The Silurian inception of inland desert ecosystems: trace fossil evidence from the Mereenie Sandstone, Northern Territory, Australia

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Abstract

The Silurian was an interval of profound change in terrestrial ecosystems as the earliest non-marine animal communities began to become established on the continents. Whilst much is known about the transition of pioneering animals from shallow marine to coastal and alluvial habitats, evidence for animal activity in contemporaneous aeolian strata is rare. Here, we present trace fossil evidence that closes this knowledge gap, indicating that Silurian desert environments, dominated by aeolian processes, were occupied by resident invertebrate communities. The evidence comes from the Mereenie Sandstone, Northern Territory, Australia, which is demonstrated to have been deposited in a wet inland aeolian system, typified by small crescentic sand dunes and extensive interdune flats. The invertebrate trace fossil associations from the Mereenie Sandstone (*Arenicolites* isp., “Burrow entrance with radial feeding traces”, *Didymaulichnus lyelli*, *Diplichnites gouldi*, *Helminthopsis* isp., *Laevicyclus* isp., *Palaeophycus* isp., *Polarichnus garnierensis*, *Skolithos* isp.) are restricted to damp interdune deposits, whereas dune strata are barren. The ichnofauna are described and

compared to those from other Palaeozoic aeolian systems, in order to re-evaluate the timing of the early stages of arthropod terrestrialization.

Introduction

Traditionally, the Palaeozoic colonization of the land by invertebrates has been understood with reference to coastal to alluvial ichnofaunas of Silurian-Devonian age: a vantage well-summarized in a seminal paper on trace fossil evidence for terrestrialization by Buatois et al. (1998a). However, over the last two decades, a consensus has begun to emerge from ichnological studies that have refined this perspective. There is now strong trace fossil evidence that invertebrates were making temporary non-marine forays throughout the Cambrian and Ordovician, well prior to the establishment of permanent habitats (e.g., Draganits et al., 2001; MacNaughton et al. 2002; Collette et al. 2010; Minter et al. 2016a; MacNaughton et al. 2019; Shillito & Davies, 2019a; b). Additionally, an improved mechanistic understanding of terrestrialization has shown that the process was characterized by a series of early bursts of behavioural disparity and ecospace occupation before non-marine ecosystems reached their maximum diversity (Minter et al., 2017).

Despite these new perspectives, almost all ichnological insights into early terrestrialization come from sedimentary successions that were deposited in environments with periodic marine influence, typically occurring in close proximity to emergent tidal facies (Draganits et al., 2001; MacNaughton et al. 2002; Shillito & Davies, 2020). There is thus a knowledge gap concerning the establishment of trace fossil communities in inland regions, with little published evidence for colonization until the latest Silurian and early Devonian (Morrissey et al., 2012a; Minter et al., 2016b; Shillito & Davies, 2017).

In this paper we report Silurian trace fossils from aeolian strata that lack evidence for marine influence, and which – from palaeogeographic and tectonic reconstructions – were deposited

in a mid-continent setting (Webby, 1978; Haines et al., 2001). The strata belong to the Mereenie Sandstone of central Australia (Figure 1), and are here shown to contain the earliest known evidence for a desert ichnofauna in the geological record.

Geological Background

The Mereenie Sandstone is a c. 580 m thick succession of siliciclastic strata, consisting entirely of very fine- to medium-grained quartz arenites, which was deposited in the Amadeus Basin of Northern Territory, Australia. Deposition of the unit followed the late Ordovician regional regression of the intracontinental Larapintine Sea (Webby, 1978; Haines & Wingate, 2007; Figure 13). The formation is typified by homogenous, white-coloured sandstones with well-rounded grains (weathered to a deep red colour, as common to central Australian outcrops), and a total lack of mudrock. The unit presently crops out as negligibly dipping strata across well-exposed escarpments, plateaus and buttes in the area around Watarrka National Park (Figure 1.).

The Mereenie Sandstone is not directly dated, but a multitude of lines of evidence suggest that it is Silurian in age. Palaeomagnetic studies have suggested that it was most likely deposited between the early Silurian and the Early Devonian (with the caveat that signals may have been overprinted) (Li et al., 1991). Gouramanis and McLoughlin (2016) favoured a late Silurian to Early Devonian age for the unit, based on comparison with other trace fossil-bearing strata across Australia: although ichnostratigraphic age estimates must be treated with caution (Egenhoff et al., 2007; Buatois & Mángano, 2011; Davies et al., 2011; Mángano et al., 2012), especially as the units with which it was compared (Tumblagooda Sandstone, Major Mitchell Sandstone, Mount Daubeny Formation, Ravendale Formation) are themselves not directly dated (Cayley & Taylor, 1997; Neef & Bottrill, 2001; Neef, 2004; McNamara, 2014; Shillito & Davies, 2020).

Neighbouring stratigraphic units provide uncontroversial age maxima and minima, derived from biostratigraphic evidence (Figure 1). The Mereenie Sandstone is unconformably overlain by the Parke Siltstone, which has an Early-Late Devonian (Emsian-Frasnian) age, revealed by vertebrate body fossils and palynomorphs (Bagas, 1988; Young, 1988; Shergold et al., 1991). It overlies strata of the Ordovician Larapinta Group, the uppermost unit of which (Carmichael Sandstone) also lacks direct age indicators. However, conodonts and other fauna from the underlying units range in age from the Tremadocian (Pacoota Siltstone) to the Katian (Stokes Siltstone) (Wells et al., 1970; Davies et al., 2011; Sansom et al., 2012). These upper and lower bounds constrain the deposition of the Mereenie Sandstone to between the Hirnantian and Emsian (approximately 445-393 Ma). Given that this interval must also account for the antecedent deposition of the Carmichael Sandstone and subsequent development of the capping unconformity, a Silurian age is extremely probable.

Sedimentary facies of the Mereenie Sandstone

The first detailed description of the Mereenie Sandstone was undertaken by Wells et al. (1970), who interpreted its depositional environment as “evidently complex” and likely to consist of a mixture of aeolian, deltaic, lacustrine, and shallow marine facies. They noted that *Skolithos* and unidentified trace fossils implied a shallow marine environment, but that sedimentological evidence of well-rounded, frosted grains and massive, extensive cross beds indicated an aeolian depositional environment. Later work by Kennard et al. (1986) and Bagas (1988) refined these observations to suggest a shallow marine depositional setting, passing upwards into a mixed aeolian-fluvial system. This explanation for the depositional environment has persisted, and the most recent study of the unit has suggested that the trace fossil-bearing strata towards the base of the Mereenie Sandstone were deposited in a dominantly shallow marine setting (Gouramanis & McLoughlin, 2016).

In this study we specifically focus on an approximately 100 metre-thick vertical succession of Mereenie Sandstone strata, stratigraphically located at the bottom of the unit, in the vicinity of Kings Canyon (Figure 1.). This is the best exposed interval of the unit, and the deeply incised local topography at Kings Canyon and neighbouring gorges mean that multiple sections throughout the same stratigraphic interval can be interrogated. Rock outcrop presents in two distinct geomorphic aspects, each of which offer different perspectives onto the ichnological and sedimentological motifs of the unit: 1) stepped plateau exposures, which make up much of the area on top of the main Kings Canyon plateau; and 2) vertical cliff exposures, which occur as large escarpments and smaller buttes that have formed due to deep Cenozoic weathering along joint planes (Figure 2.; Heimsath et al., 2010).

