears around 56 m, and the nonthrombolitic sandy limestone continues upward in massive, meter-scale blocks until approximately 68 m. This is succeeded by a 15 m interval of nonexposure, which is capped by approximately 13 m of the massive limestone.

The interval of nonexposure at Farm Arimas from 47 to 56 m is of particular taphonomic interest. Judging from material found in nearby float, these fine-grained sandstone horizons preserve a variety of microbially induced sedimentary structures as well as abundant gutter casts, which preserve a variety of scour-related and biogenic structures on their lower surfaces (Fig. 5.2; see also Jensen et al., 2000; Buatois and Mángano, 2016). The gutter cast horizons (located at ~48 and ~70 m in the section measured at Farm Arimas and at ~20 m in the section measured at Canyon Roadhouse) are observed in the fine-grained siliciclastics of the uppermost Nasep/lowermost Huns. These structures can be indicative of sediment by-pass resulting in small-scale (5–10 cm in width) downslope flows (see Mángano et al., 2002) and are a common source of trace fossils across the Nasep–Huns transition. Comparatively high trace-fossil diversity (multiple ichnotaxa indicating a range of tracemaker behaviors) is present on the underside of the gutter casts sourced from fossil horizons at Farm Arimas and Canyon Roadhouse; by contrast, nongutter casts tend to preserve the majority of body fossils in these intervals.

Microbially induced sedimentary structures.—A number of microbially induced sedimentary structures (MISSs) are present across the Nasep–Huns transition, including Kinneyia and Intrites. These structures are thought to form due to sediment deformation under the microbial mats that blanketed large swathes of the seafloor during the late Ediacaran (Bouougri and Porada, 2007; although see Pratt, 2021 for an alternative mechanism of Kinneyia formation). First described

Figure 5. Sedimentary structures from Farm Arimas: (**1**) oscillation ripples; (**2**) gutter cast trace assemblage. Dashed lines indicate approximate cast boundaries. White arrows indicate biotic structures; black arrows indicate sole marks; (**3**) parabolic flutes and (**4**) linear tool marks, both with white arrows denoting meio-faunal traces; (**5**) soft-sediment fluidization structures similar to the pseudofossil Aristophycus (see Knaust and Hauschke, 2004). Scale bars = 1 cm.
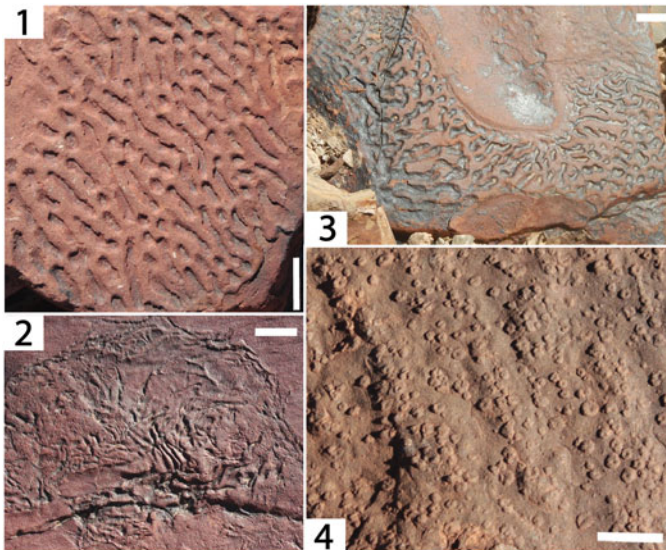

Figure 6. Microbially induced sedimentary structures from the Nasep–Huns transition at Farm Arimas: (**1, 3**) Kinneyia; (**2**) wrinkle mat fabric; (**4**) Intrites. Scale bars = 1 cm.

by Walcott (1914), Kinneyia (Fig. 6.1, 6.3) is characterized by linear to slightly curved crests separated by highly variable (0.2–2 cm) distances (Porada et al., 2008). Crests are approximately 1–2 mm wide, and the transitions into the intra-crest round-bottomed troughs is extremely steep. These structures occur on upper bedding surfaces, primarily in

sandstone or shale. Kinneyia structures appear most commonly between the Neoproterozoic and Ordovician, although similar structures have been found as early as the Archean and possibly as late as the Neogene (Hagadorn and Bottjer, 1997; Noffke et al., 2003; Carmona et al., 2012). Proposed mechanisms of formation for Kinneyia center on unstable sediments beneath the original microbial mat, although the causal forces (e.g., shear-induced mat instability, oscillation of microbial aggregates, liquefied substrate) remain debated (Porada et al., 2008; Thomas et al., 2013; Herminghaus et al., 2016). By contrast, experimental work by Mariotti et al. (2014) suggests that Kinneyia-type structures instead indicate the absence of an overlying mat, arguing the characteristic crest–trough form derives from wave-induced movement of microbial agglomerations at an exposed sediment–water interface.

Originally interpreted as a body fossil, Intrites (Fig. 6.4) was redescribed by Menon et al. (2017) as a fine-grained "sediment volcano" or fluid escape structure that forms as a result of small-scale tears in the overlying microbial mats. As material buildup progressed around the ejecta site, cyanobacteria were likely attracted to the potential for increased access to light on the raised structure; thus, the repeated sediment–biofilm–sediment accretion cycle may have produced microstromatolites in the characteristic Intrites torus form (Gerdes et al., 1994).

Trace-fossil diversity of the Nasep–Huns transition

The first account of ichnofossils in the Nama was published by Germs (1972), who documented five types of vermiform traces in the Nasep (although Archaeichium Glaessner, 1963 has since been revised to represent a body fossil; see Glaessner, 1978). Geyer and Uchman, (1995) reported a number of ichnogenera from the Nasep, including Torrowangea rosei Webby, 1970, cf. Trichophycus pedum, two ichnospecies of Palaeophycus Hall, 1847, and three ichnospecies of Planolites Nicholson, 1873 (including cf. P. montanus Richter, 1927), in addition to Skolithos Haldeman, 1840, Brooksella Walcott, 1896, Curvolithus Fritsch, 1908, and Didymaulichnus Young, 1972 noted in earlier accounts by Germs (1983) and Crimes and Germs (1982). Geyer and Uchman (1995) also described two morphotypes of Skolithos from the Nasep and Huns, a trace historically associated with the Cambrian onward (Mángano and Buatois, 2014). If accurate, this would indicate vertical burrowing was occurring far earlier than previously thought, although we note Jensen (2003) questioned these identifications, instead suggesting they more likely represent body fossils with some part of the organism rooted in the sediment. Jensen et al. (2000) focused exclusively on trace fossils from the Nasep–Huns transition, noting the presence of treptichnids, "small trace fossils," as well as the body fossils Nasepia Germs, 1973, Archaeichnium, and "annulate tubes."

