Paleontology and -ichnology of the Late Ediacaran Nasep-Huns transition

(Nama Group, southern Namibia)

By

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Thesis

Submitted to the Faculty of the

Graduate School of Vanderbilt University

in fulfillment of the requirements for the degree of

MASTER OF SCIENCE

in

Earth and Environmental Sciences

October 31, 2020

Nashville, TN

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1. 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 soft-bodied and enigmatic Ediacara biota to communities comprised 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 also 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; 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

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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 see e.g., Budd and Jensen, 2015; Smith *et al*., 2016; Zhang *et al*., 2018). Trace fossil assemblages in the latest Ediacaran therefore not only provide insights into rates and patterns of metazoan evolution, but can also help track patterns of coupling between the biosphere and geosphere, and can help establish the extent to which biological activity may have helped structure the animal-dominated ecosystems that characterize the Phanerozoic. Here, I 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; see 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 not only provides a window into the composition and functioning of late Ediacaran ecosystems, but also offers an opportunity to study potential controls on the emergence of complex animal behaviors.

2. Geologic setting

The Nama Group of southern Namibia records >3000 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 Kalahari Craton-derived material, deposited in a foreland basin formed in response to orogenic activity along the Damara and Gariep deformational belts during the assembly of Gondwana (Germs, 1983; Stanistreet *et al*., 1991; Saylor *et al*., 1995; Grotzinger and Miller, 2008).

The Nama Group is divided into three sub-basins; the Witvlei to the east, and the Zaris (north) and Witputs (south) which are separated by the paleo-topographic high Osis Arch (Germs, 1983; Grotzinger and Miller, 2008). The Zaris and Witputs sub-basins are further subdivided into (in ascending order) the Kuibis, Schwarzrand, and Fish River Subgroups. The Schwarzrand Subgroup encompasses the Ediacaran-Cambrian boundary, with the lower Ediacaran units (Nudaus and Urusis formations) unconformably overlain by the valley-infill of the Cambrian Nomtsas Formation which contains abundant *Treptichnus pedum* (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 Spitskop Member (uppermost Urusis; Linnemann *et al*., 2019). Ash beds dating from strata below the latest-known occurrence of soft-bodied Ediacaran macrofossils at Farm Swartpunt have yielded ages of 540.095 ± 0.099 Ma and 538.99 ± 0.21 Ma (Linneman *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 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 1000 m near the Gariep Belt and thinning to less than 200 m proximal to the Osis Ridge (Saylor, 2003).

2.1 Nasep Member

The Nasep is primarily composed of medium-grained, well-sorted sandstone, although at smaller scales its composition is subject to a fair degree of variability (Germs, 1983; Grotzinger and Miller, 2008). The member is comprised of a five-unit succession deposited in a variety of tide- and delta- dominated environments, although a relative lack of sedimentary structures in its lower sections makes paleoenvironmental reconstruction difficult (Saylor *et al*., 1995). The section begins in the basal Nasep with ~43 m of massive- to lightly-planar-bedded medium-grained, well-sorted sandstone (Grotzinger and Miller, 2008). This transitions into 5 to 15 m of hummocky cross-stratified grey-green sandstone that Saylor *et al*. (1995) suggest marks the transition from strong current-borne sediment deposition during sea level regression, to a deeper-water transgressive environment. The subsequent unit, a thin- to medium-bedded calcarenite with varying degrees of trough and tabular cross-bedding, indicates a shallower, subtidal environment, which is then followed by a green shale unit.

The absence of major sedimentary features in the green shale suggests deposition at or immediately below wave base. The Nasep Mb. terminates with a unit comprised entirely of monodirectional cross-bedded sandstone, indicating a coastal plain depositional environment less influenced by high-energy currents and instead dominated by ebb-tide cycles (Saylor, 2003).

2.2 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). In the east, the Huns cuts down into the Nasep and forms an erosional boundary; however, the erosion depth decreases westwards, 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) which fall along an east-to-west transect (Saylor, 2003; Saylor *et al*., 1995; Grotzinger and Miller, 2008). The lower Huns (0-40 m) is marked by shale with frequent limestone and sandstone interbeds, followed by meter-scale stromatolitic units and small patch reefs upwards through the remaining ~260 m of the section (Saylor and Grotzinger, 1996; Saylor, 2003). At maximum extent, the Huns can reach thicknesses of up to 500 m, although the unit-wide average is likely closer to 300 m (Grotzinger *et al*., 2000; Saylor and Grotzinger, 1996). The platform is capped by pinnacle reefs comprised of a thrombolitic core enveloped by stromatolitic outer layers that indicate further submergence (drowning) of the carbonate platform prior to the deposition of the overlying Feldschuhorn Shale (Saylor and Grotzinger, 1996; Grotzinger *et al*., 2005).

2.3 Study localities

Two localities in the Witputs Sub-basin, Canyon Roadhouse and Farm Arimas, expose the Nasep-Huns transition in wide lateral extent **(Figures 1 and 2).** 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.
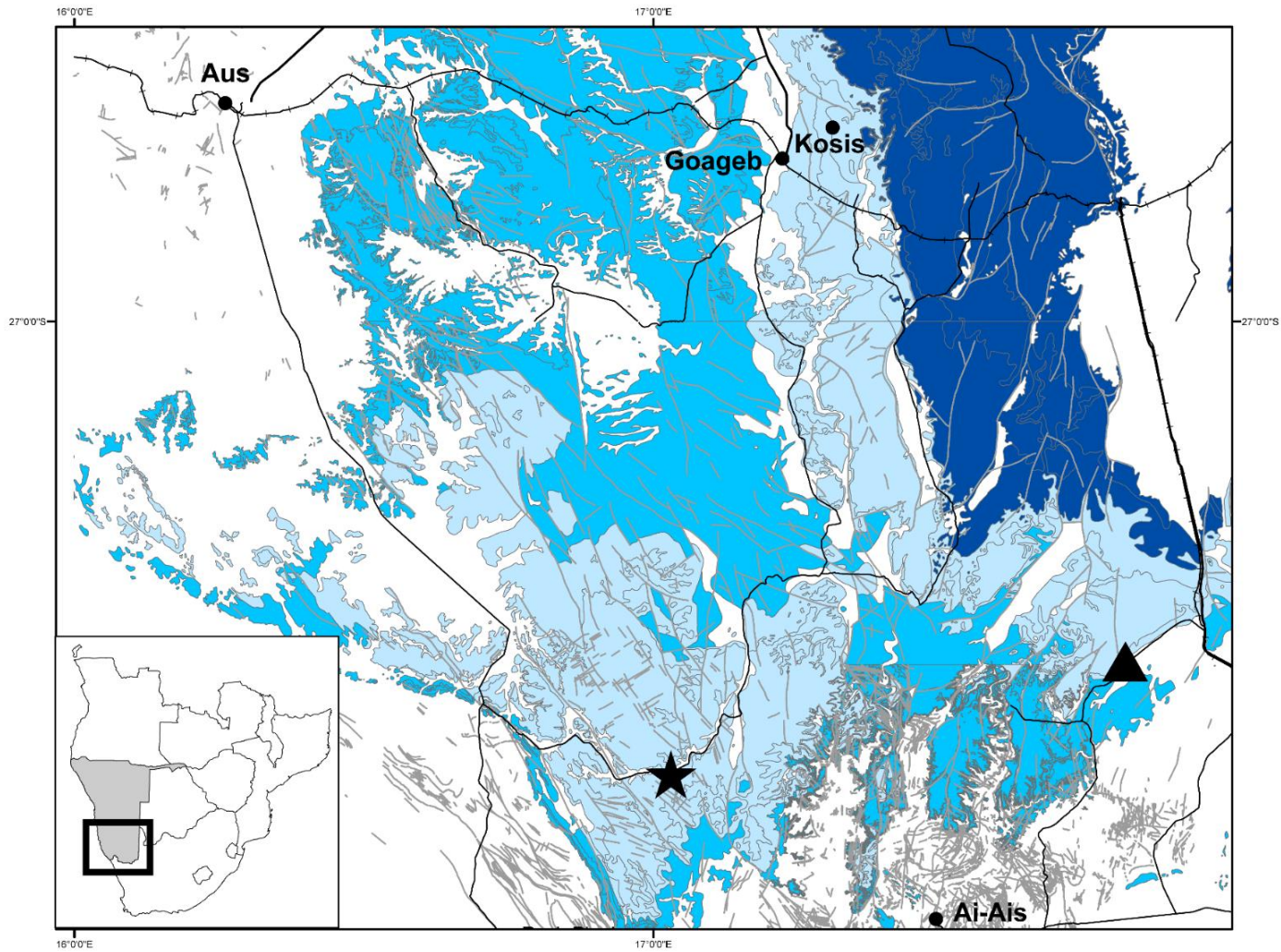
Figure 1: Map of Nama Group sediments in the proximity of Farm Arimas (star), Canyon Roadhouse (triangle), and Fish River Canyon (FRC), with inset showing approximate location in southern Africa. Kuibis Subgroup is indicated in teal, Schwarzrand in pale blue, and Fish River in navy.