The strata of the Mereenie Sandstone in this area can be divided into two broad facies based on the dominant stratification; 1) a cross-bedded facies, and 2) a flat-bedded facies. The style of stratification provides a convenient sedimentological distinction between the two facies, and has palaeoenvironmental significance because only the latter facies contains trace fossils. The two facies are interbedded with one another (Figure 3), but cross-bedded strata dominate the lower part of the studied section, and flat-bedded strata the upper part.

Cross-bedded facies

Description - This facies comprises cross-bedded, very fine- to medium-grained sandstone and is most abundant towards the base of the studied section. Cross-bedding is laterally extensive, and occurs in sets ranging from 20 cm to 3 m thick (with a mean thickness of 1.5 m). Individual sets are commonly demarcated by inclined bounding surfaces, with subtle variations in dip direction and angle to the underlying strata (Figure 4). The apparent angle of climb, measured from the lower bounding surfaces of cross-bed sets, is approximately 1°. Measurements of palaeoflow direction taken from foresets exhibit a near 360° range, with a spread of dominant

measurements clustered between directions towards the WSW to SSE (160°-230°, Figure 3). The sandstone is both compositionally and texturally very mature – it consists almost entirely of well-sorted and very well-rounded grains of quartz, with frosted veneers. Thin pinstripe lamination is observed in some beds (Figure 4C). Bedding plane exposures are rare in the cross-bedded facies because it predominantly crops out as vertical cliff sections. No trace fossils have been identified in the cross-bedded facies.

Interpretation - Thick, laterally extensive cross-beds are characteristic of aeolian dune deposits (Kocurek, 1996), and this interpretation is further supported for the cross-bedded facies by the compositional maturity of the sediment, and the rounding and frosting of individual quartz grains (Margolis & Krinsley, 1971). The discordant bounding surfaces can be interpreted as reactivation surfaces (Brookfield, 1977; Kocurek, 1981), implying some variability in wind speed and direction (Kocurek, 1981). Palaeoflow measurements suggest a prevailing northerly wind, as other directional indicators are subordinate (Figure 3).

The original dune morphology can be classed by observing the geometric relationships between the foresets and bounding surfaces (Rubin & Hunter, 1983; Kocurek, 1991). Accurate dune classification combines form (e.g., crescentic, linear, star) with orientation (transverse, oblique, or longitudinal) (Kocurek, 1991), because various combinations of these parameters exist in nature. Modern dunes can further be classed as simple (unamalgamated dunes), compound (similar dune types superimposed on top of one another), or complex (different dune types superimposed), although it is difficult to distinguish compound from complex dunes in the rock record (Kocurek, 1981, 1991).

Observable cross-bedding exhibits apparent variability in its aspect throughout the formation, as the 360° variation in outcrop orientation variably transects original duneforms that dominantly migrated towards the south (Rubin & Carter, 1987; Kocurek, 1991). The simplest

cross bedding presents an approximately repeating pattern of parallel foresets separated by discordant bounding surfaces (Figure 5). Such sections are cut parallel to the direction of migration of the dunes, revealing the climbing bedforms. In other orientations there is less regularity to the stacked cross-bedded sets, suggesting that successive bedforms were either different shapes, or that their crestlines were locally out of phase (Rubin & Carter, 1987). Comparing these observations with the models of Rubin and Carter (1987), it is probable that the dunes recorded in the Mereenie Sandstone had elongate crescentic forms and were oriented transverse to prevailing wind direction (Figure 5.). The discordant bounding surfaces in the cross-bedded facies of the Mereenie Sandstone indicate that the facies are amalgamated dune deposits which must have had either a complex or compound form (e.g. Figure 4.).

Estimating parameters of the Mereenie dunes - Quantitative estimates of dune height can be constrained from measurements of cross-bedded sets (Kocurek & Dott, 1981), assuming the original dune population was of fairly uniform dimensions (Kocurek, 1991). In most cases, set thickness does not directly represent the original height of the bedform due to truncation (Kocurek & Dott, 1981; Rubin & Hunter, 1982). Instead, original height (H) is a function of set thickness (T), bedform index (i.e., spacing-to-height ratio: I), and distance migrated (D) (Rubin & Hunter, 1982).

$$H \cong \left(\frac{TD}{I}\right)^{\frac{1}{2}} \quad (1)$$

Calculating D from ancient strata is dependent on outcrop quality and style, as it requires individual beds to be traced across their total depositional extent. The outcrop style of the Mereenie Sandstone precludes this, as many sections have been weathered into a series of discrete buttes (Figure 2). However, an alternative set of equations can be used to indirectly produce an estimate of original dune height, by first calculating dune spacing (Kocurek & Day, 2018):

$$T = S \tan \theta + 0.8225h_{SD}^2/h_M \quad (2)$$

In this equation, S is dune spacing, θ is the angle of climb, and the final term ($0.8225h_{SD}^2/h_M$) is experimentally derived as a component of set thickness resulting from scour depth (Bridge & Best, 1997; Kocurek & Day, 2018). The ratio of mean dune height (h_M) to standard deviation of dune height (h_{SD}) is not directly measurable in ancient strata, but can be approximated from modern analogue: for example, in a study of Jurassic dune facies, Kocurek and Day (2018) substituted extensively documented measurements from the White Sands Dune Field (WSDF) in New Mexico (Baitis et al., 2014). Here we follow Kocurek and Day's (2018) precedent, and also utilize the WSDF as an analogue: this is appropriate because the WSDF is dominated by crescentic dunes with damp interdunes (Kocurek et al., 2007), producing shallowly climbing strata. Accordingly, a value of 0.36 m can be approximated for h_{SD}^2/h_M (Kocurek & Day, 2018), giving an original dune spacing for this section of Mereenie Sandstone of up to 155 m, with a mean of 69 m.

In order to calculate dune heights in the Mereenie Sandstone, this value must be combined with bedform index. However, this is not a simple ratio because the relationship between bedform spacing and height is non-linear. Instead it is expressed as a power function, where dune height (H) is the product of spacing (S) raised to the power of an exponent (n) and multiplied by a constant (c) (Lancaster, 1988).

$$H = cS^n \quad (3)$$

This relationship is not consistent amongst different dunefields (Lancaster, 1988), so to estimate the value for the Mereenie Sandstone it must be compared with modern examples with dunes of similar size and morphology. Based on the limited sample of modern dunes summarized by Lancaster (1988), the Skeleton Coast of Namibia provides a good proxy because it is typified by fairly closely spaced transverse crescentic dunes. Substituting the

Skeleton Coast values for the constant (0.008) and exponent (1.40) (from Lancaster, 1988, Table 1), a reasonable estimate of a mean height of 3 m, and maximum height of 9.3 m, can be calculated for the Mereenie Sandstone dunes.

Flat-bedded Facies

Description – The flat-bedded facies of the Mereenie Sandstone is lithologically, compositionally and texturally very similar to the cross-bedded facies, but organized as apparently horizontally-bedded very-fine to medium-grained sandstones. The facies frequently crops out as laterally-extensive bedding planes, but can also be recognised in cliff exposures as 0.2-5 m thick finely-bedded packages of beds, individually between 1 cm and 25 cm thick. In some locations, the flat-bedded facies is truncated by erosional bounding surfaces that juxtapose the overlying cross-bedded facies (Figure 4).