The primary trace fossils found within Nasep and Huns exposures at Farm Arimas and Canyon Roadhouse represent simple, horizontal vermiform pascichnia or fodinichnia, although there are a number of morphologically distinct forms present under this greater classification (Archaeonassa Fenton and Fenton, 1937, Gordia Emmons, 1844, Helminthoidichnites
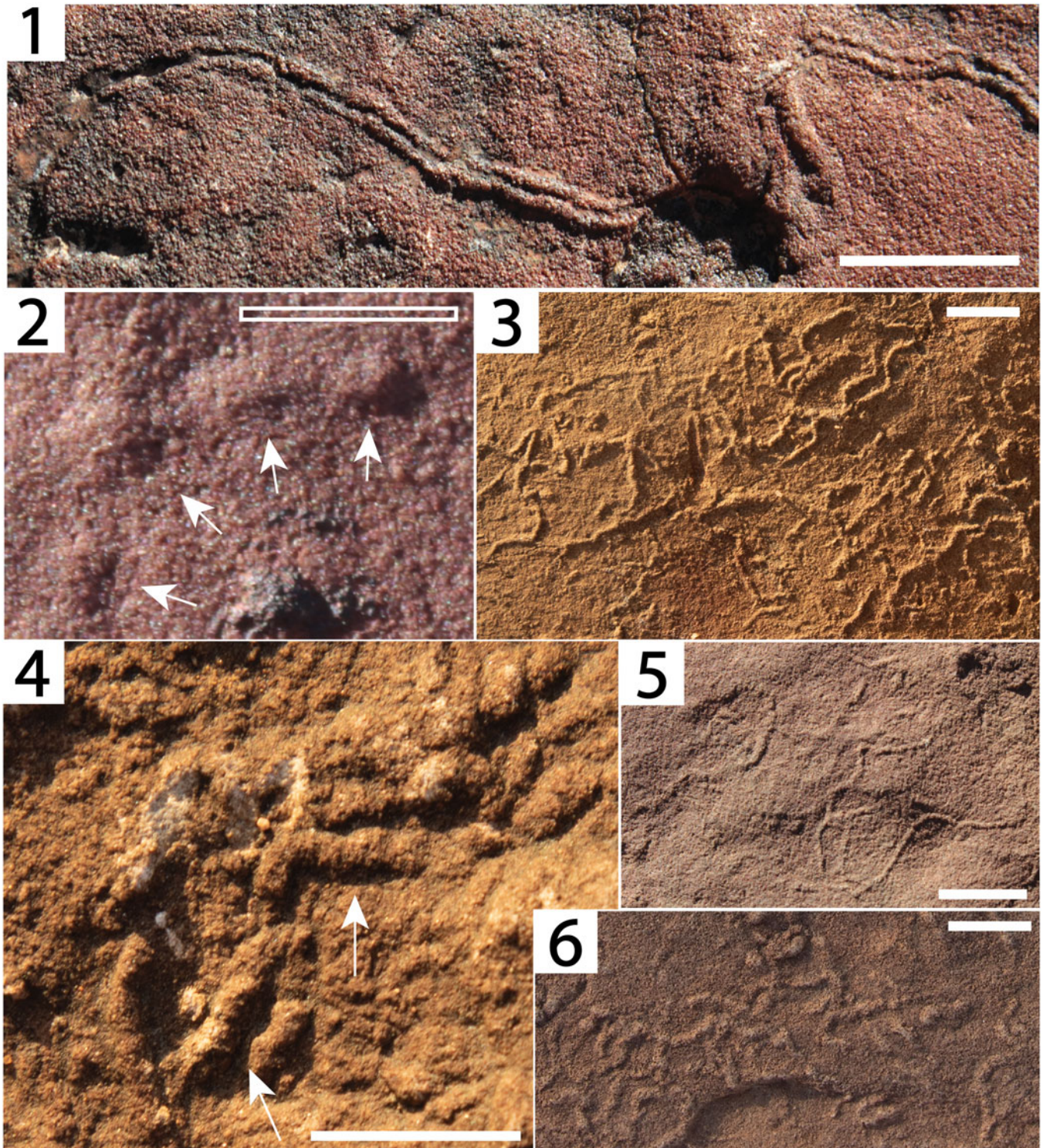
Figure 7. Nasep–Huns ichnofauna: (**1**) *Archaeonassa* from Canyon Roadhouse; (**2**) treptichnids from Farm Arimas, with arrows denoting individual segments; (**3**) *Helminthoidichnites* from Canyon Roadhouse; (**4**) *Torrowangea* from Canyon Roadhouse, with irregular constrictions indicated by arrows; (**5**) *Helminthopsis* from Canyon Roadhouse; (**6**) *Gordia* from Canyon Roadhouse. Filled scale bars = 1 cm; hollow scale bar = 2.5 mm.

Fitch, 1850, and *Helminthopsis* Heer, 1877; see Fig. 7.1, 7.3, 7.5, 7.6). Also present to a lesser extent are actively filled horizontal forms (*Torrowangea*; see Fig. 7.4), horizontal burrows with vertical components (treptichnids; see Fig. 7.2), and irregular meiofaunal networks (Fig. 8). These ichnogenera will be described in greater detail in the following.

