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New evidence on the taphonomic context of the Ediacaran *Pteridinium*

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New material collected from the Kliphoek Member of the Nama Group (Kuibis Subgroup, Dabis Formation) on Farm Aar, southern Namibia, offers insights concerning the morphology of the Ediacaran organism *Pteridinium*. *Pteridinium* fossils previously described as being preserved in situ have been discovered in association with scour-and-fill structures indicative of transport. Additionally, two *Pteridinium* fossils have been found within sedimentary dish structures in the Kliphoek Member. A form of organic surface with a discrete membrane-like habit has also been recovered from Farm Aar, and specimens exist with both *Pteridinium* and membrane-like structures superimposed. The association between *Pteridinium* fossils and membrane-like structures suggests several possibilities. *Pteridinium* individuals may have been transported before burial along with fragments of microbial mat; alternately they may have been enclosed by an external membranous structure during life.

Key words: *Pteridinium*, Petalonamae, Vendobionta, taphonomy, palaeoecology, Kliphoek Member, Nama Group, Ediacaran.

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Introduction

Members of the genus *Pteridinium* were first described as impressions of soft-bodied organisms preserved in sandstone of the Kliphoek Member (Nama Group, Kuibis Subgroup, Dabis Formation) in Namibia (Gürich 1930, 1933). “Three-dimensional” preservation is typical of fossils from the Kuibis Subgroup (Dzik 1999) and has been well documented for specimens of *Pteridinium* (Pflüg 1970).

The Kuibis Subgroup consists of sediments deposited in a foreland basin setting on the edge of the Kalahari Craton (Germes 1974), during a period of ocean basin closure to the west and north of the modern outcrop (Hartnady et al. 1985; Stanistreet et al. 1991). This unit includes shallow marine sediments with predominantly east-to-west flowing palaeo-currents (Gresse and Germes 1993), and multiple lines of evidence indicate a provenance on the Kalahari Craton (e.g., Horstmann et al. 1990). The Kuibis Subgroup was deposited in two subbasins, the Zaris to the north and the Witputs in the south, separated by a topographic high mapped in the region of Osis (Gresse and Germes 1993). The specimens discussed in this paper were collected from the Aus region of southern Namibia, representing Witputs Subbasin deposits. The Kuibis Subgroup in this basin is characterised by upward deepening feldspathic sandstone-orthoquartzite-limestone cycles, with sandstones giving way to limestone toward the west and

up-section. The Kliphoek Member represents the sandstone phase of the second of these cycles (Gresse and Germes 1993; Saylor et al. 1995).

In the Kliphoek Member, specimens of *Pteridinium* sometimes occur in close proximity to membrane-like structures of various shapes. The preserved state of these structures is variable, and they appear to represent the remains of a flexible mass or membrane. It is almost certain that these *Pteridinium* specimens were transported before burial, raising questions as to the association between *Pteridinium* fossils and such membranous features in life. This paper documents sedimentary features not previously reported in association with *Pteridinium*, along with previously unreported forms of membrane-like structure.

Institutional abbreviations.—NGS, Namibian Geological Survey, Windhoek, Namibia; UNESCO, United Nations Educational, Scientific, and Cultural Organisation, Paris, France.

Fieldwork and observations

Fossils discussed in this paper were collected during 2006, 2008, and 2009 from Farm Aar in southwest Namibia (Fig. 1). Numbers used for specimens are field allocation and specimens are part of the collections of the Namibian Geological Survey, Windhoek, where they will be lodged.