Figure 2: a) transect map of Canyon Roadhouse. Numbers indicate progression of transect; b) transect map of Farm Arimas; c) far view of Arimas stratigraphy. Dashed line indicates the approximate position of the Nasep-Huns boundary.

3. Sedimentology

At Canyon Roadhouse, the lowest Nasep exposures begin with 0.5 m of recrystallized limestone with mud chip inclusions. This is immediately followed by 1.5 m of coarse-grained sandstone, which bears lithological and textural similarities to *Ernietta* horizon**s** foun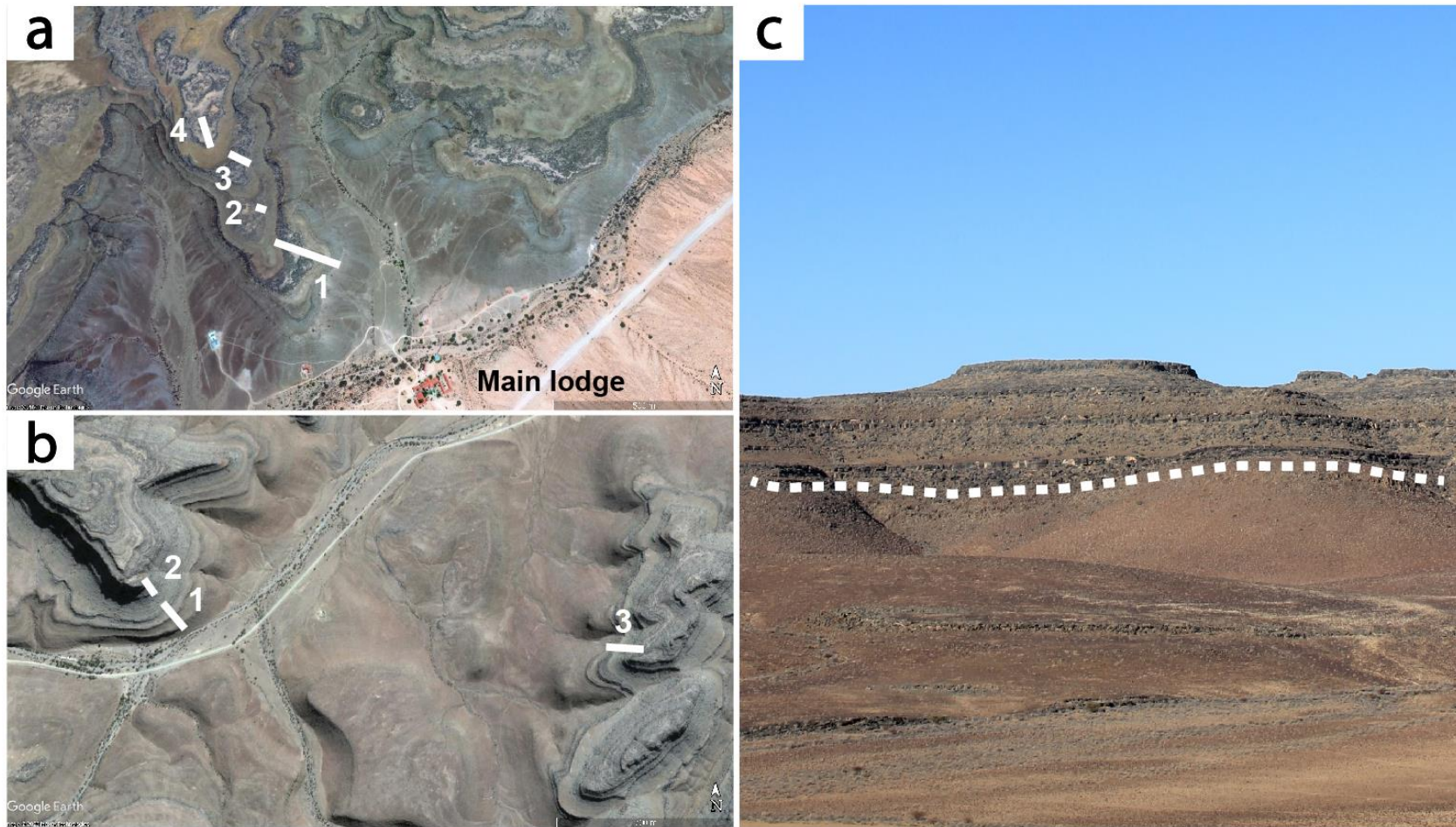d at localities such as Farm Hansburg (see Bouougri *et al*., 2011; Gibson *et al*., 2019; Maloney *et al*., 2020); however, these beds have yet to yield any Ediacaran body fossils. These exposures fine upwards over 2 m into a medium-grained sand with larger-scale clasts and are capped with a thin fine layer of heavily-structured sand. Another fining-upwards interval occurs from 6 m to 9 m, recording 20 cm beds of thick, coarse-grained sandstone. These are interbedded with ~30 cm layers of finer sandstone with bidirectional ripples. The Nasep-Huns boundary likely falls somewhere in the intermediate ~6 m of non-exposure, as the next outcrops appear at around 15 m and consist of > 2 m layers of interbedded mudchip-dominated limestone and micaceous fine-grained silt/sandstone, some containing coarser-grained sand. At least one limestone bed in these Huns exposures preserves evidence of smaller ripples with some hummocky cross-stratification. This sequence disappears around 27 m, and the next exposure at 35 m records ~4 m of weathered black limestone. 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 jagged Huns carbonate, before ceasing at approximately 56 m.

The Nasep-Huns transition at Farm Arimas is more extensive, with approximately 96 m of vertical exposure. The uppermost Nasep constitutes the lower 15 m of the section, and is comprised of reddish-brown medium-grained sandstone with intermittent ripples and channelization, as well as meiofaunal traces. The Nasep-Huns boundary is presumed to fall

within the successive 10 meters of non-exposure, 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 the aforementioned 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 non-thrombolitic sandy limestone continues upwards in massive, meter-scale blocks until approximately 68 m. This is succeeded by a 15 m-interval of non-exposure, which is capped by approximately 13 m of the massive limestone **(Figure 3)**.