Archaeonassa are described as convex furrows separated by a midline groove, 1–7 mm in width and often preserved in positive epirelief (Fig 7.1; also see Darroch et al., 2020, fig. 9g). Traces are commonly straight to mildly sinuous and are thought to represent pascichnia attributable to a range of invertebrate taxa (Yochelson and Fedonkin, 1997). In their original
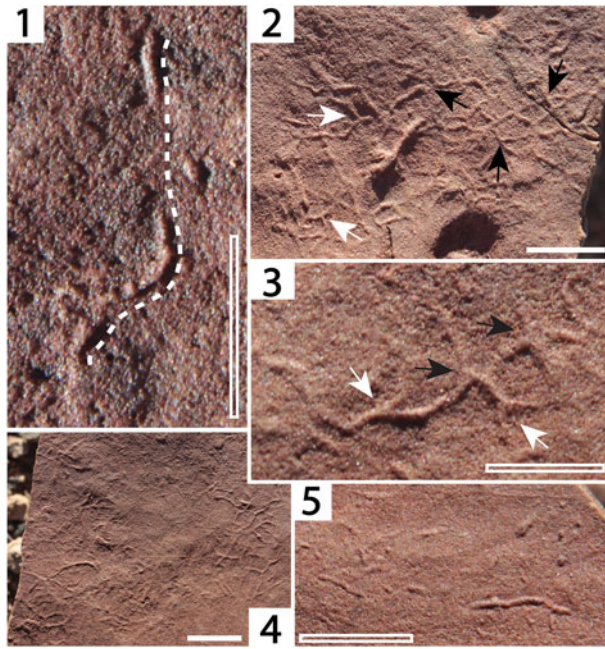
Figure 8. Meiofaunal traces from the upper Nasep at Farm Arimas: (**1**) individual exhibiting movement in and out of the sediment, with dotted line providing trajectory visualization; (**2, 3**) meiofaunal networks exhibiting both branching (white arrows) and overcrossing (black arrows); (**4**) trace network; (**5**) individual specimen dipping below surface and reemerging. (**1, 3, 5**) Hollow scale bars = 5 mm; (**2, 4**) filled scale bars = 1 cm.

description, Fenton and Fenton (1937) suggested a gastropod origin for *Archaeonassa* (although this was contested by Yochelson and Fedonkin, 1997); Buckman (1994) later posited potential attribution to echinoderms or arthropods. However, neoichnological work by Matz et al. (2008) found similar bilobate traces could plausibly be left by nonbilaterian giant protists such as *Gromia*. *Archaeonassa* found in late Ediacaran strata from Ukraine suggest a degree of undulation in and out of sediment underneath microbial mats, as well as general movement perpendicular to the paleoshoreline and parallel to tides, potentially indicating very early taxis (Uchman and Martyshyn, 2020). *Archaeonassa* is present at both Canyon Roadhouse and Farm Arimas despite being noticeably rarer than at Farm Haruchas (basal Vingerbreek Member, Nudaus Formation, lower Schwarzrand Subgroup; see Bouougri and Porada, 2007).

Gordia (Fig. 7.6; also see Darroch et al., 2020, fig. 9d) is composed of nonbranching traces displaying a high degree of self-crossing, a criterion used to differentiate it from the morphologically similar *Helminthoidichnites* and *Helminthopsis* (Getty et al., 2017). *Gordia* is most frequently interpreted as unspecialized infaunal pascichnia of annelids or priapulids (Buatois et al., 1998; Wang et al., 2009). Occasional abrupt terminal segments ("pustules") suggest a movement of a proboscid frontal organ into the vertically adjacent sediment, which could indicate priapulid affinities (Wang et al., 2009). *Gordia* is most typically found in gutter casts from the uppermost Nasep/lowermost Huns but is scarce outside of these structures. A number of the basal Huns specimens record the aforementioned pustules, indicating the tracemakers possessed a degree of vertical movement capabilities.

Helminthoidichnites represents nonmeandering, straight to curved horizontal traces 1–10 mm wide, most typically interpreted as pascichnia and attributed to nematomorphs (Buatois et al., 1998; Schlirf et al., 2001; Fig. 7.3). Specimens are generally preserved in negative epirelief or positive hyporelief (Darroch et al., 2020). Individuals of *Helminthoidichnites* exhibit overcrossing between individuals, and some degree of "looping" is observed; however, computer simulations have demonstrated these loops exhibit greater randomness than do those of *Gordia* (Hofmann, 1990). *Helminthoidichnites* is abundant across the Nasep–Huns transition and is most often found on the underside of gutter casts in concert with other vermiform traces.

In contrast to *Helminthoidichnites*, *Helminthopsis* (Fig. 7.5; also see Darroch et al., 2020, fig. 7b) are nonlooping horizontal trails 1–10 mm wide interpreted as unspecialized fodinichnia and most often preserved in negative epirelief or positive hyporelief (Hofmann and Patel, 1989). Traces are winding to meandering and do not touch or self-cross (Fillion and Pickerill, 1990). Individuals are typically preserved in negative epirelief. The presence of marginal ridges suggests the trails were formed by displacement of sediment by the tracemakers and that these structures remained open for a time post passage (Jensen et al., 2006). *Helminthopsis*, together with *Helminthoidichnites,* represent the most abundant traces found at Canyon Roadhouse and Farm Arimas. As with many of the vermiform traces present at these sites, this ichnotaxon is largely confined to preservation within the gutter cast communities from ~70 m at Farm Arimas and ~20 m at Canyon Roadhouse.

Torrowangea is the sole example of actively filled burrows from the Nasep–Huns (Fig. 7.4; also see Darroch et al., 2020, fig. 9e). This ichnogenus is composed of transversely annulated, meandering to sinuous horizontal burrows characterized by intermittent constrictions thought to indicate a degree of peristaltic motion (Narbonne and Aitken, 1990; Kim and Pickerill, 2003; Jensen et al., 2006). Specimens are always preserved in positive epirelief, and backfill has the same sedimentary composition as the surrounding matrix. *Torrowangea* is most often interpreted as a vermiform deposit feeder burrowing below the sediment–water interface (Buatois and Mángano, 2016); however, some studies demonstrate the formation of structurally similar traces by benthic foraminiferal pseudopoda (Severin et al., 1982; Kitazato, 1988). *Torrowangea* is present at both Farm Arimas and Canyon Roadhouse and typically presents as 3–5 mm wide burrow structures interweaving to form a greater tangled structure. Individual burrows are meandering and characterized by sporadic constrictions, which provide for differentiation from the visually similar *Archaeichnium*. *Torrowangea* is found at the gutter cast horizons, although it is not typically associated with the vermiform trace-dominated gutter cast communities. Instead, it typically forms monospecific occurrences.