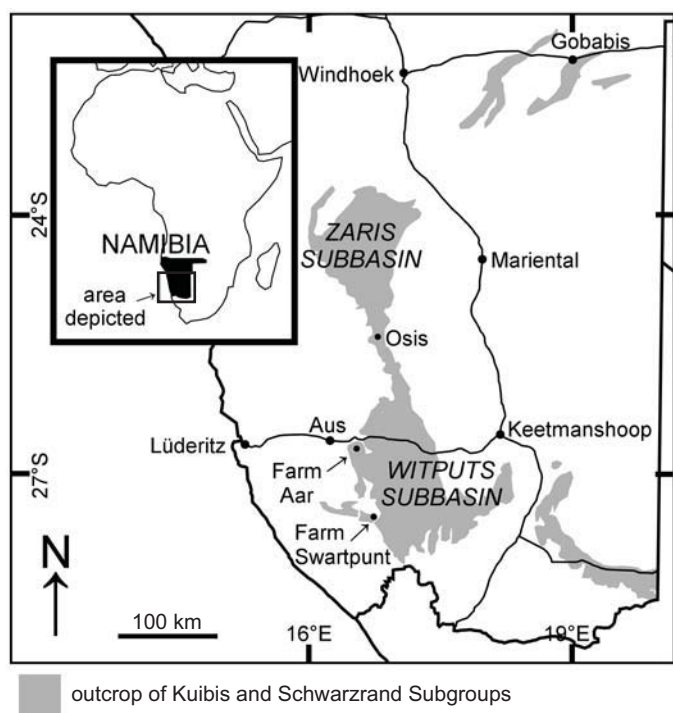


Fig. 1. Location of the Kuibis and Schwarzrand Subgroups in Namibia.

The Kliphoek Member consists mainly of sandstone, cross-bedded on a 1–2 metre scale, indicative of a shallow marine setting influenced by downslope avalanches and currents from tides or river deltas (Saylor et al. 1995). Saylor et al. (1995) reported “abundant channelized and scoured surfaces”, indicative of the occurrence of high-energy events within this member. This member is overlain by limestone beds belonging to the Mooifontein Member (Gresse and Germs 1993) indicative of marine transgression. New *Pteridinium* specimens were collected from the upper part of the Kliphoek Member and in the lower part of an overlying, 30–50 m thick shale dominated section that lies between the Kliphoek Member and the base of the massive Mooifontein Limestone (Fig. 2).

The sandstone is dominantly fine to very fine-grained orthoquartzite. Individual beds range up to 35 cm in thickness but are mostly thinner than 15 cm. Within the shale section, the bases and tops of the sandstone beds are sharp, but gently undulating, and sometimes exhibit very low angle scouring of the underlying shale. Sandstone beds are usually parallel laminated. Symmetric ripples occur on some bedding surfaces, while pelloidal structures resembling rip-up clasts are common on others.

The upper part of the Kliphoek Member was likely deposited in an extensive, sandy, braided fluvial system, partly reworked into vast inter-tidal sand flats along a low gradient coastal plain. The overlying shale beds are interpreted as intertidal to shallow subtidal muds deposited at the beginning of a regional transgression. Individual sandstone beds within these shales were likely deposited by sheet flood events into shallow water over mud-dominated inter-tidal to

sub-tidal sediments. A detailed study of this unit by the current authors is in preparation.

Pteridinium taphonomy

Pteridinium fossils are preserved within a well-sorted quartzite containing mica flakes visible in hand specimen, and occur in both negative and positive relief. Beds of *Pteridinium* are present in at least three widely separated localities at Farm Aar. These fossiliferous beds can extend over several metres. The discontinuous nature of the outcrop prevents mapping in entirety. *Pteridinium* fossils lie parallel to the bedding but exhibit no preferred orientation.

At one locality, a *Pteridinium*-rich bed is underlain by a scour-and-fill structure (Fig. 3), indicating that *Pteridinium* deposition occurred as part of a high-energy mass flow event. At two other localities, extensive dish structures are present, the largest outcrop covering an area of at least 60 square metres. The dish structures can be stacked up to 26 layers deep, forming a distinctive facies composed entirely of well-sorted quartzite (Fig. 4). Two specimens of *Pteridinium* are present within this facies, as well as rare features