Many exposed bedding planes are featureless, but some are true substrates (Davies and Shillito, 2018), preserving sedimentary structures that attest to them having been ancient sediment-water/air interfaces. These structures include symmetrical ripple marks, raindrop impressions, and adhesion marks (Figure 6), in addition to the entirety of the ichnofauna known from the Mereenie Sandstone (see Trace fossil associations).

Interpretation - The bedding planes in the flat-bedded facies provide direct evidence for both subaerial exposure (adhesion marks, raindrop impressions) and subaqueous sculpting (symmetrical wave ripple marks) of sediment at the time of deposition. The lack of evidence for dune topography and interbedding with cross-bedded facies implies that the flat-bedded facies are interdune deposits. The evidence for both subaqueous and damp subaerial conditions suggests that the interdunes acted as areas where water could pool, and they can thus be considered damp interdunes (Mountney & Thompson, 2002).

Depositional Setting

A depositional model for the lower Mereenie Sandstone is shown in Figure 7. This shows a wet aeolian system, interpreted from the extensive evidence for subaqueous and emergent sedimentary structures in the flat-bedded interdune facies. Damp aeolian interdunes are a function of an elevated water table (Carr-Crabaugh & Kocurek, 1998; Mountney & Thompson, 2002), in contrast with dry aeolian interdunes that form as simple depressions between successive dunes (Kocurek & Havholm, 1993; Mountney, 2012). In wet aeolian systems, the elevation of base-level through the heightening of the water table enables extensive accumulations of interdune strata, which climb in tandem with dune strata (Kocurek & Crabaugh, 1993; Mountney, 2012). The high frequency of damp interdune deposits in the Mereenie Sandstones implies frequent floodwater recharge, which would also have subdued rates of aeolian dune migration and restricted supply of aeolian sediment (Mountney & Thompson, 2002).

Flat bedded facies (damp interdunes) are not uniformly abundant throughout the Mereenie Sandstone, and are subordinate to the cross-bedded facies (crescentic dunes) in the lower part of the studied section. A possible explanation for this is that the succession records a progressively wetter climate, with later elevation of the water table increasing the ratio of interdune to dune. When the water table was heightened, the sediment budget was restricted due to the trapping of sediment in contact with the capillary fringe (Mountney & Thompson, 2002). Conversely, when the water table was relatively low, more sediment would have been liberated to contribute to dune formation (Mountney & Russell, 2009; Mountney, 2012). However, even in the lower part of the Mereenie Sandstone, it is apparent that the net aeolian sediment budget was still limited, evidenced by the estimated c. 3 m mean height of the dunes.

An alternative explanation for facies variability is that the Mereenie Sandstone records an incipient and subsequently developing aeolian system, which fits with the regional context of marine regression: the Mereenie Sandstone being the first non-marine unit to overlie the marine Carmichael Sandstone (Bagas, 1988). Typically, in the early stages of evolution of an aeolian system, dune fields emerge with many small dunes and evolve towards a system with fewer, larger dunes, spaced further apart (Ewing & Kocurek, 2010; Gao et al., 2015; Kocurek & Day, 2018). In light of the facies signatures of the Mereenie Sandstone, this explanation would fit the small stature dunes of the lower cross-bedded facies, whereas the upper part of the succession is dominated by interdune sediments simply because large dune deposition was centred away from the current outcrop area. However, the total absence of any evidence for large dunes suggests that this explanation may be less likely. It is also possible that non-marine conditions were well-established prior to the onset of Mereenie Sandstone deposition because it remains uncertain how conformable its basal contact with the Carmichael Sandstone is (Lindsay & Korsch, 1991).

Regional sedimentary context

Direct sedimentological evidence strongly suggests that the Mereenie Sandstone was deposited in a wet aeolian system, but provides no indication of the distance by which the dunefield was separated from the sea. Previous investigations of the unit have favoured the hypothesis that the dunefield was coastal, in part because of its ichnofauna (e.g. Gouramanis & McLoughlin, 2016), which could explain the elevated interdune water table (Clemmensen et al., 2001; Kocurek et al., 2001). However, a coastal locale appears unlikely in a regional context, because the Mereenie Sandstone depocenter was in the middle of the Amadeus Basin, which was located in northern Gondwana, surrounded by other continental basins (Haines et al., 2001). The pancontinental Larapintine Sea, which had inundated the Amadeus Basin with marine waters for much of the Ordovician (Webby, 1978; Haines et al., 2001; Haines & Wingate,

2007; Davies & Sansom, 2009), had begun to recede during the late Ordovician. This regression was associated with the Rodingan Movement at the onset of the Alice Springs Orogeny (Wells et al., 1970; Haines et al., 2001), during which 3 km of sedimentary strata was uplifted and eroded in the northeast of the basin (Figure 13.; Webby, 1978; Haines & Wingate, 2007). The absence of other Silurian strata directly east of the Mereenie Sandstone outcrop belt also suggests that there was a region of uplift immediately adjacent to the Mereenie depocenter, cutting off the centre of the Amadeus Basin from the influence of the eastwards-receding Larapintine Sea (Haines et al., 2001).

The inland setting implied from palaeogeographic reconstructions suggests that the Mereenie aeolian system was well divorced from marine influences, which raises questions about why the local water table was apparently so elevated. One plausible explanation is that the Rodingan topographic highs to the north and east would have influenced regional groundwater flow. These neighbouring highlands could have instigated basinward groundwater flow (Haines & Wingate, 2007), leading to a perched water table on impermeable sub-Mereenie strata within the Larapinta Group (e.g., the Stokes Siltstone; Bagas, 1988). This inland hypothesis has some supporting evidence because, despite evidence for intermittent drying of substrates, no salts or pseudomorphs are known from the Mereenie Sandstone, as would be expected to result from evaporating marine waters. The absence of evaporite signatures is additionally notable because they are present in the underlying Larapinta Group, and contemporaneous groundwater might be expected to have liberated some salts from these sub-strata (Bagas, 1988). However, if the water table was perched above the antecedent evaporites, hydrological connectivity would have been limited. Such a situation is plausible given the modern hydrological profile of the region, where the Mereenie Sandstone forms a significant aquifer, underlain by clay-rich units with low hydraulic conductivity (Brown et al., 1990).

The palaeogeographic and tectonic context of the Mereenie Sandstone thus favour that it was deposited some distance from any marine influence, with a high perched water table due to local groundwater flow, which rose further as the basin centre continued to subside (Shaw et al., 1991). In light of this assessment, the ichnofauna of the succession may have global significance in comparison with known Silurian-Devonian continental ichnofaunas from settings that retained some marine connectivity (Draganits et al., 2001; Krapovickas et al., 2016; Shillito & Davies, 2020).

The regional context has further significance because the Mereenie Sandstone was deposited at an equatorial latitude – for the entirety of its possible age range, central Australia only migrated from approximately 10 degrees north to 10 degrees south (Torsvik & Cocks, 2016). Climatically, this means that the setting would have been equatorial or tropical; settings in which deserts are rarer today as they are typified by biodiversity hotspots with high rates of precipitation (Sorooshian et al., 2000; Dirzo & Raven, 2003). It is possible that desert conditions persisted in the Amadeus Basin in part as a result of the anactualistic biological conditions of the Silurian (i.e., the minimal extent, small-stature vegetation that existed at the time (Davies and Gibling, 2010; Gensel et al., 2020)). However, such conditions would have been exacerbated by syn-depositional palaeogeography. Modern analogue shows that low latitude deserts predominantly occur in topographic rain shadows (e.g., the Taru Desert, adjacent to Mount Kilimanjaro (Butynski & de Jong, 2018), and the Atacama Desert, adjacent to the Andes (Hartley, 2003)). A similar scenario would have been likely during Mereenie deposition, as it occurred in the lee of significant highlands arising both from the Alice Springs orogeny to the north and the Petermann Ranges Orogeny to the south (Haines et al., 2001).