Treptichnids are an informal grouping of serial vertically penetrating burrows; in the Nasep–Huns, these are represented by discrete ovoid probes typically ~1–3 mm long that follow a curvilinear to semicircular pathway and are characteristically preserved in positive hyporelief (Fig 7.2; also see Darroch et al., 2020, fig. 13a, b). The first report of these traces from the Nasep (Germs, 1972) details parallel-ridged trails ~3 mm wide that terminate and reappear at regular intervals. Jensen et al. (2000) later identified these traces as *Treptichnus*
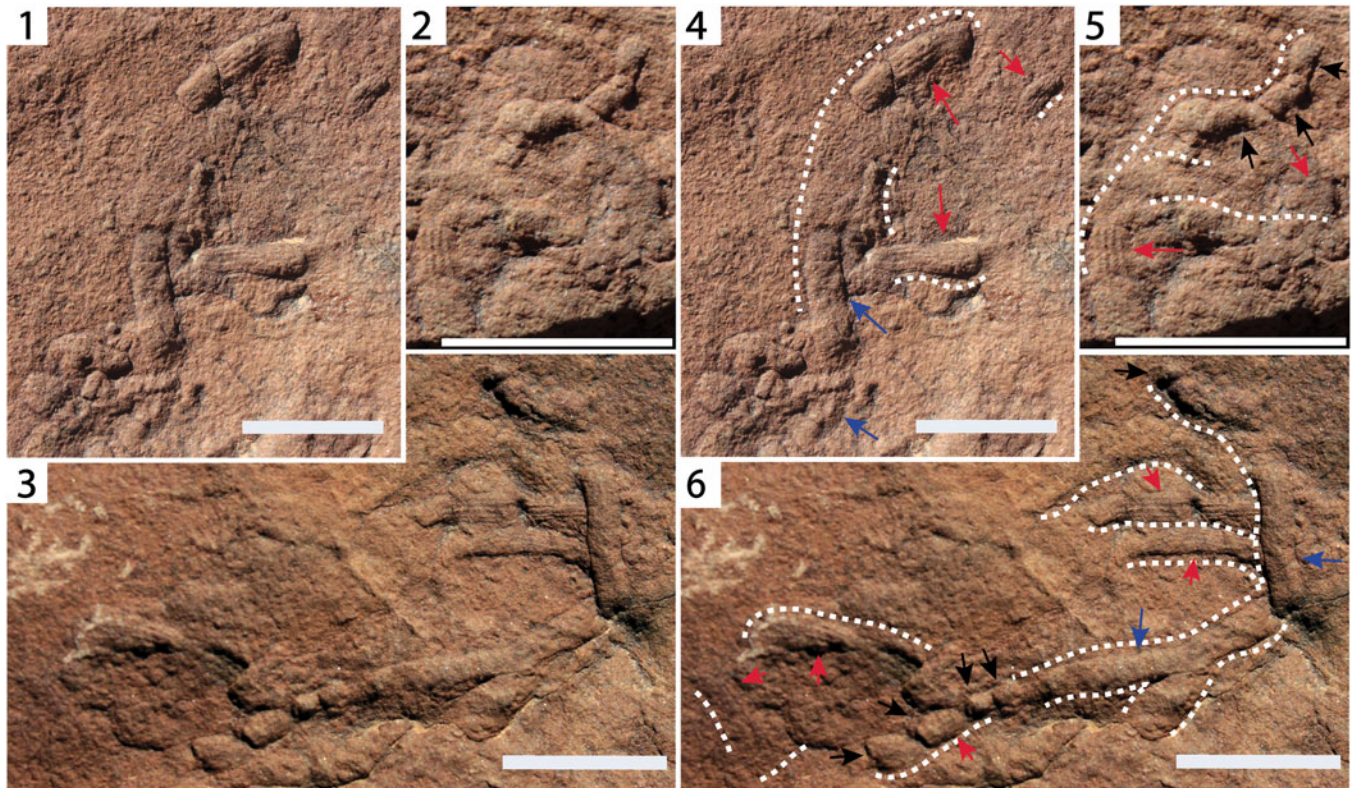
Figure 9. Indeterminate trace fossils from Farm Arimas (GSN F1643): (**1–3**) original images; (**4–6**) annotated material. White dotted lines indicate individual overcrossing probe structures, including indications of subsurface movement. Colored arrows denote dichotomous surface patterns, with blue showing posterior transverse annulation and red marking anterior longitudinal striations. Black arrows indicate abrupt probing "nubs" similar to those of *Gordia*. Scale bars = 1 cm.

isp., noting their morphological similarities to *Treptichnus pedum,* albeit at a far smaller scale and with greater unidirectional probe tendencies. This suggests the treptichnids (determined by Jensen et al., 2000 to be from the Huns rather than the Nasep originally documented by Germs) likely represent more "advanced" bilaterian behavior below the Cambrian boundary (Jensen et al., 2000). Treptichnid specimens are found in both the uppermost Nasep and basal Huns at Canyon Roadhouse and Farm Arimas; at both sites, these traces are preserved as part of the larger gutter cast ichnofossil assemblages but are much smaller relative to the other traces.

Meiofaunal networks from this interval are high-density assemblages composed of millimeter-scale horizontal trace fossils 0.3–0.5 mm wide and exhibiting a high degree of overcrossing (Fig. 8). First described by Germs (1972) as "thread-like trails" from the Nasep of Farm Arimas, these traces are often found in conjunction with treptichnids and other vermiform burrowers. Individual traces over- or undercross but do not pass through each other. Some specimens exhibit slight vertical movement in and out of the horizontal plane similar in character to *Yichnus levis* (Xiao et al., 2019) from the terminal Ediacaran Shibantan member of China, although at a much smaller scale. Traces of similar appearance to those figured by Germs (1972) are found in the upper Nasep and lower Huns at both Farm Arimas and Canyon Roadhouse, where they are most commonly preserved within the greater gutter cast trace assemblage and exhibit occasional instances of dichotomous branching (Fig. 8.2, 8.3). Further inspection of these specimens suggests

morphological differences between these traces ("Form A" as described by Darroch et al., 2020) and those found in the terminal Ediacaran Spitskop Member ("Form B" from Darroch et al., 2020, frequently displaying right-angle branching and regular movement above and below the sediment surface), indicating the possibility of two distinct meiofaunal behaviors within the Urusis Formation.