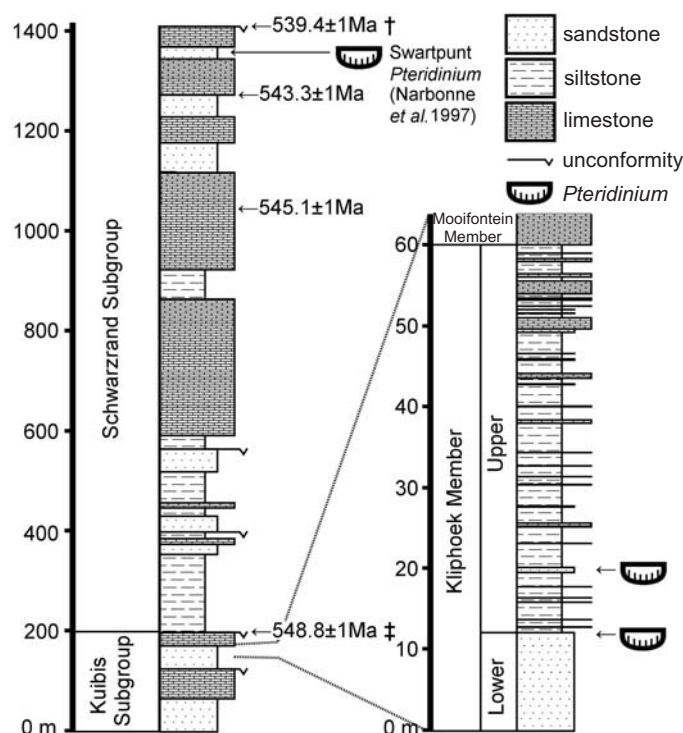


Fig. 2. Generalised stratigraphic section of the Nama Group south of Osis (left) and the uppermost part of the Kliphoek Member on Farm Aar (right). Dates refer to U-Pb zircon dates of ash beds, after Saylor et al. (1998). † U-Pb zircon date from an ash bed in the early Cambrian Nomtsas Formation (Grotzinger et al. 1995), which cuts unconformably into limestone of the upper Schwarzrand subgroup. ‡ U-Pb zircon date from an ash bed in the Hoogland Member of the Kuibis Subgroup, which outcrops north of Osis (Grotzinger et al. 1995). Trends in $\delta^{13}\text{C}$ suggest that this postdates deposition in the Kuibis Subgroup south of Osis (Saylor et al. 2005).

Fig. 3. Bed of *Pteridinium* fossils underlain by a scour-and-fill structure. Laminations are visible in the underlying sediment, cross-cut by the material containing *Pteridinium* fossils. From the top of the Lower Kliphoek on Farm Aar (see Figs. 1 and 2).