Speculatively, the palaeolatitude of the depositional environment may provide circumstantial clues to the age of the succession. If the prevailing northerly wind recorded in palaeocurrent directions (Figure 3) were equivalent to the northeasterly trade winds that today occur close to

the equator in the northern hemisphere, then deposition might be expected to have occurred when the region was still north of the equator: suggesting an early-mid Silurian age (Torsvik & Cocks, 2016). However, this interpretation requires further supporting evidence, as more localized constraints on wind direction (e.g. topography) cannot be ruled out.

Ichnology of the Mereenie Sandstone

Trace fossils were first recognised in the Mereenie Sandstone by Wells et al. (1970), who reported "Scolithus-like pipes" and "a few trace fossils". The first focussed ichnotaxonomic assessment of the strata was undertaken by Gouramanis and McLoughlin (2016), who identified four named ichnotaxa (*Beaconites antarcticus*, *Diplichnites*, ?*Laevicyclus*, and *Taenidium barretti*) and three unnamed ichnotaxa ("Small indeterminate trail", "Small burrow openings", and "Burrow entrance with radial feeding traces"). Here we expand the number of known ichnotaxa from the Mereenie Sandstone to nine, reassign Gouramanis & McLoughlin's (2016) "*Taenidium barretti*" to *Polarichnus garnierensis*, and discuss their previously unnamed ichnotaxa. We omit the *Beaconites* reported by Gouramanis and McLoughlin (2016; their Fig. 5.), because although these particular specimens were also observed in this study, they appear to be stratigraphically below the base of the Mereenie Sandstone, within the Carmichael Sandstone.

The chief signature of the Mereenie Sandstone is a low abundance of trace fossils, with a low to moderate ichnodiversity (9) and ichnodisparity (7). The ichnofauna is concentrated on a limited number of bedding planes within the flat-bedded (interdune) facies. The assemblage, abundance, and sedimentological context is shown in Table 1.

Ichnotaxa

Arenicolites isp. Salter 1857

Ten occurrences of paired burrows in positive epirelief as paired apertures are identified as *Arenicolites* (Figure 8.G). The burrows have homogenous infill that is compositionally similar to the surrounding sediment, and the paired apertures are 4-10 mm in diameter, and separated by approximately 20-40 mm. Paired burrows are distinguished from the tops of the simple vertical burrows due to the consistent close association of apertures. There is no evidence of spreite between burrow shafts, distinguishing these traces from *Diplocraterion*. Even given the uncertain precise age of the Mereenie Sandstone, these are definitively amongst the earliest non-marine examples of *Arenicolites*, which is not known elsewhere in non-marine strata before the Pridoli (Morrissey et al., 2012a; Shillito & Davies, 2017). The known examples occur dominantly on two bedding planes, one within the Garden of Eden (Figure 1), and the other immediately to the east of there. A vermiform tracemaker is considered most likely, through analogy with modern burrows (Häntzschel, 1975).

“Burrow entrance with radial feeding traces”

A single specimen of a “Burrow entrance with radial feeding traces” was identified by Gouramanis and McLoughlin (2016) in their study of the Mereenie ichnofauna (Figure 8.I). This specimen was not witnessed in the field, and whilst it resembles *Gyrophyllites* based on the images and description in Gouramanis and McLoughlin (2016), it cannot be confidently assigned to an ichnogenus, and so is left in open nomenclature. The trace is approximately circular, comprised of a featureless core surrounded by radiating unbranched, club-shaped lobes. It is preserved in a combination of positive and negative epirelief, and is 37 mm in diameter (Gouramanis & McLoughlin, 2016). *Gyrophyllites* elsewhere are thought to have been produced by vermiform organisms, and are known from throughout the Phanerozoic, with the earliest specimens from shallow water settings (Muñoz et al., 2019a; b).

Didymaulichnus lyelli Rouault 1850

Seven examples of short, bilobate paired grooves in negative epirelief separated by a median ridge are identified as *Didymaulichnus* (Figure 8.B). The trails are smooth, with no internal structure or ornamentation, and occur on two bedding planes. Ten of these examples form a single trail that is discontinuous along its length, as it is associated with asymmetrical ripples and occurs only on the ripple crests, and the other four form a similar discontinuous trail close by. The grooves are approximately 3 mm apart, and the separation between successive pairs in the trail is 18-22 mm, dependent on separation between successive ripple crests. All of these occur close to the trail on the north side of the King's Canyon Rim walk. There is some discussion whether *Didymaulichnus* was produced by molluscs or arthropods (Häntzschel, 1975), but arthropods are most widely favoured (Bradshaw, 1981).

Diplichnites gouldi Gevers 1971

Seven examples of symmetrical trackways, each consisting of two rows of closely spaced imprints in negative epirelief, with no medial markings, have been identified as *Diplichnites*. The trackways range in width from 80-160 mm, with five between 120-160 mm. The imprints are not connected to one another, although some overlap, and are ellipsoidal to circular in shape, oriented approximately perpendicular to the trace axis (Figure 8.C). They correspond to *D. gouldi* form B, as described by Trewin and McNamara (1994). *Diplichnites* occur on multiple different bedding planes, with most examples close to Cotterill's Lookout. *Diplichnites* is known to be produced by arthropods, and may be produced by many different classes including myriapods, eurypterids, and xiphosurans (Trewin & McNamara, 1994).

Helminthopsis isp. Heer 1877

A single occurrence of a simple, smooth walled horizontal trail with a short, irregular, meandering path was observed (Figure 8.A). The trail is 3 mm wide, preserved in positive epirelief, and has a compositionally-similar infill to the host sediment. It occurs in close

association with *Arenicolites* near the Garden of Eden. *Helminthopsis* is a systematic deposit-feeding trace produced by vermiform organisms, with polychaetes and priapulids both considered possible tracemakers (Han & Pickerill, 1995).

Laevicyclus isp. Quenstedt 1879

Thirty-five of the burrows observed in the Mereenie Sandstone are identified as *Laevicyclus*. These are cylindrical vertical burrows with a passively filled core, surrounded by an actively filled mantle (Figure 8.E). The apertures of the burrows are preserved in mixed positive and negative epirelief, and typically appear to be funnel-shaped, ranging from 55-140 mm in diameter. The infilling sediment is compositionally similar to the bedding planes which they occupy. One bedding plane at the Garden of Eden exhibits twenty *Laevicyclus*, and they typically occur in clusters rather than in isolation. The dense accumulation implies preferential colonization of some substrates by the tracemakers. Some forms described as *Laevicyclus* elsewhere have been interpreted as the product of a sweeping motion produced by a tethered object (Jensen et al., 2002). This interpretation can be rejected for specimens in the Mereenie Sandstone as the burrows are irregularly asymmetric, have no concentric markings, and are variably in positive and negative epirelief at different points along continuous arcs. Various invertebrate tracemakers have been considered for *Laevicyclus*, but have not been identified with certainty (Knaust, 2015).