Of note from Arimas is an indeterminate trace fossil (GSN F1643; Fig. 9) composed of meandering 1–3 cm (length) tubes that intertwine to create a larger, braided form. Tubes are 2–3 mm wide, with longitudinal striations ~0.4 mm apart present toward the distal ends. A number of specimens display a shift from the grooved pattern into faint transverse annulations in the medial portion (see Fig. 9.4, 9.6). In multiple instances, tubes appear to dip below the sediment surface and reemerge consistent with the direction of motion, suggesting a degree of bioturbative activity (see Fig. 9.5, 9.6). Structures terminate with minimal evidence of tapering, and some appear to exhibit *Gordia*-type probing "nubs." A number of individual tubes are capped by a slightly wider, rounded structure, producing a bulbous effect. This trace material is present on a single slab composed of multiple individuals from Farm Arimas. The horizon lies in the upper portions of Huns exposure (a few meters above the gutter cast/trace horizon at ~70 m) and are likely also the source of *Corumbella* body fossils described in the next section.

These striated traces are similar to the material described by Glaessner (1963) as *Archaeichnium haughtoni.* While originally

classified as a trace, Glaessner (1978) later revised his assessment of *Archaeichnium* to that of a body fossil, although he noted definitive assignment to either one of these categories is difficult. Traces exhibiting similar flexible collapse have been described from the Cambrian of Sweden (see Jensen, 1997, fig. 49). In addition, both the individual tubes and the greater braided mass of the Huns material bear noticeable similarities to priapulid trace material described from the lower Cambrian of Sweden by Kesidis et al. (2019).

The longitudinal striations are consistent (both in approximate size and placement) with sensory papillae ridges (scalids) present on the proboscides of extant scalidophoran priapulids such as *Priapulus caudatus* Lamarck, 1816 (see Hammond, 1970a, b, fig. 1). These grooves remain equidistant throughout the anterior portion of the probes. However, as this material is preserved in positive semirelief, assessment of the full number of striations is difficult.

The materials recovered by our group also exhibit two distinct surface patterns that support scalidophoran affinities: a striated, bulbous distal portion that transitions into a transversely annulated proximal section. Modern priapulids move through sediment by evagination of the frontal introvert (see Calloway, 1975, fig. 1), followed by peristaltic contractions that shorten the annulated trunk. As the peristaltic wave reaches the posterior praesoma, the introvert retracts and the body shifts into the now-vacated anterior space (see Elder and Hunter, 1980, table 1 and fig. 1). Neoichnological experiments by Kesidis et al. (2019) demonstrated that this method of locomotion results in dual-patterned burrows strikingly similar to the specimens described here. In addition, while the burrows of larger priapulids such as *P. caudatus* tend to close immediately post passage, smaller species (e.g., *Halicryptus spinulosus* von Siebold, 1849) can leave smaller open structures behind, which likely provide greater preservation potential as sediment is infilled (Powilleit et al., 1994); however, the presence of microbial mats may affect this taphonomic paradigm (see Yallop et al., 1994). This preservational tendency toward smaller burrows is consistent with the specimens collected for this study, which are smaller in both length and width than the exceptionally preserved material described by Kesidis et al. (2019).

The horizontality and slight penetrative behavior of the traces are also consistent with some accounts of priapulid burrowing behavior investigated under laboratory settings. Experiments by Vannier et al. (2010) demonstrated that when constrained to a single horizontal plane, *P. caudatus* will produce burrow traces morphologically similar to the material described here (see Vannier et al., 2010, fig. 1D). However, their imposed vertical restrictions are largely artificial and do not reflect the natural environment of priapulids, which also display tendencies to burrow vertically. As such, our interpretations should be viewed cautiously.

Body fossils

While this study is focused primarily on the ichnofauna of the Nasep–Huns transition, there are also body fossils preserved in the sections that provide important supplementary evidence as to the temporal placement of the units and the suite of ecologies present.
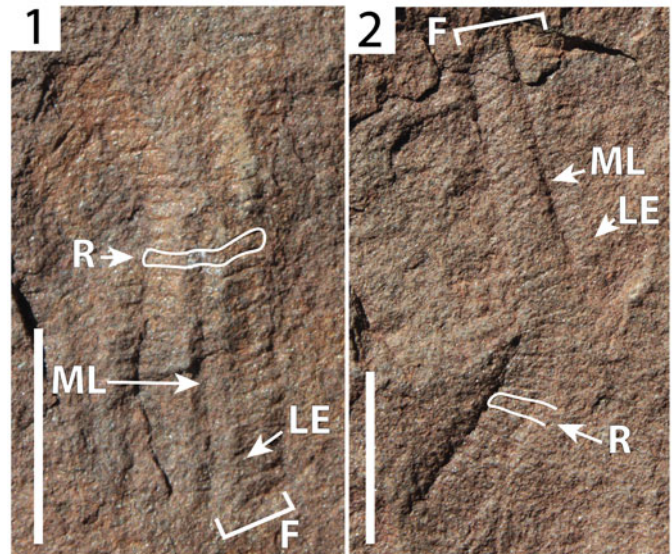

Figure 10. Two Huns *Corumbella* specimens from Farm Arimas (GSN F1644): (**1**) individual with multiple faces preserved; (**2**) specimen with single face preserved exhibiting degree of flexibility. Labels included reference to Pacheco et al. (2015). F = face; LE = lateral edge; ML = midline; R = ring. Scale bars = 1 cm.

Corumbella Hahn et al., 1982 is described as an annulated tubular structure of length up to ~80 mm and diameter up to 25 mm extending from a basal aboral region (often found extending into the substrate) into an oral region (Babcock et al., 2005; Pacheco et al., 2015). Tubes possess fourfold radial symmetry and suggest a high degree of flexibility. Hagadorn and Waggoner (2000) described a second form of the genus from the Great Basin of the western United States, termed *Corumbella* new species A, which exhibits a helical twist and lacks the secondary branched polypar of the specimens originally described by Hahn et al. (1982). However, Babcock et al. (2005) noted the presence of a similar helical twist in *C. werneri* Hahn et al., 1982 specimens from Brazil, and thus suggested it may in fact bear no taxonomic significance. While members of the genus are most often interpreted as scyphozoan cnidarians, recent work by Walde et al. (2019) has suggested *Corumbella* might instead represent calcareous sinotubulitids.