The interval of non-exposure at Arimas from 47 – 56 m is of particular taphonomic interest. Based on material found in nearby float, these sandstone horizons preserve a variety of microbially-induced sedimentary structures (see section 3.1 below) as well as abundant gutter casts, which preserve a variety of scour-related and biogenic structures on their lower surfaces **(Figure 4c)**. Of particular note are the gutter casts horizons (located at ~48 and ~70 m in the section measured at Arimas, and at ~20 m in the section measured at Canyon Roadhouse) observed in the fine grained siliciclastics of the uppermost Nasep/lowermost Huns. These structures indicate sediment instabilities resulting in small-scale (5-10 cm in width) downslope sediment flows, and are the primary 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 Arimas and Canyon Roadhouse; in contrast, material from outside of presumed gutter casts preserves relatively few trace fossils.
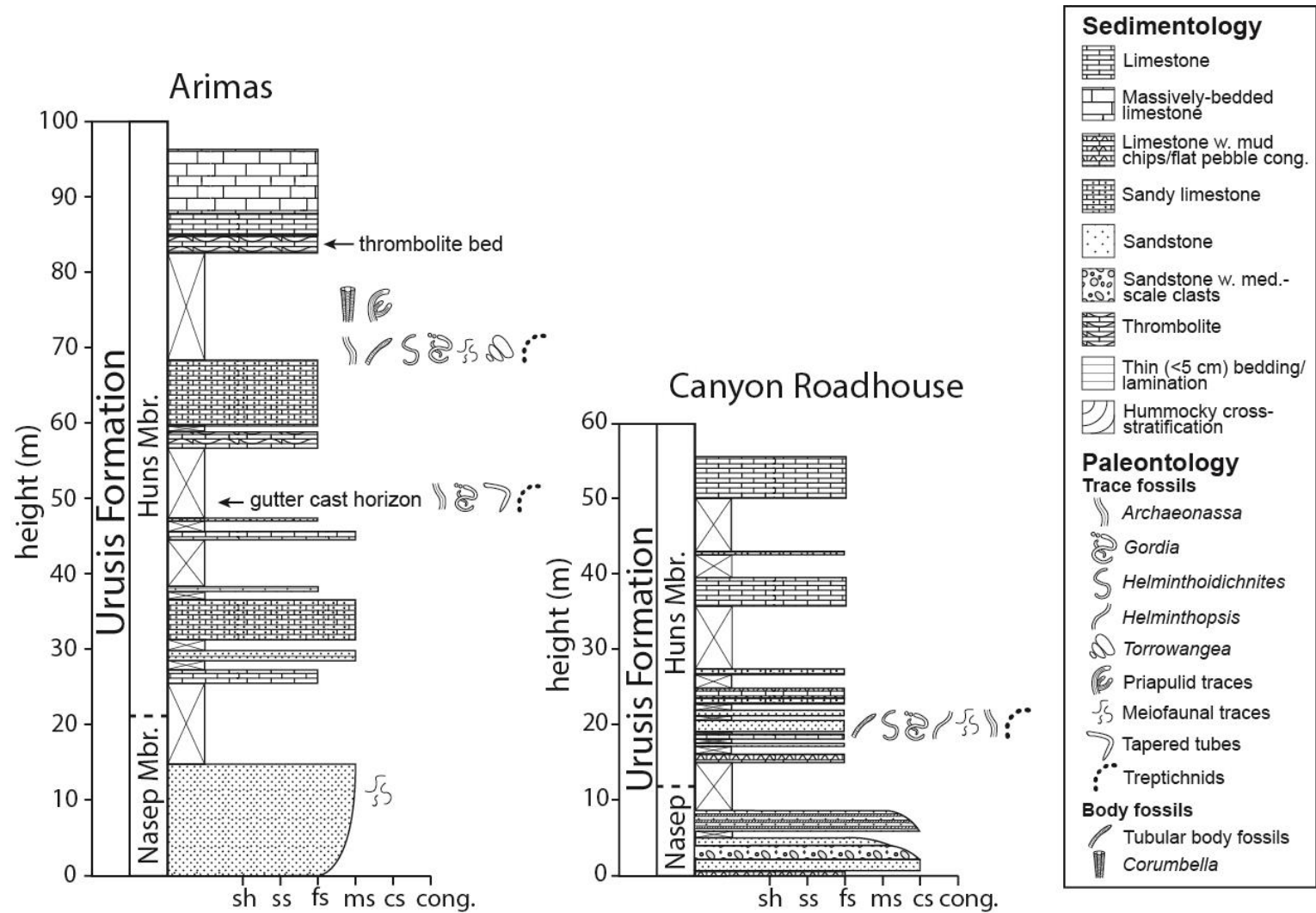
Figure 3: Composite stratigraphy of the Nasep-Huns exposures at Arimas (left) and Canyon Roadhouse (right).

Figure 4: Sedimentary structures from the Nasep-Huns. a) Climbing ripples from Canyon Roadhouse; b) Mudchips (arrowed) from Canyon Roadhouse; c) Gutter cast from Farm Arimas. Dashed lines indicate approximate cast boundaries. White arrows indicate biotic structures, black indicate sole marks (scale bar 1 cm); d) bidirectional ripples from Canyon Roadhouse; e) Ripples from Arimas.

Overall, the regional stratigraphy records a transition from reddish Nasep sandstone at the base, to a more poorly-exposed intermediate portion with coarsening upward intervals capped by interbedded sandstone and limestone, and finally the Huns carbonate in the upper portions of the section. The sheer amount of exposure at Arimas lends itself well to finer-scale examination of faunal change throughout the section. The meiofaunal traces in the lower section (uppermost

Nasep) shift into a more matground-dominated environment towards the middle of the section as mentioned above. While the meiofaunal traces appear to be absent from the lower potions of the Canyon Roadhouse section, we instead find a layer of comparatively very coarse-grained sediment, followed later in the Nasep by beds of abundant vermiform traces.

3.1 Microbially-induced sedimentary structures

A number of microbially-induced sedimentary structures (MISS) are present across the Nasep-Huns transition, including *Kinneyia* and *Intrites.* These structures are thought to form due to sediment deformation under the rigid microbial mats that blanketed large swathes of the seafloor during the late Ediacaran (Bouougri and Porada, 2007).

First described in 1914 by Walcott, *Kinneyia* **(Figure 5, a and b)** is characterized by linear-to-slightly curved crests separated by highly variable (2 mm – 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*-type structures appear most commonly between the Neoproterozoic and the 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 algal mat, though 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;). In 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.

While originally interpreted as a body fossil, *Intrites* (**Figure 5d**) was re-described 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 greater sunlight energy available on the raised structure; thus, the repeated sediment-biofilm-sediment accretion cycle would have likely produced microstromatolites in the characteristic *Intrites* torus form (Gerdes *et al*., 1994).
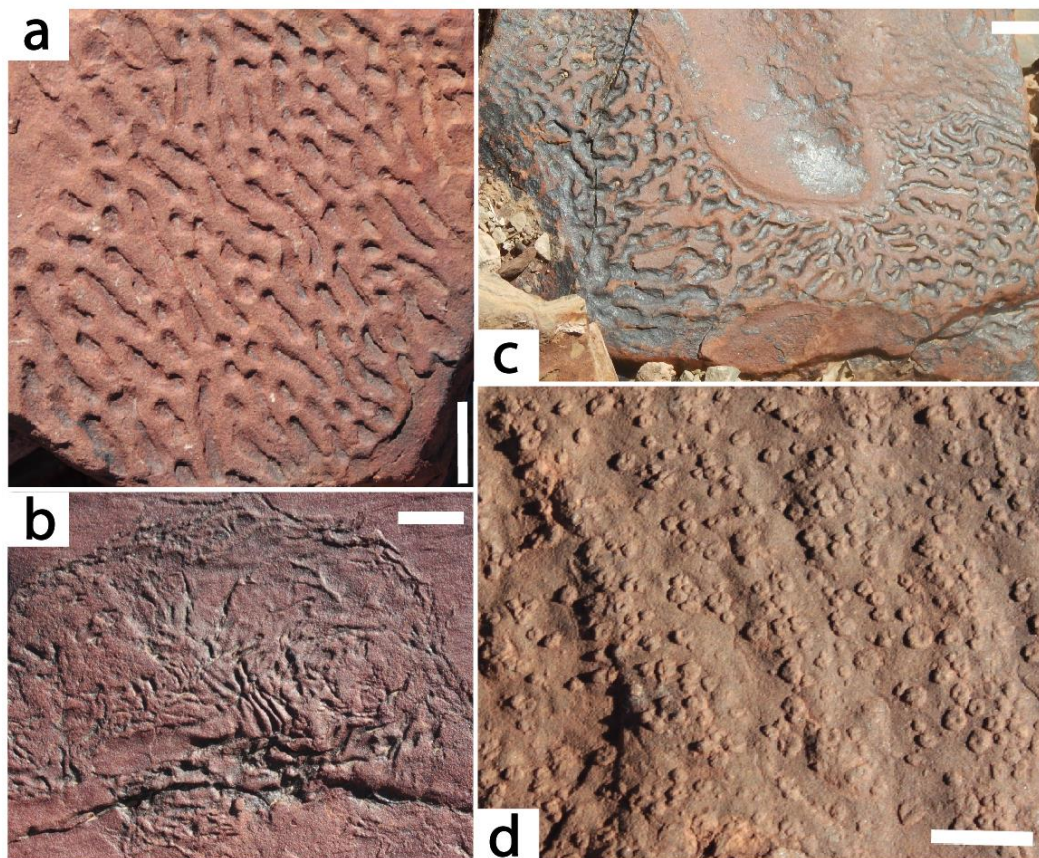

Figure 5: MISS from the Nasep-Huns. a and b) *Kinneyia*; c) wrinkle mat fabric; d) *Intrites*. All scale bars 1 cm.