Palaeophycus isp. Hall 1847

Eight specimens of smooth, unornamented, approximately cylindrical and predominantly horizontal burrows in positive epirelief, with a structureless infill of similar lithology to the host sediment, are ascribed to *Palaeophycus* (Figure 8.D). The burrows are variably straight to curved, and all of the specimens that were observed are unbranched. They range from 9-20 mm in length, and from 4-7 mm in diameter. The known examples occur dominantly within the

Garden of Eden in association with *Laevicyclus*, but two were observed at the north end of the Giles Track, close to King's Canyon. *Palaeophycus* is thought to record selective feeding or predatory behaviour, and is likely produced by a range of vermiform organisms (Osgood, 1970).

Polarichnus garnierensis Narbonne et al 1979

Polarichnus is the most abundant trace fossil observed in the Mereenie Sandstone, with sixty-three individual occurrences observed on many different surfaces throughout the section. These traces were originally described as *Taenidium barretti* (Gouramanis & McLoughlin, 2016), and have been reidentified as surficial striations curve in opposite directions either side of the mid-point of the burrow, a feature which is incompatible with the previous diagnosis. *Polarichnus* comprises a shallow U-shaped burrow with no spreite, which is typified by domed sedimentary laminae between the arms of the burrow. Asymmetric folds and thrusts in the domed sediment give the appearance of irregular striations perpendicular to the shaft (Figure 8.H, 9). The shaft and infill of the burrow are commonly impossible to ascertain in clastic strata, and so the ichnospecies is identified from the domed laminae on the top surface (see Davies et al., 2006, for similar expressions). All examples were observed in positive epirelief, and range in length from 95-610 mm and in width from 45-60 mm. These dimensions are distinct from the other burrows and trackways in the Mereenie Sandstone, suggesting unique tracemakers. *Polarichnus* is a poorly understood trace, with no modern analogue, and is presently only known from four successions worldwide, all of late Silurian and early Devonian age (Narbonne et al., 1979; Pollard et al., 1982; Davies et al., 2006; Shillito & Davies, 2020). The tracemaker of *Polarichnus* is unknown, but burrows in both Norway and Canada closely match the dimensions of eurypterid body fossils from those locations (Narbonne et al., 1979; Davies et al., 2006), although none are known from the Mereenie Sandstone.

Two burrows are identified as *Skolithos* from transverse cross sections through simple, unbranched vertical or near vertical tubes. The infill of these burrows is homogenous and similar to the surrounding sediment, and the diameters of the apertures ranges from 10-12 mm. The specimens appear on bedding planes in positive epirelief as raised circles (Figure 8.F) which are not clearly directly associated with any other burrows, allowing them to be distinguished from the paired burrows of *Arenicolites*. The known examples come from east of the Garden of Eden. Similar modern burrows are known to be produced by filter feeding polychaetes, but other tracemakers and life habits are possible (Curran & Frey, 1977).

Trace fossil associations

Direct associations between different ichnotaxa are uncommon in the Mereenie Sandstone, and most colonized bedding planes host monospecific assemblages (Figures 10-12). This is especially notable for the most common ichnotaxon, *Polarichnus*, where multiple bedding planes typically contain between one and eight specimens, but no other trace fossils (Figure 10). Only two bedding planes provide exceptions to this. One contains most of the known occurrences of *Laevicyclus*, in association with a single *Polarichnus* and abundant, small *Arenicolites* (Figure 11). The second hosts a diverse assemblage of six different infaunal traces: *Arenicolites*, *Helminthopsis*, *Laevicyclus*, *Palaeophycus*, *Polarichnus*, and *Skolithos* (Figure 12).

All of the known trace fossils from the Mereenie Sandstone occur on bedding planes, some of which appear to be true substrates (Davies & Shillito, 2018). As such, the palimpsesting of trace fossils and sedimentary surface textures can inform about the sequence of events during sedimentary stasis, and how the fauna responded to changing conditions (Davies et al., 2017; Davies & Shillito, 2018). For example, in the monospecific *Polarichnus* assemblages (e.g.

Figure 10), 44% of all known examples of *Polarichnus* occur on bedding planes that also contain adhesion marks, and 25% on rippled surfaces. As adhesion marks only form when a surface is subaerially exposed, due to wind transporting sediment over a damp substrate (Kocurek & Fielder, 1982), at least some of the *Polarichnus* tracemakers must have interred themselves in the substrate during intervals of subaerial exposure. Interestingly, all of the other four known instances of *Polarichnus* in the global Silurian-Devonian record are also associated with evidence for emergence, such as desiccation cracks or adhesion marks (Narbonne et al., 1979; Pollard et al., 1982; Davies et al., 2006; Shillito & Davies, 2020). The type specimens of the ichnotaxon were hypothesised to record animals constructing U-shaped burrows to escape unfavourable environmental conditions (Narbonne et al., 1979), and this could explain the close association of *Polarichnus* with emergent sedimentary structures. Subaerial exposure would have been a particular problem for the first animals to exploit non-marine niches, as they would have had to contend with desiccation due to evaporative water loss, and associated challenges to respiration and excretion (Davenport, 1985; Truchot, 1990). Considering *Polarichnus* as an adaptive solution to avoid water loss by early non-marine pioneers explains both its global rarity and its local abundance, in strata with a very specific stratigraphic and palaeoenvironmental range.

Another informative true substrate is the *Laevicyclus* bed at the “Garden of Eden” (Figure 1). It reveals an assemblage of interface feeding traces (*Laevicyclus* and *Arenicolites*), alongside a solitary *Polarichnus* (Figure 11). The distribution of *Laevicyclus* on the surface is approximately uniform, so the traces may be constituents of a contemporaneous feeding assemblage, spaced to minimise unnecessary competition (Pemberton & Frey, 1984; Davies et al., 2009). The lack of sedimentary structures on the bedding plane means its palaeoenvironmental context is uncertain, but the absence of otherwise common adhesion marks might indicate that *Laevicyclus* and *Arenicolites* developed in intervals when interdunes

were flooded. It is unclear whether the sole *Polarichnus* was contemporaneous with the other burrows, or a later palimpsest.

The most diverse assemblage of trace fossils occurs approximately 10 metres stratigraphically above the *Laevicyclus* bed, and contains *Arenicolites*, *Helminthopsis*, *Laevicyclus*, *Palaeophycus*, *Polarichnus*, and *Skolithos*. This assemblage includes both interface (*Arenicolites*, *Laevicyclus*, *Skolithos*) and deposit feeding (*Helminthopsis*, *Palaeophycus*) traces, along with the enigmatic *Polarichnus*. The distribution of the trace fossils is non-uniform, and the surface lacks physical sedimentary structures for the interpretation of its palaeoenvironmental context. However, the range of feeding styles that are recorded suggests this is an assemblage formed by opportunist tracemakers, exploiting temporarily favourable conditions.

The only trackway trace fossil in the Mereenie Sandstone, *Diplichnites*, occurs on six known bedding planes, but surfaces rarely contain more than one individual trackway, and the trace fossil only ever occurs as a monospecific assemblage. The dimensions of the trackways are significantly larger than those of any of the burrows, including *Polarichnus* (Table 1), suggesting that the Mereenie interdunes hosted a subordinate population of large arthropods that were distinct from any infaunal tracemakers. No trackways are associated with emergent sedimentary structures and two are associated with symmetric ripple marks with no evidence for exposure, suggesting that these largest denizens of the ecosystem favoured subaqueous conditions.