The *Corumbella* specimens (GSN F1644; Fig. 10) recovered by our group from the Huns represent the first-known occurrence of the genus from Namibia. These individuals are preserved on a single upper-Huns (~73 m) slab from Farm Arimas, with some exhibiting a degree of lateral flexibility consistent with corumbellids from other Ediacaran sites (see, e.g., Hagadorn and Waggoner, 2000, figs. 5.4–5.5; Pacheco et al., 2015, fig. 4; Vaziri et al., 2021, fig. 2). Septa are clearly visible and form ~0.5 mm rings with defined midlines; neither the oral nor aboral regions appear preserved for any individual. As such, assignment to either *C. werneri* or a separate species is difficult; the lack of clearly defined torsion in the Huns specimens would suggest affinity with *C. werneri*, but the limited extent of the preserved individuals prevents assessment as to the presence/absence of the second polypar.

A suite of tubular body fossils 1–5 mm in diameter displaying a high degree of morphological variability is found
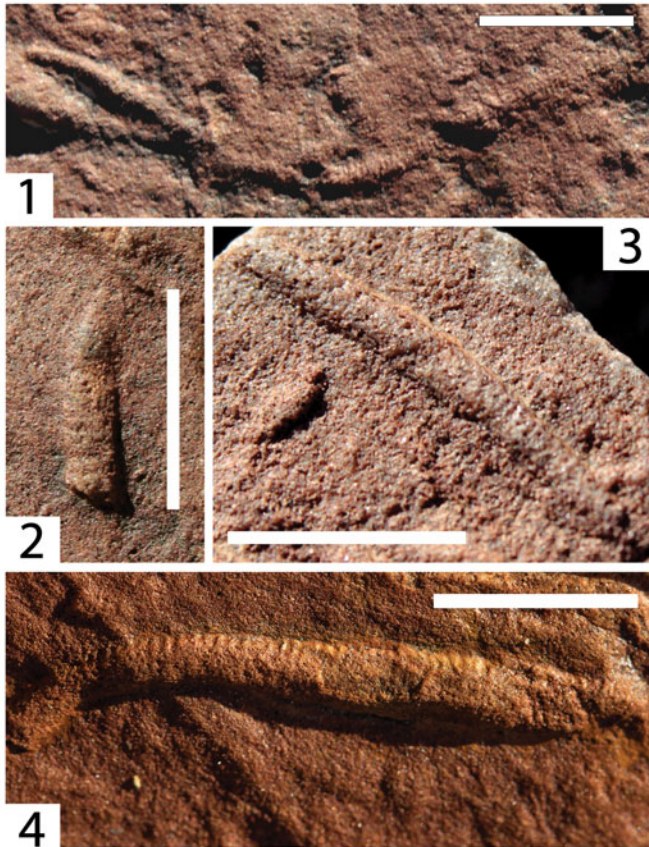
Figure 11. Tubular body fossils from the Nasep–Huns: (**1, 2, 4**) examples from Farm Arimas; (**3**) example from Canyon Roadhouse. Note preservation of tapered ends (**1, 3**) and defined annulations (**1, 2, 4**). Scale bars 1 = cm.

throughout the study area (Fig. 11). Specimens similar to this type have historically been assigned to *Archaeichnium*; however, this singular taxonomic designation likely obscures the breadth of tubular morphological diversity present across the Nasep–Huns.

Unlike the possible priapulid trace material, these tubular body fossils do not possess longitudinal striations and are instead characterized by transverse annulations spaced approximately 1 mm apart (Hagadorn and Waggoner, 2000). These structures are thought to be flexible due to lack of clean breaks, and the body orientations suggest current alignment. Tentative interpretations suggest similarities to other late Ediacaran tubular metazoans (cf. Droser and Gehling, 2008; Cai et al., 2011; Cortijo et al., 2015; Smith et al., 2016; Schiffbauer et al., 2020). A number of individuals possess conical terminal tapers, and diagnoses are reliant on the presence of these tapered ends. As such, due to the number of annulated and tubular metazoan taxa associated with the Nama Group, identification can be more difficult when the conical tapers are absent. Other tubular taxa present across this interval include "kinked-funnel" structures and stacked cone-in-cone forms that bear similarities to the "cloudinomorph" form grouping described by Selly et al. (2020). Further systematic work is needed to address the breadth of tubular morphological disparity across the Nasep–Huns transition.

Discussion

Detailed investigations of the Nasep–Huns transition at Canyon Roadhouse and Farm Arimas confirm this interval preserves among the highest diversity of trace fossils known from latest Ediacaran-aged sediments anywhere (see Darroch et al., 2020). Moreover, the presence of the terminal Ediacaran index fossil *Corumbella* in these sections bolsters biostratigraphic links between Brazil, Paraguay, Iran, the southwestern United States, and Namibia (Hagadorn and Waggoner, 2000; Babcock et al., 2005; Warren et al., 2011; Vaziri et al., 2018). We first discuss the composition of fossil communities, followed by paleoenvironmental reconstruction and potential controls on trace-fossil preservation.