4. Trace fossils of the Nasep-Huns transition

4.1 Previous work

The first account of ichnofossils in the Nama was published by Germs (1972), who documented five types of vermiform traces in the Nasep (although from amongst these five, *Archaeichium* 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*, cf. *Tricophycus pedum*, two forms of *Palaeophycus*, and three forms of *Planolites* (including cf. *montanus*), in addition to the *Skolithos*, *Brooksella*, *Curvolithos*, and *Didymaulichnus* noted in earlier accounts by Germs (1983) and Crimes and Germs (1982). Geyer and Uchman also described two morphotypes of *Skolithos* from the Nasep and Huns, a trace historically associated with the Cambrian onwards (Mángano and Buatois, 2014), and if accurate, would indicate vertical burrowing was occurring far earlier than previously thought (although I note that Jensen, 2003 questioned these identifications, and instead suggested that 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*, *Archaeichnium*, and "annulate tubes."

4.2 Trace diversity and occurrence

The primary trace fossils found within Nasep and Huns exposures at Arimas and Canyon Roadhouse are vermiform pas- or fodichnia, although there are a number of morphologically-distinct forms present under this greater classification.

Archaeonassa (Fenton and Fenton, 1937) **(Figure 6f)** – Convex furrows separated by a midline groove, 1 to 7 mm in width between furrow crests. Traces are most often straight, with some specimens recording a degree of sinuosity, and are thought to represent fod- or pasichnia attributable to a range of invertebrate taxa (Yochelson and Fedonkin, 1997). In their original description, Fenton and Fenton (1937) suggested a gastropod origin for *Archaeonassa* (though this is 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 non-bilaterian giant protists such as those within the genus *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 paleo-shoreline and parallel to tides, suggesting some evidence of very early taxis (Uchman and Martyshyn, 2020).

Occurrence – Archaeonassa is present at both Canyon Roadhouse and Farm Arimas; however, it is noticeably rarer at these two localities than at Farm Haruchas (basal Vingerbreek Mbr, Nudaus Fm, lower Schwarzrand Subgroup) (see Bouougri and Porada., 2007). Much like other vermiform traces, the Nasep-Huns specimens are primarily associated with the gutter casts, including one specimen from Arimas that appears to run along the apex point of the gutter cast (corresponding to the nadir of the original gutter; see **Figure 4c**).
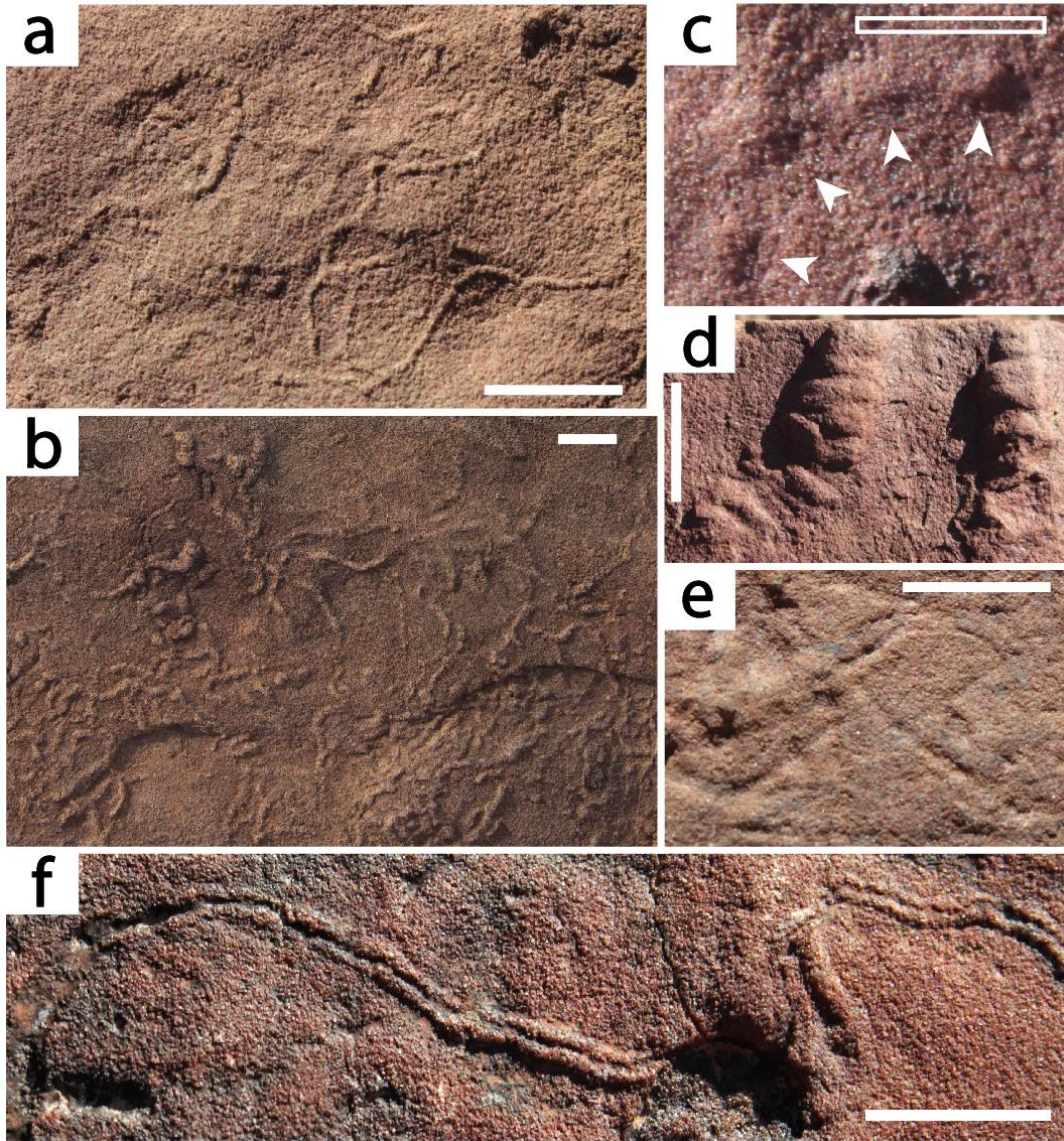
Figure 6: Nasep-Huns ichnofauna. a) *Helminthoidichnites*; b) *Gordia*; c) treptichnid, with arrows denoting individual segments; d) *Torrowangea*; e) *Helminthopsis*; f) *Archaeonassa*. Filled scale bars 1 cm, hollow scale bar 2.5 mm.

Gordia (Emmons, 1844) **(Figure 6b)** – Winding, non-branching vermiform 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 fodichnia or pasichnia of annelids or

priapulids (Buatois and Mángano, 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).

Occurrence – Gordia is most typically found in gutter casts from the uppermost

Nasep/lowermost Huns, but is scarce outside of these structures. In the horizons where it is

present, *Gordia* represents an outsize portion of the bioturbative activity occurring on individual

slabs (Cribb *et al*., 2019). A number of the basal Huns specimens record the aforementioned

pustules, indicating the tracemakers possessed a degree of vertical movement capabilities.

Helminthoidichnites (Fitch, 1850) **(Figure 6a)** - *Helminthoidichnites* represents non-

meandering, straight-to-curved horizontal traces 1-10 mm in width, most commonly interpreted

as pasichnia and often attributed to nematomorphs (Buatois *et al*., 1998; Schlirf). Specimens

commonly exhibit overcrossing between individuals. Some degree of "looping" is observed;

however, computer simulations have demonstrated these loops exhibit greater randomness than

do those of *Gordia* (Hofmann, 1990).

Occurrence – Helminthoidichnites is common across the Nasep-Huns transition, and is

most often found on the underside of gutter casts in concert with other vermiform traces.

Helminthopsis (Heer, 1877) **(Figure 6e)** – Non-looping, non-branching horizontal trails

1-10 mm wide, interpreted as unspecialized feeding/grazing traces (fodichnia) (Hofmann and

Patel, 1989; Wetzel and Bromley, 1996; Buatois and Mángano, 1998). Traces are winding-to-

meandering and do not touch or self-cross (Fillion and Pickerill, 1990). Individuals are most

often preserved in hyporelief or 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).