It is possible that the apparent absence of trace fossils from the cross-bedded facies is due to nature of the outcrop (Figure 2). This is because all trace fossils were observed on bedding plane exposures, yet the bedding surfaces are almost entirely the tops of planar beds from the flat-bedded facies. The systematic underrepresentation of horizontal surfaces from the cross-

bedded facies is significant, as were any horizontal traces to exist within this facies they would not be observed. Additionally, horizontal traces would have a lower preservation potential in the cross-bedded facies, due to reworking of the surficial sediment through avalanching down foresets. However, of the 129 individual trace fossils observed throughout the formation, 91.5% have a vertical component, and as there is no evidence of any vertical trace fossils in the extensive cliff exposures of the cross-bedded facies, it is reasonable to consider the apparent absence of trace fossils to be a true absence.

Comparison with other ichnofaunas

The record of aeolian ichnofaunas from the Lower Palaeozoic is sparse (Krapovickas et al., 2016). The earliest Cambrian and Ordovician examples record only temporary excursions into coastal aeolian dunefields (MacNaughton et al., 2002; Hagadorn et al., 2011), and even known Lower Devonian instances are restricted to trackways in coastal aeolian dune facies (Draganits et al., 2001; Krapovickas et al., 2016).

The earliest uncontroversial record of an inland aeolian ichnofauna dates from the Middle Devonian, within the Kilmurry Sandstone (Caherbla Group) of Ireland (Morrissey et al., 2012b; Krapovickas et al., 2016). Like the Mereenie Sandstone, the Kilmurry Sandstone is split into two distinct facies associations corresponding to aeolian dunes and interdunes. The aeolian facies of the two units are sedimentologically similar, as both record compound transverse crescentic duneforms (Dodd, 1986). However, the units exhibit a pronounced contrast in terms of their ichnology: the Kilmurry Sandstone dune facies contain a low diversity ichnofauna (ichnodiversity of 10 and ichnodisparity of 6; Morrissey et al., 2012b), contrasting the total absence of trace fossils in similar facies of the Mereenie Sandstone (Figure 14). The interdune facies of the two units are both sedimentologically and ichnologically distinct. The Kilmurry Sandstone interdune facies indicate a pervasive ephemeral fluvial influence (Dodd, 1986;

Morrissey et al., 2012b), and its ichnofauna is less diverse than that of the Mereenie Sandstone, with no shared ichnotaxa between the units (Figure 14).

The dissimilarity between the Mereenie and Kilmurry ichnofaunas enables a number of generalized observations to be made. 1) *The lack of trace fossils from permanently dry settings in the Mereenie Sandstone but presence in the Mid Devonian Kilmurry Sandstone*: it is not until Devonian-aged strata that there is evidence of desert organisms capable of surviving for long periods in desiccating environments, or capable of burrowing in dry sand (requiring different physiological adaptations than burrowing in wet, adhesive substrates [Dorgan et al., 2006; Dorgan, 2015]). 2) *The presence of U-shaped burrow ichnotaxa (such as *Polarichnus*) in the Mereenie Sandstone but not in the Kilmurry Sandstone*: U-shaped burrows are known to serve as refuges from unfavourable environmental conditions (Narbonne et al., 1979), so the Silurian ichnofauna bears more hallmarks of opportunistic pioneer colonists than the well-established Devonian ichnofauna. 3) *Lower ichnodiversity in the Kilmurry Sandstone interdune facies than the Mereenie Sandstone interdune facies*: this appears to have an environmental control and implies fewer ichnotaxa were present in fluvially-influenced interdune deposits than groundwater-controlled interdune deposits. It mirrors trends in Palaeozoic alluvial facies where a lower abundance and diversity of traces occur in higher energy channel deposits than lower energy floodplains (Morrissey et al., 2012a; Minter et al., 2016b; Shillito & Davies, 2017).

The Mereenie ichnofauna can additionally be compared with near-contemporaneous and geographically-proximate marine strata, such as those of the underlying Ordovician Stairway Sandstone (Figure 1) (little work has been done on the intervening Stokes Siltstone and Carmichael Sandstone, although unspecified trace fossils and *Cruziana* have been reported from both formations [Wells et al., 1970; Bagas, 1988]). The Stairway Sandstone was deposited in shallow water and occasionally emergent conditions of the Larapintine Sea, and can be

confirmed as fully marine from the diverse invertebrate and vertebrate body fossil fauna (Webby et al., 2000; Davies et al., 2011). As expected, the Stairway ichnofauna is significantly more diverse than the Mereenie Sandstone, with an ichnodiversity of 16 ichnogenera, and an ichnodisparity of 12 (Figure 15). It contains widespread deposit feeding traces (e.g. *Arthropycus*; Rindsberg & Martin, 2003), typical of contemporaneous tidal environments (e.g. Bradshaw, 1981; Hunter & Lomas, 2003; Shillito & Davies, 2020), but lacks the archetypal *Polarichnus* seen in the Mereenie Sandstone. However, there is significant overlap between the two ichnofaunas in that five of the eight ichnotaxa from the Mereenie Sandstone are also present in the Stairway Sandstone, and two of the remaining taxa are mirrored by similar traces filling the same ecological niches (*Palaeophycus* with *Planolites*, and *Helminthopsis* with *Gordia*).

The ichnotaxa observed in both the Mereenie and Stairway sandstones are known to be facies-crossing, and continue to be present in both continental and marine settings through the rest of the Phanerozoic, and as such, it is uncertain whether there is a causal link between the ichnofaunas. However, the comparison between the Mereenie and Stairway sandstones suggests that some of the earliest aeolian invertebrate fauna may be similar to organisms that occupied the shallow marine realm millions of years earlier, but that they developed ethological adaptations to cope with the major environmental shifts in the region. For example, the presence of widespread *Polarichnus* suggests novel adaptive solutions were necessary to avoid desiccation in the Mereenie ecosystem, while the absence of widespread deposit feeding traces could imply a limited supply of food resources.

Figure 16 illustrates this with a hypothesized progression from the shallow marine Stairway Sandstone ecosystem, through the restricted subaqueous Carmichael Sandstone ecosystem, to the Mereenie dune field ecosystem. It is hypothesized that during the long-term subaerial uplift of the centre of the Amadeus Basin, groups of invertebrate fauna that could adapt to survive

increased continentality exploited new niches. The diversity of these pioneers progressively reduced as the hostility of the setting increased until only a restricted community of survivors persisted, recorded as the Mereenie ichnofauna. The tracemakers that were most suited to this long-term environmental shift included those that created trackways and vertical burrows. The ethologies recorded by such traces are versatile and can serve a useful function to the tracemaker independent of environment (Buatois et al., 1998; Schlirf & Uchman, 2005). Other behaviours, such as those recorded by *Polarichnus*, emerged out of necessity to counter the challenges posed by a novel habitat. *Polarichnus* appears to be an ichnological artefact of an evolutionary “stepping stone”, appearing in a restricted window during the colonization of subaerial environments. Finally, many behaviours (and by extension tracemakers), that were unsuited to the novel conditions, did not make the transition from water to land at this time. Examples of such include systematic deposit-feeding behaviours, which are well suited to subaqueous environments where sediment and nutrients are frequently reworked, but are poorly suited to gradually accumulating interdunes, where replenishment is significantly slower.