Fossil communities.—The Nasep–Huns transition preserves a varied suite of trace and body fossils from a shallow marine environment that was at least intermittently colonized by seafloor microbial mats. These ichnofossil communities, comprising *Archaeonassa*, *Helminthopsis*, *Helminthoidichnites*, *Gordia*, *Torrowangea*, sub-centimeter-scale treptichnids, and meiofaunal burrow systems represent a trace-fossil assemblage that is either of comparable diversity to, or significantly more diverse than, those described from other late Ediacaran localities worldwide (Narbonne and Aitken, 1990; Weber et al., 2007; Högström et al., 2013; Parry et al., 2017; Tarhan et al., 2020). Material from the upper Nasep/lower Huns is further notable for its relatively high intraslab trace diversity, including a number of ichnotaxa in direct association with each other (Fig. 5.2). In terms of behavioral complexity, several ichnotaxa (*Archaeonassa, Gordia,* treptichnids) exhibit both movement along the sediment–water interface and a degree of movement above and below the sediment surface. In the case of *Gordia* and the treptichnids, this likely represents probing behavior, indicating the tracemakers were exploiting vertical space in search of nutrients. While the primary trace attributions (fodinichnia and pascichnia) suggest a community dominated by mat grazers (Buatois et al., 2014), these sections are punctuated by organisms that may have been exploiting the mat-free substrate provided by the gutters. *Torrowangea* provides supplementary support for subsurface life habits, likely representing a deposit feeder outside of the gutters. The presence of these ichnotaxa suggests there is likely a higher diversity of depth-related niches present in these assemblages than has been described for most coeval localities and thus a degree of ecological complexity that is higher than usually attributed to late Ediacaran communities (Darroch et al., 2020).

The meiofaunal traces noted here bear superficial morphological similarities to Ediacaran nematode traces from Brazil (see Parry et al., 2017) and are of comparable size. Although these burrows exhibit frequent overcrossing (and thus give the impression of forming genuine "networks"), they also appear to possess rare instances of dichotomous branching (see Fig. 8). In addition, they exhibit a similar surface-level vertical tiering and share an overall sinuosity with the meiofauna from Brazil; however, they are far more linear than the sinuous Ordovician *Cochlichnus*-like meiofaunal traces described by Baliński et al. (2013). Modern meiofauna plays important roles in a

number of ecological processes, including nutrient cycling and vertical chemostratigraphic flux (Schratzberger and Ingels, 2018), implying similar styles of ecosystem engineering may have been active in the latest Ediacaran of Namibia.

The material tentatively identified here as probes left by priapulid worms also has significant implications for the complexity of late Ediacaran ecosystems. Priapulids are crown-group ecdysozoans; this indicates the presence of crown-group Bilateria before the Cambrian boundary and in turn significant metazoan overlap between Ediacaran and Cambrian benthic communities. The presence of scalidophorans in these strata would suggest some degree of active predation was occurring, as modern priapulids have been overwhelmingly predatory since the early Paleozoic (Brett and Walker, 2002). While scavenging behaviors have been documented from the Ediacaran of Australia (Gehling and Droser, 2018), and definitive examples of macroscopic predation are known from the uppermost Ediacaran of China (Hua et al., 2003), priapulid traces in the Nasep–Huns would provide significant support for the Precambrian advent of metazoan predation, suggested to be a major ecological driver of the Cambrian Explosion (Erwin et al., 2011; Erwin and Tweedt, 2012).

In addition, the putative priapulid material could shed light as to the nature of the substrate during deposition. Priapulids can burrow both vertically and horizontally; however, when vertical space is constrained, they will often produce more lateral burrows (Vannier et al., 2010). When moving in this way, they will frequently leave their frontal introverts or caudal portions at the sediment–water interface, which Kesidis et al. (2019) suggested likely serves a respiratory function. While these vertical restrictions are artificial when introduced in a laboratory setting, it is possible that the paleoenvironments of the late Ediacaran imposed similar controls, such as the presence of a redox discontinuity surface (RDS) at a comparatively shallow depth (Buatois and Mángano, 2011; Kesidis et al., 2019). This would be consistent with our understanding of Ediacaran sediments in the lead-up to the Cambrian substrate revolution, in which a positive feedback loop of increasing bioturbation frequency and intensity led to deepening of the RDS (Bottjer et al., 2000; Mángano and Buatois, 2014). These proposed priapulid traces exhibit shallow movement above and below the sediment–water interface. This could suggest some form of natural constraint against their tendency to burrow vertically, perhaps indicating a chemostratigraphic or physical barrier to deeper movement.

Paleoenvironmental reconstruction.—The stratigraphy of this interval suggests an overall shoreline transgression resulting in a transition from a coastal-plain/shallow-water environment to a lower-shoreface setting (Saylor, 2003). At Canyon Roadhouse, the presence of climbing ripples (Fig. 3.1) within the Nasep Member indicates lateral sediment migration coupled with net lateral deposition (Allen, 1970). In this case, the combination of lateral and vertical sediment accumulation points to increased sediment supply while the presence of turbidity flows indicates a general level of sediment instability (Saylor, 2003). This idea is supported by the abundance of gutter casts at Farm Arimas (Fig. 5.2) and Canyon Roadhouse, although we note that gutter casts can also be generated by storm-generated flows (Myrow, 1992a; Pérez-López, 2001).

The large numbers of centimeter-scale tool marks (Figs. 3.5, 5.3, 5.4) and current-aligned tubular body material found in these strata are also indicative of relatively high-energy transport during deposition (Darroch et al., 2020). In addition, the lowermost Huns exposures at Canyon Roadhouse are composed of limestone with mudstone chip inclusions (Fig. 3.2), indicating high-energy erosional flows were occurring during this interval (Myrow, 1992b; Myrow and Southard, 1996). As the section transitions further into the Huns Member, the facies indicate corresponding change in sediment supply and lithology and shift to a lower-shoreface environment. The relative paucity of sedimentary structures stratigraphically higher in the Huns suggests deposition was occurring below wave base (Saylor, 2003).

Potential controls on trace-fossil preservation.—Several ichnotaxa, in particular the small treptichnids and meiofaunal burrows, are most commonly found preserved in positive hyporelief on the bases of gutter casts, raising an interesting question as to whether the tracemakers were actively exploiting these areas. The presence of widespread MISS (in particular, Kinneyia and Intrites) suggests that much of the sedimentary surface in the Nasep–Huns transition was colonized by microbial mats and may have posed a physical and chemical barrier to penetration by small metazoan fauna. In this scenario, the removal of microbial mats through the formation of gutter casts may have exposed organic-rich sediments that could be quickly exploited by opportunistic bilaterian metazoans (see Pemberton et al., 1992). In addition, the lack of an obscuring mat layer in these instances could have facilitated the preservation of these traces as further sediment deposition occurred; we note that this scenario requires an interval of stasis between the formation of the gutter and subsequent deposition of the sediment cast to preserve the "true substrate" (see Davies and Shillito, 2021).