Occurrence – Helminthopsis, together with *Helminthoidichnites,* represents the largest

propotion of 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 Arimas and ~20 m at Canyon Roadhouse..

Torrowangea (Webby, 1970) **(Figure 6d)** – Transversely annulated, meandering-to-

sinuous horizontal burrows characterized by intermittent constrictions thought to indicate a

degree of peristaltic motion (Jensen *et al*., 2006; Kim *et al*., 2003; Narbonne and Aitken, 1990).

Specimens are always preserved in convex epirelief, and backfill has the same composition as

the surrounding matrix. *Torrowangea* is most often interpreted as a vermiform deposit feeder

typically 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).

Occurrence – 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 is most often found on slabs where *Torrowangea* is the only

represented ichnogenus.

Treptichnus isp. **(Figure 6c)** – The first report of treptichnids from the Nasep (Germs, 1972) details parallel-ridged trails ~3 mm in width that terminate and reappear at regular intervals. Jensen *et al*. (2000) later identified these traces as *Treptichnus isp.*, noting their morphological similarities to *Treptichnus pedum,* albeit at a far smaller scale and with greater unidirectional tendencies of the probes. This suggests the Huns treptichnids (determined by Jensen *et al*. (2000) to be the source of the material, rather than the Nasep originally documented by Germs) likely represent more "advanced" bilaterian behavior below the Cambrian boundary (Jensen *et al*, 2000).

Occurrence – Specimens of *Treptichnus isp.* occur in both the uppermost Nasep and basal Huns at Canyon Roadhouse and Farm Arimas. Discrete ovoid probes are typically ~1-3 mm in length and follow a curvilinear to semi-circular pathway. The treptichnids at both sites are often preserved as part of the larger gutter cast ichnofossil assemblages, but are much smaller in relation to the other traces.

Meiofaunal traces **(Figure 7)** – high-density assemblages of >1 mm horizontal trace fossils, 0.3-0.5 mm in width and exhibiting a high degree of overcrossing. First described by Germs (1972) as "thread-like trails" from the Nasep of Farm Arimas, and often found in conjunction with treptichnids and other vermiform burrowers. Individual traces within the greater structure often vertically over- or under-cross, but do not pass through each other. Some specimens exhibit slight vertical movement in and out of the horizontal plane, and branching is uncommon.
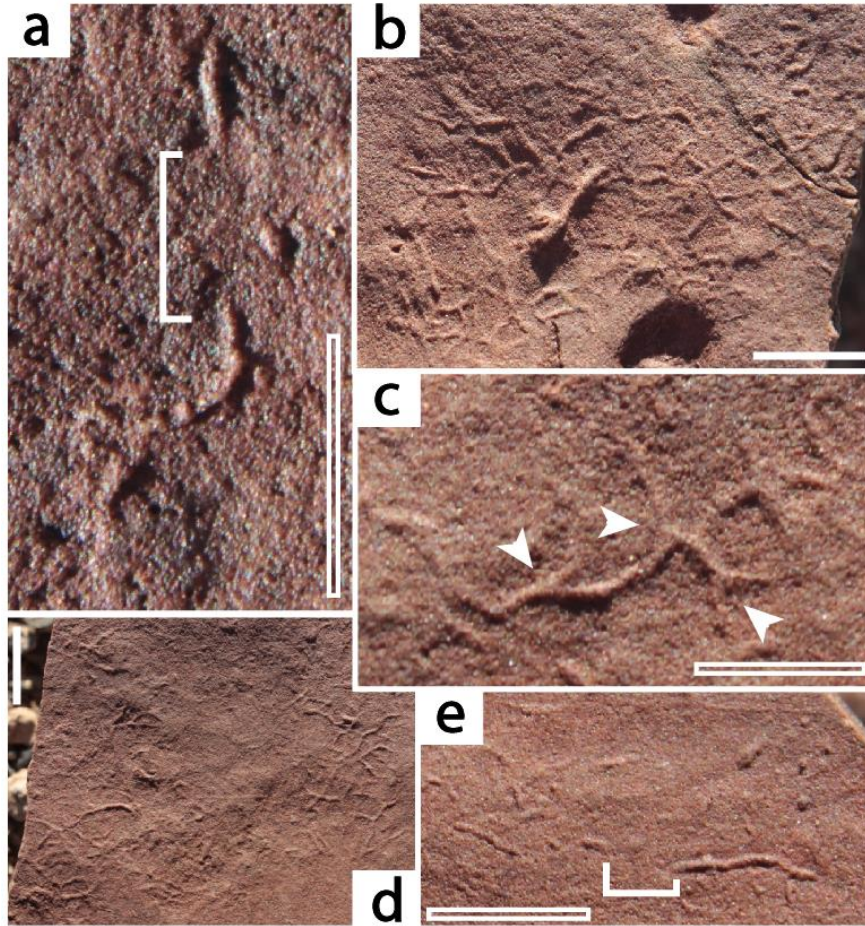
Figure 7: Meiofaunal traces. a) trace showing movement in and out of bedding plane; b) dense meiofaunal network exhibiting high degree of overcrossing; c) close-up of individual trace with branching indicated by arrows; d) trace network with multiple instances of branching; e) individual specimen dipping below surface and reemerging. Filled scale bars 1 cm, hollow scale bars 5 mm.

Occurrence – Meiofaunal traces of similar appearance to those figured in Germs (1972) are found in the upper Nasep and lower Huns at both Arimas and Canyon Roadhouse, where they are most commonly preserved within the greater gutter cast trace assemblage. Further inspection of these specimens suggests morphological differences between these traces and those found in the terminal Ediacaran Spitskop Member, indicating the possibility of two distinct meiofaunal tracemakers within the Urusis Formation.

Indet. trace fossil **(Figure 8)** – meandering 1-3 cm (length) tubes that intertwine to form a larger, braided structure. Tubes are 2-3 mm wide, with longitudinal striations ~0.4 mm apart present towards the distal ends. A number of specimens display a shift from the grooved pattern into faint transverse annulations in the medial portion **(see Figure 8, a and c)**. 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. 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 affect.

These traces are similar to the material described by Glaessner (1963) as *Archaeichnium haughtoni.* While originally classified as a trace, Glaessner later revised his assessment of *Archaeichnium* to that of a body fossil, although he notes definitive assignment to either one of these categories is difficult (1978). The degree of plasticity seen in this new material is unusual for a trace fossil; however, similar traces exhibiting flexible collapse have been described from the Lower Cambrian of Sweden (see Jensen, 1997, Figure 49). In addition, both the individual tubes and the greater braided mass of the Huns material bear noticeable similarities to priapulid trace material described by Kesidis *et al.* (2019) from the Lower Cambrian of Sweden.
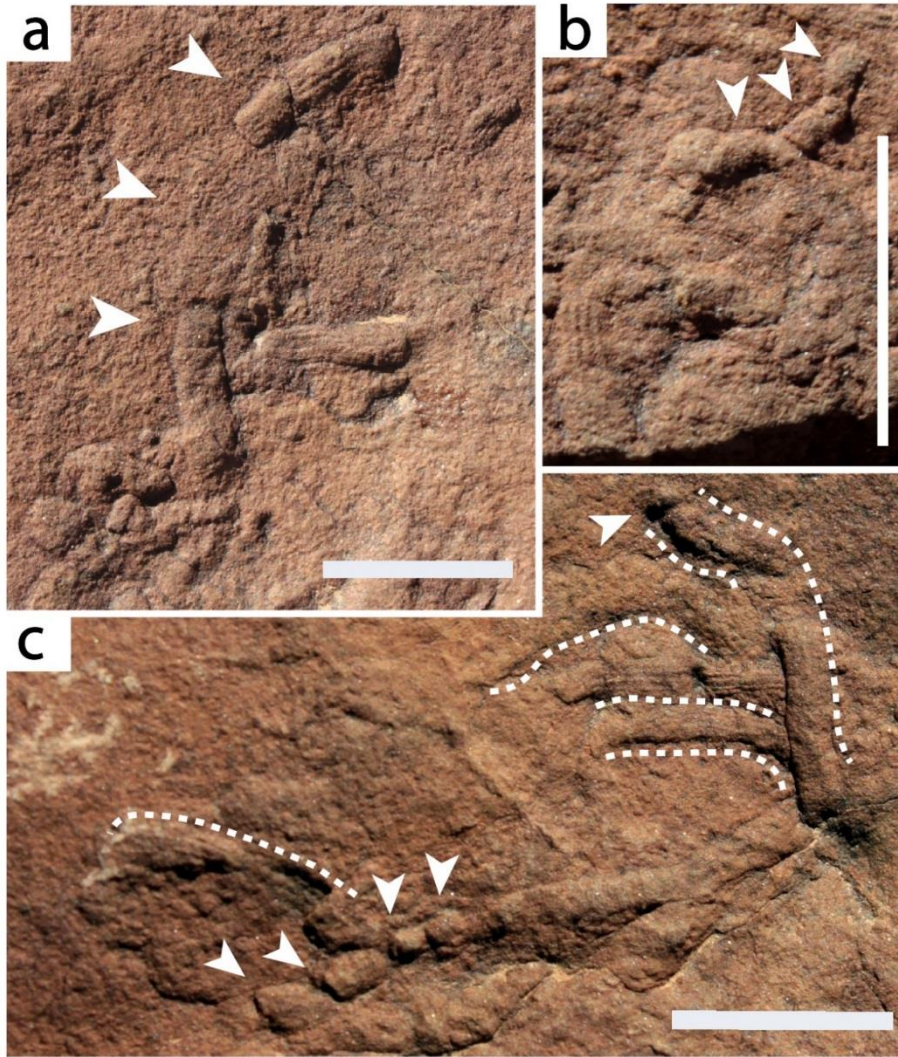
Figure 8: Putative priapulid trace fossils from Arimas. Arrows in (a) indicate possible movement in and out of bedding plane. Arrows in (b) and (c) mark abrupt probing "nubs" similar to those of *Gordia.* Dashed lines in (c) show individual, overcrossing extended probes, with the leftmost exhibiting undulation below the sediment surface. Scale bars 1 cm.