Conclusions

- The Silurian Mereenie Sandstone was most likely deposited in a wet inland aeolian environment, typified by c. 3 m-high crescentic dunes and wide damp interdunes, in a topographic rain shadow setting near the equator.
- A low diversity ichnofauna indicates that invertebrates permanently inhabited the interdunes. The fauna contended with stressed conditions through adaptive strategies such as self-burial to avoid desiccation during the evaporation of interdune ponds (as typified by *Polarichnus*).

- This is the earliest known record of an inland aeolian ichnofauna, pre-dating the previous earliest report from the Mid Devonian, and provides an insight into the inception of desert ecosystems.
- The regional context of the unit is broadly contemporaneous with the draining of the Larapintine Sea. The similarity between some of the trace fossils of the Mereenie Sandstone and those of earlier marine units implies that there is some commonality between the faunas. It is possible that local environmental change may have been adapted to and exploited by some existing shallow marine fauna at the onset of terrestrialization.

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885 **Figure Captions**

886 Figure 1. Location Map and regional stratigraphy of the Mereenie Sandstone. A) A map of
 887 Watarrka National Park, where the Mereenie Sandstone crops out, showing key walking trails
 888 where observations took place. B) A close up of the King’s Canyon area of Watarrka National
 889 Park. C) A larger scale map of the area around Alice Springs, showing the location of Watarrka
 890 National Park. D) The regional stratigraphy of the Mereenie Sandstone and the underlying
 891 Larapinta Group. Satellite images © CNES / Airbus, © Google Earth. Age of the Larapinta
 892 Group units from Davies et al. (2011) and Sansom et al. (2012); Age of the Parke Siltstone
 893 from Shergold et al. (1991).

894 Figure 2. An overview of the two distinct types of outcrop of the Mereenie Sandstone that occur
 895 in the Watarrka National Park (cf. Shillito and Davies, 2020). This reveals a mixture of stepped
 896 plateau, and cliff exposure types, with an abundance of horizontal outcrop types in trace-
 897 bearing strata. Block diagrams show the hypothetical distribution of observed trace fossils in a

898 3x3 unit cube, if units contain vertical (blue), horizontal (red) or no (yellow) traces. Grey shows
899 areas which cannot be observed, and absent units show those lost to erosion. Pie charts show
900 proportion of existing vertical traces (blue/grey) and horizontal traces (red/grey) which can be
901 observed with a given outcrop style, and the relative bias towards observed vertical/horizontal
902 traces (red/blue) given equal proportions existing within the volume. Upper block diagrams
903 and pie charts assume vertical and horizontal traces in every unit cube. Lower block diagrams
904 and pie charts assume vertical and horizontal traces in every alternate unit cube. Examples of
905 the outcrop types come from the King's Canyon region of Watarrka National Park.

906 Figure 3. Representative sedimentary log and palaeoflow rose from the Mereenie Sandstone.
907 A log of interbedded cross-bedded and flat-bedded facies very fine sandstone, with sedimentary
908 surface textures and trace fossils marked. Log records a representative section 14 m thick with
909 two *Polarichnus* beds, the lower containing 8 traces, and the upper a single specimen.
910 Palaeoflow measurements taken from throughout the observed thickness of the cross-bedded
911 facies indicate a dominant flow to the South.

912 Figure 4. Aeolian sedimentary structures from the cross-bedded facies of the Mereenie
913 sandstone. Palaeoflow direction illustrated following Davies et al., 2018. A) Large scale,
914 shallow cross bedded sandstone, with reactivation surfaces (thick white lines). Thin white lines
915 show where cross bedded sandstone is cutting down through flat bedded sandstones. Image
916 looking to the east (80°). B) Large scale, shallow cross bedded sandstone, with many
917 reactivation surfaces (thick white lines). Image looking to the east (110°). C) Pinstripe
918 lamination, formed as aeolian ripple lamination. Black scale bar – 1 m. Red scale bar – 1 cm.

919 Figure 5. Cross bedding used to determine dune morphology. All cross bedded sets are between
920 corresponding sets of flat-bedded interdune facies. A) Laterally continuous cross-bedded sets
921 with inclined bounding surfaces, as seen in Figure 4. B) Pseudo-random cross bedded sets,

truncating against each other and over/underlying flat-bedded deposits. C) Multiple laterally extensive cross-bedded sets. This highlights the difficulty tracing cross-bedded sets along their full duration in the Mereenie Sandstone, as outcrops are weathered into individual buttes between which it is difficult to correlate sets. D) Dune morphology and resultant bedding pattern model from Rubin and Carter (1987). A combination of laterally extensive cross-bedded packages (corresponding to cross sections parallel to direction of dune migration) and pseudo-random cross bedding (corresponding to cross sections perpendicular to direction of dune migration) are likely associated with transverse crescentic duneforms. White scale bar – 1 m.

Figure 6. Sedimentary surface textures from the flat-bedded facies of the Mereenie Sandstone. A) A bedding plane with symmetrical ripple marks to one side and adhesion marks to the other, revealing emergence of part of the substrate. B) A ripple marked surface within F2 with sand cracks palempsesting the ripple marks, showing evidence of emergence of the substrate. C) Laddered ripple marks, showing evidence for drainage and emergence of the substrate. Black scale bar – 10 cm.

Figure 7. Depositional model for the Mereenie Sandstone. Main schematic shows the broad depositional environment for all both associations together. Small schematics show a more detailed plan view highlighting the different sub-environments that are included within each facies association. Cross sectional interpretation is modified from Mountney (2012), and illustrates the relative abundance of interdune facies increasing up-section.

Figure 8. Trace fossils in the Mereenie Sandstone identified in this study. A) *Helminthopsis* in positive epirelief. B) *Didymaulichnus* in negative epirelief crossing ripple crests. C) *Diplichnites* in negative epirelief. D) *Palaeophycus* in positive epirelief (multiple examples). E) *Laevicyclus* burrow top in positive epirelief. F) *Skolithos* burrow top in positive epirelief.

G) *Arenicolites* presenting as paired burrow tops in epirelief. H) *Polarichnus* in positive epirelief. I) “Burrow entrance with radial feeding traces”, modified after Gouramanis & McLoughlin, 2016. Black scale bar – 10 cm. Red scale bar – 5 cm. White scale bar – 1 cm.

Figure 9. Different expressions of *Polarichnus* from the Mereenie Sandstone. A) A specimen with a smooth outside and apparent opening to the left of the burrow, a similar form to that illustrated in 8H. B) *Polarichnus* split by a fractured bedding surface, viewed in two bedding planes at different levels. This shows the internal structure has intense striations whereas the outside can appear smooth. C) A curved specimen of *Polarichnus* showing increased weathering towards the centre of the burrow. The arms of the burrow are more striated than the core. D) An elongate example of *Polarichnus* (30 cm) showing the typical striations on the arms of the burrow. Black scale bar – 10 cm.

Figure 10. *Polarichnus* associations from the Mereenie Sandstone. A) A monospecific assemblage containing only *Polarichnus* (Po), on a ripple marked bedding plane. B) A close up of the *Polarichnus* overprinting faint ripple marks. C) A close up of two overlapping *Polarichnus* burrows, a large clear burrow overprinting the outline of an earlier trace. Black scale bar – 10 cm.

Figure 11. *Laevicyclus* associations from the Mereenie Sandstone. A) An assemblage dominated by *Laevicyclus* (La), with small specimens of *Arenicolites* (Ar) in between the larger burrows. B) A close up of a *Laevicyclus* in close association with small paired burrow tops, interpreted as *Arenicolites*. C) The sole instance of *Polarichnus* known from this bedding surface, in association with a *Laevicyclus*. It is possible that the *Polarichnus* is a later palimpsest. Black scale bar – 10 cm.