An alternative scenario involves these tracemakers being widespread throughout the paleoenvironment but preserved only in gutter casts (as in the preceding, during an interval of stasis between formation of the gutter and subsequent infilling by sediment) where the overlying microbial mat has been removed. Wray (2015) suggested that the microbial mats that typify much of the late Ediacaran may not have been ideal for preserving surface structures as the object (or organism) had to penetrate the mat and disturb the sediment underneath for the structure/trace to be recorded; this would be especially true for extremely small tracemakers (although Buatois and Mángano, 2012, 2016 pointed out that microbial mats can often enhance the preservation of smaller-scale ichnofossils due to their inherent microbial binding capabilities, while Gingras et al., 2011 noted that modern microbial mats are often found associated with high infaunal animal diversities, due in large part to the increased oxygen content relative to overlying water). This preservation potential would, however, depend on a number of factors, including mat type (epi- versus endobenthic) and thickness. We also note that lithological contrast at the interface between underlying and infilling sandstones may have played a role in preserving these traces; the smallest fossils are most often found in positive relief on the underside of gutter casts (i.e., positive hyporelief), which could conceivably be the result of finer

material casting small burrows formed in underlying substrate. However, given that we have thus far found gutter casts only as loose blocks, this taphonomic model remains a hypothesis. If correct, however, it follows that small bilaterian traces (including treptichnids) might be more widespread in these intervals than is currently recognized and that gutter casts may represent valuable taphonomic windows in which optimal rheological conditions can help preserve traces left by tiny metazoans.

A final alternative involves the tracemaking organisms being caught up in flow and deposited at the interface of the gutter casts during burial. This might imply that traces preserved on the bases of gutter casts thus represent escape behavior ("fugichnia"); however, the observation that most traces found in these slabs appear typical (e.g., the regular "probes" formed by small treptichnids; see Fig. 7) might constitute an argument against this. A detailed reinvestigation of these traces, along with a fine-scale characterization of the internal sedimentary structure of gutter casts themselves, would help to test between these three models (with potential implications for finding complex burrowing behavior even lower in the Nama succession).

In summary, the Nasep–Huns ichnofossils first described by Jensen et al. (2000) and expanded upon here represent among the oldest examples of complex infaunal activity known. Coupled with this unusual mode of preservation in gutter casts, it is possible this comparatively early assemblage represents a stage in which the bioturbative behavior of the tracemakers was not yet robust enough to breach the matground boundary. We note that, in Namibia, these complex trace-fossil assemblages are restricted to the last few million years of the Ediacaran (rather than the entire "Nama" interval; see also Mángano and Buatois, 2020); however, if late Ediacaran mats were preventing some of the smallest traces from being recorded, these assemblages could possibly extend further back in time.

Environmental controls on latest Ediacaran evolutionary ecology.—The comparative ichnodiversity of the Nasep–Huns in relation to other late Ediacaran sites may in part reflect oxygen availability in the Witputs sub-basin during deposition (Wood et al., 2015; Tostevin et al., 2016). As described, this interval likely represents a transgressive sequence, shifting from the high-energy, shallow-marine conditions of the Nasep into the comparatively quieter—but still heavily storm-dominated—outer shelf facies of the Huns (Saylor, 2003; Darroch et al., 2020). Wood et al. (2015) suggested a favorable mid-ramp setting would have provided the most consistent access to oxygen, with deeper-water settings possessing insufficient oxygen levels to sustain communities capable of complex behavior. By contrast, shallower environments would have experienced only transient oxygenation (Wood et al., 2015). During this episode of shoreline transgression, the Nasep–Huns fauna may thus have been positioned at an optimal location within the greater carbonate ramp setting, allowing for greater diversity and the evolution of more complex and oxygen-intensive behaviors such as macropredation. However, an argument could also be made that oxygen levels shortly beneath the sediment–water interface may have been just as, if not more, relevant to late Ediacaran infaunal tracemakers than oxygen levels in the overlying water column. Within other late Ediacaran sections characterized by abundant matgrounds, microbial mats themselves have been suggested as providing oxygen "oases" that could be exploited by emerging bilaterians (Gingras et al., 2011; Xiao et al., 2019) while leaving the underlying sediment relatively oxygen poor. In settings such as the Nasep–Huns transition in Namibia, however, where microbial mats were arguably patchier (being locally removed by storms and other sources of sediment instability), it is possible that the sediment substrate may have been oxygenated to greater depths, allowing it to be exploited by bilaterian tracemakers. Both hypothesized controls on the appearance of these more complex trace fossils in the Nasep–Huns transition do, however, emphasize the potential close relationship between terminal Ediacaran animals and redox dynamics (Xiao et al., 2019).

Conclusions

Paleontological and paleoenvironmental analysis of the Nasep–Huns transition in southern Namibia illustrates that diverse communities of bilaterian metazoan tracemakers were thriving before the Cambrian. This adds to our understanding of the pattern and timing of the latest Neoproterozoic rise of animals, demonstrating that many of these complex behaviors not only emerged much earlier than previously thought, but also evolved in concert with matground-dominated Ediacaran environments. Detailed paleontological investigation of the Nasep–Huns transition has also revealed new trace- and body-fossil taxa for the region, including the first documented appearance of the late-Ediacaran index fossil *Corumbella* from Namibia. While more detailed investigation will be required to determine the exact nature of the indeterminate trace fossils described here, putative assignment to Ecdysozoa raises new hypotheses surrounding the diversity of feeding behaviors in the latest Ediacaran, perhaps indicating the emergence of predation as a component of these benthic ecosystems. Finally, the sedimentological characteristics of the Nasep–Huns transition, in particular the preservation of meiofaunal trace fossils and small treptichnids in gutter casts, raise the possibility that these behaviors may be more widespread than is currently thought but rarely well preserved due to the presence of widespread seafloor mats in the late Ediacaran. Gutter casts and other seafloor-disruptive features may thus represent an unusual taphonomic window preserving sub-centimeter trace fossils; future investigations focusing on these features may thus reveal even older examples of complex infaunal behaviors. The breadth of both taxonomic and behavioral diversity present in the Nasep–Huns transition adds to a changing view of the latest Ediacaran, revealing the roots of the agronomic revolution that followed.

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Competing interests

The authors declare none.

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