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* (see Hammond, 1970a, 1970b, Figure 1). These grooves remain equidistant though the length of the anterior portion of the probes. However, as this material is preserved in convex semirelief, assessment of the full number of striations is difficult.

The material recovered by our group also exhibit two distinct surface patterns that support scalidophoran affinities; namely, a striated, bulbous distal portion that transitions into a transversely-annulated proximal section **(Figure 8).** Modern priapulids move through sediment by evagination of the frontal introvert (see Calloway, 1980, Figure 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 Figure 1). Neoichnological experiments by Kesidis *et al.* (2019) demonstrate 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*) are capable of leaving smaller open structures behind, which likely provide greater preservation potential (Powilleit *et al.*, 1994). This 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 overall horizontality and slight penetrative behavior of the traces are also consistent with some accounts of priapulid burrowing behavior, albeit these studies have largely been confined to 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, Figure 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.

While the sinuousity and overlapping nature of the individual probe structures likely preclude their assignment as sedimentary structures, the possibility that these specimens instead represent body fossils requires closer examination. Jensen *et al*. (2006) note a number of meandering structures that they argue have been incorrectly interpreted as traces (rather than tubular body fossils). These include palaeopascichnids and winding structures they assert likely represent tubular body fossils. The medial latitudinal annulations could indicate these structures are indeed body fossils. The overlapping form could also plausibly represent branches of a single body fossil. Specimen width is generally consistent except in the case of the aforementioned probing nubs **(see Figure 8, b, and c)**; Jensen *et al*. (2006) argue that while abrupt diameter changes are diagnostic criteria for body fossils in carbonized compressions, this same assertion cannot be made for casts and molds due to loss of definition during the fossilization process.

Occurrence – This trace material is present on a single slab comprised 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 below).

5. Body fossils

While this study is primarily focused on the ichnofauna of the Nasep-Huns transition, there are a number of body fossils preserved in the sections which provide important supplementary evidence as to the temporal placement of the units and the suite of behavioral diversity present.

Corumbella sp. (Hahn *et al*., 1982) **(Figure 9)** – annulated tubular structure of length up to ~80 mm/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 US, 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). While members of the genus are most often interpreted as scyphozoan cnidarians, recent work has suggested *Corumbella* might instead represent calcareous sinotubulitids (Walde *et al*., 2019).

Occurrence – The *Corumbella* recovered by our group from the Huns represents the first-known occurrence of the genus in Namibia. These specimens are present on a single upper-Huns (~73 m) slab from Arimas comprised of multiple individuals, some exhibiting a degree of lateral flexibility consistent with corumbellids from other Ediacaran sites (see e.g., Pacheco *et al.*, 2015, Figure 4; Hagadorn and Waggoner, 2000, Figure 5.4-5.5). 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

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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. In addition, Babcock *et al.* (2005) note the presence of a similar helical twist in *C. werneri* specimens from Brazil, and thus suggest it may in fact bear no taxonomic significance.
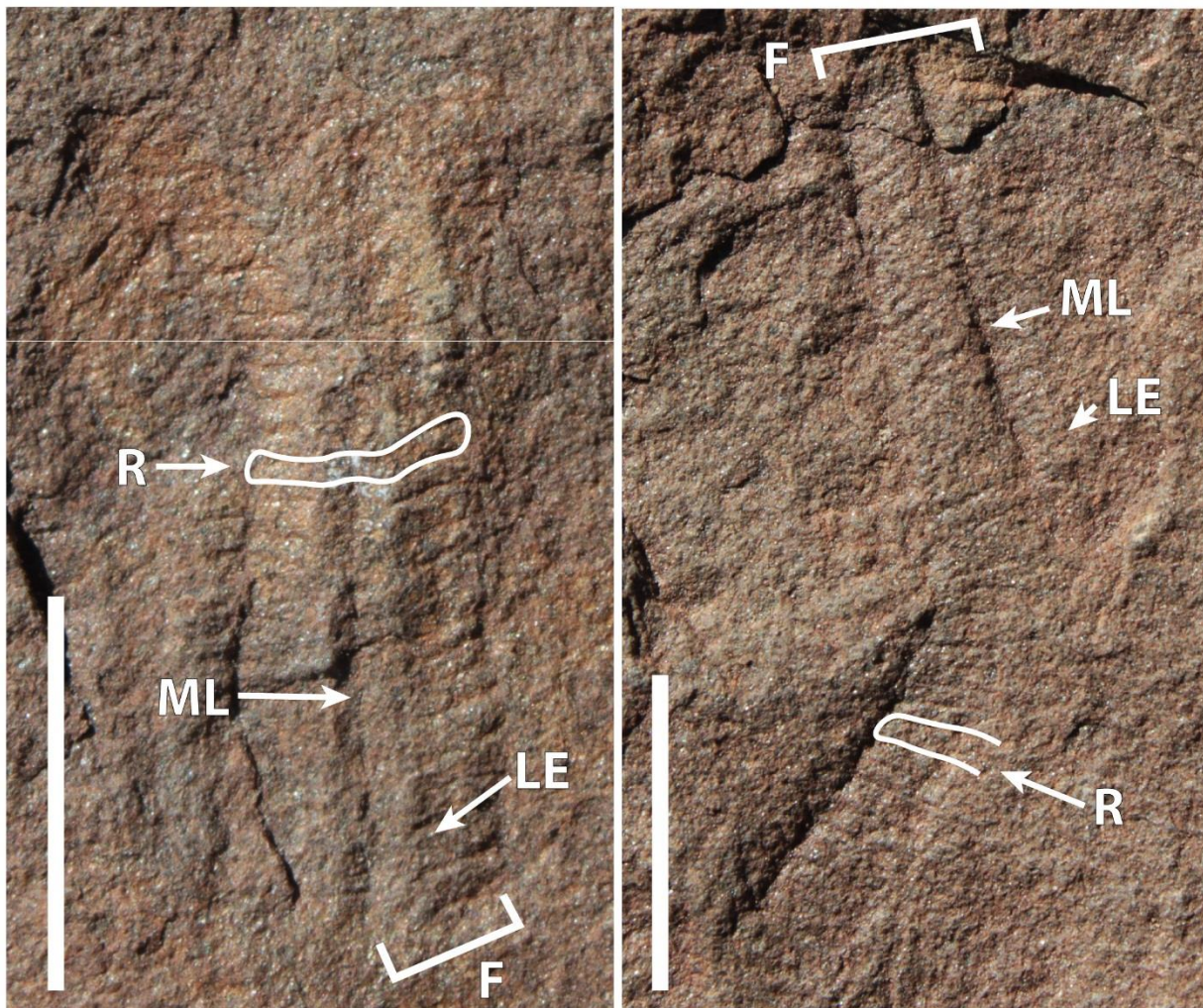
Figure 9: Two *Corumbella* specimens from Arimas, anatomically labeled using Pacheco *et al.* (2015) as reference. 'R' – ring; 'ML' – midline; 'LE' – lateral edge; 'F' – face. Scale bars 1 cm.