Figure 12. Highest diversity trace fossil associations from the Mereenie Sandstone. A) The most diverse trace fossil bed known from the Mereenie Sandstone, containing *Arenicolites*

(Ar), *Palaeophycus* (Pa), *Skolithos* (Sk), and *Polarichnus* (Po). Small burrows are clustered to the centre and left of the image, with two *Polarichnus* on the right side. B) A close up of *Arenicolites*, *Palaeophycus* and *Skolithos* in close association with one another. C) A close up of one of the *Polarichnus*, with associated *Arenicolites* burrow tops. Black scale bar – 10 cm.

Figure 13. A palaeogeographic map illustrating the closure of the Larapintine Seaway from the Ordovician (pre-Mereenie) to Silurian (during Mereenie deposition), following Webby, 1978. This shows how the area where the Mereenie was deposited was part of a pan-continental seaway during deposition of the Larapinta Group. Preceding deposition of the Mereenie Sandstone, large areas were uplifted due to the Alice Springs Orogeny, and the margin of the remnants of the Larapintine Seaway retreated to the east.

Figure 14. Comparison of the ichnofaunas from dune and interdune facies associations of the Kilmurry Sandstone Formation with the ichnofauna from the Mereenie Sandstone. All three ichnofaunas have a lot of differences, but the Mereenie and Kilmurry dune ichnofaunas share key components such as arthropod trackways and trails, and simple vertical and horizontal burrows. Numbers correspond to categories of architectural design defined by Buatois et al. (2017): 1) Simple horizontal trails, 5) Bilobate trackways and paired grooves, 6) Trackways and scratch imprints, 8) Bilaterally symmetrical short, scratched impressions and burrows, 10) Passively filled horizontal burrows, 12) Simple actively filled (meniscate) horizontal to oblique structures, 35) Vertical unbranched burrows, 36) Vertical single U- and Y-shaped burrows.

Figure 15. Comparison of the ichnofaunas of the Stairway Sandstone (from Davies et al., 2011) and the Mereenie Sandstone. The marine Stairway Sandstone ichnofauna has a significantly greater diversity and disparity, despite predating the Mereenie ichnofauna and occurring at approximately the same geographic location, providing further evidence that the Mereenie Sandstone was non-marine. Numbers correspond to categories of architectural design defined

by Buatois et al. (2017): 1) Simple horizontal trails, 3) Chevronate trails, 5) Bilobate trackways and paired grooves, 6) Trackways and scratch imprints, 8) Bilaterally symmetrical short, scratched impressions and burrows, 10) Passively filled horizontal burrows, 11) Simple actively filled (massive) horizontal to oblique structures, 17) Horizontal burrows with horizontal to vertical branches, 30) Isolated and serial oval to almond-shaped burrows, 35) Vertical unbranched burrows, 36) Vertical single U- and Y-shaped burrows, 43) Horizontal, branched concentrically filled burrows. a) Specimens of *Protovirgularia* were originally described as *Uchirites*, however that ichnogenus has since been reevaluated as a junior synonym of *Protovirgularia* (Buatois et al., 2017). b) *Laevicyclus* was originally identified as *Monocraterion* in the Stairway Sandstone, but following a recent review of radial and rosette ichnotaxa (Muñoz et al., 2019a) all specimens of *Monocraterion* from outside of the Mickwitzia sandstone have been synonymized with *Laevicyclus*.

Figure 16. Development of the Mereenie fauna, a progression from the Stairway Sandstone to the Mereenie Sandstone. This figure shows the transition from the shallow marine Stairway Sandstone to the aeolian Mereenie Sandstone, and how the ichnofaunas have changed alongside environmental changes. In the Stairway Sandstone, diverse burrows are widespread throughout the submerged strata. In the Carmichael Sandstone the ichnofauna is less certain, but there is widespread evidence for emergence. In the Mereenie Sandstone the ichnofauna has a low diversity, with vertical burrows localised to wet areas of the substrate and *Polarichnus* in association with emergent surface textures. Relict burrows (dashed lines) are shown remaining in areas that were previously submerged, indicated by ripple marks.

Table 1. The ichnofauna of the Mereenie Sandstone. Table details observed relative abundances of traces (Single – 1 known occurrence, Multiple – 1-10 known occurrences, Abundant – >10 known occurrences). Architectural design categories correspond to those defined by Buatois et al. (2017).

Trace	Abundance	Associated sedimentary structures
Simple horizontal trails - 1		
<i>Helminthopsis</i>	Single	-
Bilobate trails and paired grooves - 5		
<i>Didymaulichnus</i>	Multiple	Ripples
Trackways and scratch imprints - 6		
<i>Diplichnites</i>	Multiple	Ripples
Passively filled horizontal burrows - 10		
<i>Palaeophycus</i>	Multiple	-
Radial to rosette structures - 19		
"Burrow entrance with radial feeding traces"	Single	-
Vertical unbranched burrows - 35		
<i>Laevicyclus</i>	Abundant	-
<i>Skolithos</i>	Multiple	-
Vertical single U- and Y-shaped burrows - 36		
<i>Arenicolites</i>	Multiple	-
<i>Polarichnus</i>	Abundant	Adhesion marks, ripples

[Click here to access/download;figure;Figure 3. Mereenie Logs.jpg](#)

	1	5			6			8		10	12				19	35			36	
	<i>Helminthopsis</i>	<i>Cruziana</i>	<i>Didymaulichnus</i>	<i>Bilobed trail</i>	<i>Diplichnites</i>	<i>Palmichnium</i>	<i>Protichnites</i>	<i>Rusophycus</i>	<i>Selenichnites</i>	<i>Palaeophycus</i>	<i>Ancorichnus</i>	<i>Entradichnus</i>	<i>Scoyenia</i>	<i>Taenidium</i>	Burrow entrance with radial feeding traces	<i>Laevicyclus</i>	<i>Pustulichnus</i>	<i>Skolithos</i>	<i>Arenicolites</i>	<i>Polarichnus</i>
Kilmurry Sandstone (Dune)		●		●	●	●			●	●	●	●					●	●		
Kilmurry Sandstone (Interdune)							●	●					●	●						
Mereenie Sandstone	●		●		●					●					●	●		●	●	●

	1		3	5		6		8	10	11	17		19	30	35		36			43
	<i>Gordia</i>	<i>Helminthopsis</i>	<i>Protovirgularia</i> ^a	<i>Cruziana</i>	<i>Didymaulichnus</i>	<i>Diplichnites</i>	<i>Monomorphichnus</i>	<i>Rusophycus</i>	<i>Palaeophycus</i>	<i>Planolites</i>	<i>Arthropycus</i>	<i>Phycodes</i>	Burrow entrance with radial feeding traces	<i>Lockeia</i>	<i>Laevicyclus</i> ^p	<i>Skolithos</i>	<i>Arenicolites</i>	<i>Diplocraterion</i>	<i>Polarichnus</i>	<i>Asterosoma</i>
Stairway Sandstone	●		●	●	●	●	●	●		●	●	●		●	●	●	●	●		●
Mereenie Sandstone		●			●	●			●				●		●	●	●		●	

Deposition of Stokes Siltstone
 Closure of Larapintine Seaway
 Regional Uplift - Rodingan movement
 Major unconformity

Uplift ends
 Deposition becomes fully terrestrial
 Minor unconformity