Tubular body fossils **(Figure 10, a-d)** – tubes 1-5 mm in diameter, displaying a high degree of morphological variability. Specimens of this type have historically been assigned to *Archaeichnium*; however, given the similarities of the *Archaeichnium* type material (Glaessner, 1963) to the indet. trace fossils described above, it is likely that many of these tubular body fossils have thus been misidentified as such.

Figure 10: Annulate tubes from both Canyon Roadhouse and Arimas. All scale bars 1 cm.

Unlike the putative trace material, these specimens 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 b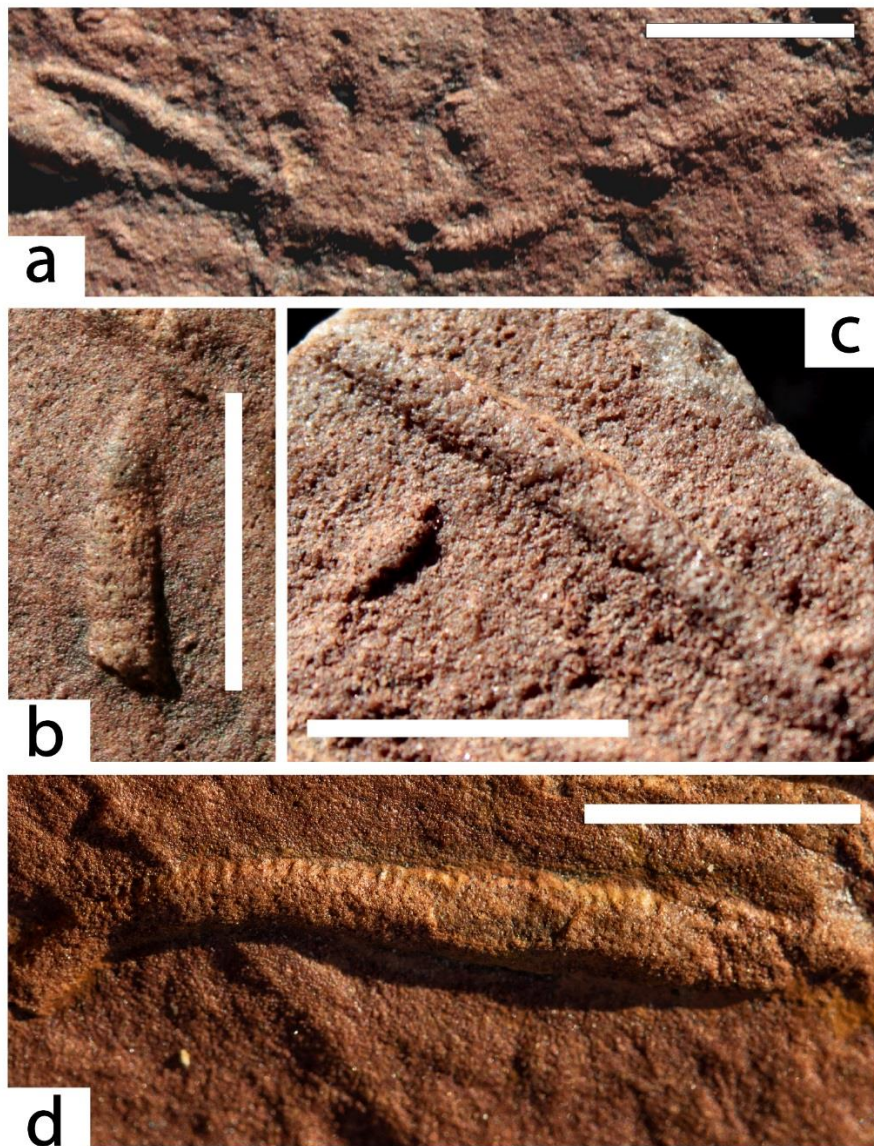ody orientations suggest current alignment. Tentative interpretations suggest similarities to other Late Ediacaran tubular metazoans (c.f. Droser and Gehling, 2008; Cai *et al*., 2011; Cortijo *et al*., 2015; Smith *et al*., 2016; Schiffbauer et al., 2020). A number of individuals possess conical terminal tapers. Diagnoses are often made contingent on the presence of these tapered ends; identification can be more difficult when the conical tapers are not preserved, due to the number of annulated and tubular metazoan taxa associated with the Nama Group. Other tubular taxa present across this interval include kinked-funnel structures and stacked cone-in-cone forms which bear similarities to the "cloudinomorph" form-grouping described by Selly *et al*. (2019). Further systematic work is needed to address the breadth of tubular morphological disparity across the Nasep-Huns transition.

*Occurrence –*Tubular body fossils are fairly common within the fossil horizons at both Arimas and Canyon Roadhouse. The kinked-funnel and conical-taper structures described above were recovered from the gutter cast horizon at Arimas.

6. Discussion

Detailed investigation of the Nasep-Huns transition at these two localities confirms this interval preserves among the highest diversity of trace fossils known from latest Ediacaran-aged sediments anywhere **(Table 1)**, as well as new taxa that have not yet been described from Namibia. Moreover, the presence of *Corumbella* in these sections bolsters biostratigraphic and paleogeographic links between Brazil, Paraguay, Iran, the southwestern US, and Namibia in the terminal Ediacaran (see Babcock *et al.*, 2005; Hagadorn and Waggoner, 2000; Vaziri *et al.*, 2018; Warren *et al.*, 2011). I will first discuss the composition of fossil communities, followed by paleoenvironmental reconstruction potential controls on trace fossil preservation.

6.1 Fossil communities

The Nasep-Huns transition preserves a varied suite of trace and body fossils from a Late Ediacaran shallow marine environment that was at least intermittently colonized by seafloor microbial mats. The ichnofossil communities, comprised of *Archaeonassa*, *Helminthopsis*, *Helminthoidichnites*, *Gordia*, *Torrowangea*, sub-cm scale treptichnids, and meiofaunal burrow systems represent a diverse assemblage comparable to other Late Ediacaran sites worldwide (Högström *et al.*, 2013; Narbonne and Aitken, 1990; Parry *et al,* 2017; Tarhan *et al.*, 2020; Weber *et al.*, 2007). Material from the upper Nasep/lower Huns is further notable for the degree of intra-slab trace diversity, including a number of ichnotaxa in direct association with each other (**Figure 4c**). This is an unusual feature among the aforementioned coeval trace assemblages, which tend to preserve only one or two ichnogenera in concert.

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Table 1: Summary of ichnodiversity among coeval deposits

Site	No. of ichnogen.	Species present	Inferred paleoenvironment
Nasep-Huns Mbrs. (Namibia)	5+	*Archaeonassa*, *Gordia*, *Helminthoidichnites*, *Helminthopsis*, *Torowangea*, treptichnids, meiofaunal traces, indet. trace material (c.f. *Archaeichnium*)	High-energy shallow water ramp
Blueflower Fm. (NW Canada)	11	*Aulichnites* isp., *Helminthoida* isp., *Helminthoidichnites tenuis*, *Helminthopsis abeli*, *Helminthopsis irregularis*, *Helminthopsis?* isp., *Lockeia* isp., *Neonereites* isp., *Palaeophycis tubularis*, *Planolites montanus*, *Torrowangea rosei*	Deep-water basin slope below wave base
Dengying Fm.. (S. China)	5	*Helminthoidichnites*, *Lamonte trevallis*, *Neonereites*, *Palaeophycus-Planolites* ichnoguild, *Torrowangea rosei*	Shallow-water carbonate platform
Deep Spring Fm. (SW USA)	8	*Bergaueria*, *Cochlichnus*, *Helminthoidichnites*, *Helminthopsis*, *Planolites*, treptichnids, cf. *Belorhaphe**, cf. *Helicolithus**	Low-energy, peritidal-to-shoreface marine
Corumbá Grp.. (Brazil)	2	*Didymaulichnus lyelli*, *Multina minima*	Shallow carbonate platform below fair-weather wave base
Manndraperelva Mbr. (Norway)	9	*Arenicolites*, *Cochlichnus*, *Curvolithus*, *Palaeophycus-Planolites*, *Palaeopascichnus*, *Treptichnus pedum*, cf. *Bergaueria*, cf. *Helicolithus*, treptichnids, trilobed trace fossils	Shallow marine with distal and proximal turbidites

*See McIlroy and Brasier, 2017
References: Narbonne and Aitken 1990, Weber *et al.* 2007, Meyer *et al.* 2014, Tarhan *et al.* 2020, Parry *et al.* 2017, Högström *et al.*, 2013

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 (fod- and pasichnia) suggest a community dominated by mat grazers (see Buatois *et al*., 2014), these sections are punctuated by small treptichnids exploiting the mat-free gutter substrate. *Torrowangea* provides supplementary support for subsurface life habits, likely representing an undermat deposit feeder. The presence of these ichnotaxa suggest that there is a diversity of vertical niches present in these assemblages, and thus a degree of ecological complexity that is higher than usually attributed to Late Ediacaran communities.

The meiofaunal traces noted here bear superficial morphological similarities to Ediacaran nematode traces from Brazil (see Parry *et al*., 2017), but are (on average) larger in size and form sparser networks. In terms of similarities, the Nasep-Huns specimens exhibit occasional dichotomous branching, but no evidence of polychotomous branching. The Nasep-Huns specimens exhibit a similar surface-level vertical tiering and share an overall sinuosity with the meiofauna from Brazil; however, they are far less sinuous than the Ordovician *Cochlichnus*-like meiofaunal traces described by Baliński *et al*. (2013). Modern meiofauna play important roles in a number of important ecological processes, including nutrient cycling and vertical chemostratigraphic flux (Schratzberger and Ingels, 2018), implying similar levels of ecosystem engineering in the latest Ediacaran of Namibia.

The *Archaeichnium* traces tentatively identified here as probes left by priapulid worms also have significant implications for the complexity of late Ediacaran ecosystems. Priapulids are

crown-group ecdysozoans, and thus indicates the presence of crown-group bilateria prior to the Cambrian boundary, and in turn significant metazoan overlap between Ediacaran and Cambrian benthic communities. The presence of scalidophorans in these strata would also suggest some degree of active predation was occurring as modern priapulids are overwhelmingly predatory, and their fossil record indicates this has remained the case since at least 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. The existing body of work surrounding priapulids has shown they are able to 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) suggest likely serves a respiratory function. While these vertical restrictions are artificial when introduced in a laboratory setting, it is possible that the paleo-environments 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.*,

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2000; Mángano and Buatois, 2014). These proposed priapulid traces exhibit shallow movement above and below the sediment-water interface, periodically re-emerging consistent with the overall direction of motion. This could suggest some form of natural constraint against their tendency to burrow vertically, perhaps indicating a chemostratigraphic or physical barrier to deeper movement.

6.2 Paleoenvironmental reconstruction

The stratigraphy of this interval suggests an overall sea level transgression resulting in a transition from a coastal plain/shallow water environment, to a lower-shoreface environment (see Saylor, 2003). At Canyon Roadhouse, the presence of climbing ripples **(Figure 4a)** within the Nasep Member indicate lateral sediment migration coupled with net lateral deposition (Allen, 1970). In this case, the combination of lateral and vertical sediment accumulation points to the presence of turbidity flows, indicating a general level of sediment instability (Saylor, 2003). This idea is supported by the abundance of gutter casts at Arimas and Canyon Roadhouse **(Figure 4c)**, albeit at far smaller scales. These two factors suggest the lower portion of the section is dominated by relatively high-energy paleoenvironments with significant sediment movement and deposition. In addition, the lowermost Huns exposures at Canyon Roadhouse are comprised of limestone with mud chip inclusions **(Figure 4b)**, indicating storm-dominated deposition during this interval (Myrow, 1992; Myrow and Southard, 1996). As the section transitions further into the Huns Member, the facies indicate corresponding change in lithology and shift to a lower-shoreface shelf environment. The relative paucity of sedimentary structures stratigraphically higher into the Huns suggests deposition was occurring below wave base (Saylor, 2003).

6.3 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 sediment and a significant food source which could be quickly exploited by bilaterian metazoans. An alternative scenario involves these tracemakers being widespread throughout the paleoenvironment, but only preserved in gutter casts 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 in order for the structure/trace to be recorded; this would be especially true for extremely small tracemakers (although see Buatois and Mángano, 2016 for an alternative viewpoint). In this light, small bilaterian traces (including treptichnids) might be more widespread than is currently recognized, and consequently gutter casts may represent valuable taphonomic windows in which optimal rheological conditions can help preserve traces left by tiny metazoans.

Along with the Mt. Dunfee assemblage described by Tarhan *et al*. (2020), the Nasep-Huns ichnofossils initially noted by Jensen *et al*. (2000) and expanded upon in this work represent the stratigraphically-lowest (and thus furthest below the Cambrian boundary) examples of complex, Cambrian-type trace activity known. Coupled with the unique mode of gutter cast

preservation, 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. However, given the non-gutter-restricted nature of the coeval Mt. Dunfee material, the specific preservation of the Nasep-Huns material is most likely a taphonomic control of this particular site. In addition, most of the assemblages summarized in Table 1 are characterized by low-energy depositional environments below fair-weather wave base; the high-energy environments of the Nasep-Huns would have been comparatively deleterious to quieter-water methods of trace preservation.

6.4 Controls on latest Ediacaran evolutionary ecology

The comparative ichno-diversity of the Nasep-Huns in relation to other Late Ediacaran may in part reflect oxygen availability in the Witputs sub-basin during deposition. Wood *et al*. (2015) suggest a favorable, mid-ramp setting would have provided the most consistent access to oxygen; redox structure analysis shows deeper water was both too anoxic (ferruginous) to sustain communities capable of complex behavior. In contrast, shallower environments would have only experienced transient oxygenation. 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. As sea level was rising at this time, one would expect to see a window of complex communities during the interval at which the depositional environment was at an ideal depth; this is reflected in the uppermost Nasep/basal Huns fossil horizons that reduce in frequency moving into the deeper-water thrombolitic pinnacle reefs.

Finally, the diversity of behaviors present across the Nasep-Huns transition is consistent with findings by Cribb *et al*. (2019) that indicate bedding-plane bioturbation intensity in the Nama Group increases moving into the Nasep and further into the Cambrian. Vertical movement by *Gordia, Archaeichnium,* treptichnids, and others away from the sediment surface indicates these underlying sediments were at least partially oxygenated, suggesting small-scale bioturbation was occurring long before these traces were made. These behaviors would have played a significant part in the substrate-exploitation feedback loop, allowing for incremental increases in burrowing depth.

7. Conclusion

Paleontological and paleoenvironmental analysis of the Nasep-Huns transition in southern Namibia illustrates that diverse assemblages of bilterian metazoan tracemakers were thriving prior to the Cambrian. This assertion holds significant import for our understanding of the Precambrian evolution of animals, demonstrating that not only did these complex behaviors emerge much earlier than previously thought, but also evolved in concert with matground-dominated Ediacaran environments.

Assessment of this interval has also revealed novel trace- and body fossil taxa for the region, including the first documented appearance of *Corumbella* from Namibia. While more work remains necessary to determine the exact nature of the longitudinal scratch traces, putative assignment to Ecdysozoa adds another dimension of our understanding to the late Ediacaran, perhaps indicating modern animal fauna and their associated life habits (i.e., predation) were important players in these benthic ecosystems. Finally, this interval provides a unique preservational snapshot of the complexities of the Ediacaran seafloor through the lens of gutter casts. The disruption of the oft-obscuring algal mat layer through these small-scale sediment instabilities allows for evidence that diverse ichno-assemblages were flourishing at and below the sediment-water interface. Both these behaviors and the breadth of diversity present across this interval add to a changing view of the latest Ediacaran, involving clear examples of ecological escalation and complexity, and laying bare the roots of the agronomic revolution yet to come.

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