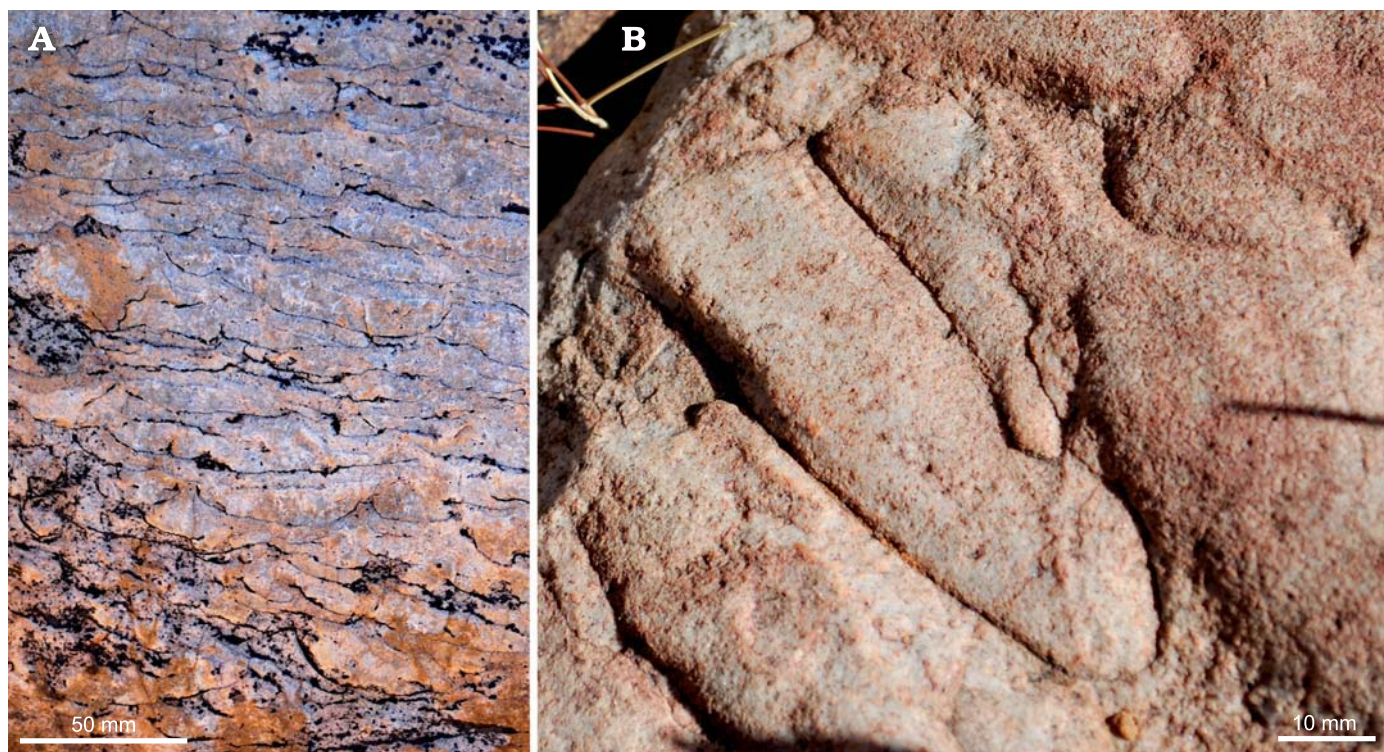


Fig. 4. **A.** Side view of a section bearing dish structures. The top of the bed is toward the top of the photograph. **B.** *Pteridinium* fossil embedded within dish structures, indicating that *Pteridinium* fossils formed a component of consolidating sediment, underlying rapidly deposited beds. Both from the top of the Lower Kliphoek on Farm Aar (see Figs. 1 and 2).

that resemble aspects of *Pteridinium* anatomy (Fig. 4B). At one of the two localities where they are observed, the dish structures are present less than a metre stratigraphically below a bed of *Pteridinium*. The structures superficially resemble linguoid ripples (see Wynn et al. 2002: fig. 5b), but they lack a convex ripple crest. It is possible that they represent a form of load-casting, but this must be considered unlikely on the basis of the uniformity between underlying and overlying sediment and the thinness of overlying beds. The structures are preserved concave-upward, and the possibility that the

facies has been overturned can be discounted, as at one of the two sites these structures are present above a sequence of sediments of the Kliphoek Member with distinct cross-bedding and a clear younging direction. This fact rules out phenomena such as gas doming (Gerdes et al. 1993) and hummocks in the sediment, and obscures comparisons with those cyanobacterial mats that display a convex-upward “domal” morphology (Scheiber 1999). Apart from the inclusion of at least two fossil *Pteridinium*, there are no immediately identifiable biologically-controlled features. The surfaces do not



Fig. 5. Specimen NGS-F-V-258 collected on Farm Aar. Multiple membrane-like surfaces are visible. These are interpreted as flexible organic structures, see discussion for more information.

resemble previously identified sedimentary structures associated with microbial mats (see Scheiber 2004 for an overview), and thus cannot be regarded as microbially induced sedimentary structures (Noffke et al. 2001; Noffke 2009), leaving dish structures as the most robust interpretation.

Associations of *Pteridinium* and membrane-like structures

Membrane-like structures have been collected from the top of the lower Kliphoek Member and the base of the upper Kliphoek Member. These structures are preserved as casts or moulds in massive quartzite. They occur as distinct surfaces within the quartzite, often taking on a sub-cylindrical or sub-discoidal shape (Fig. 5). Membrane-like structures usually possess folded surfaces and often display an overall contorted appearance. In one specimen, a membrane-like structure occurs in close proximity to a specimen of *Pteridinium* (Fig. 6).

Two localities produced *Pteridinium* fossils and membrane-like structures which are clearly associated with each other. Figure 6 illustrates a specimen of *Pteridinium* associated with a membrane-like structure. The membrane-like structure consists of a moulded surface within the quartzite with clear folds, and closely follows the contours of the *Pteridinium* specimen. Between the membrane-like structure and the *Pteridinium* specimen is a zone of massive quartzite (Fig. 6).

Close examination of the surface of this structure with a low angle light source reveals a subtle series of parallel lineations (Fig. 6). Lineations separate ridges with a modal

width of $\frac{1}{4}$ of a millimetre, roughly the size of the sandstone grains. The low angle of the light source and the uniformity of size would ordinarily suggest an artifact of chance grain alignment. However, if this were the case, the alignment of the lineations would vary as the light angle varied.

The lineations reported here are consistent over different light angles. Additionally, moulded surfaces immediately adjacent to the lineated surfaces lack lineations, despite being composed of grains of the same size in the same rock-type (see Fig. 6B). Lineations are generally continuous across discrete areas of membrane-like structure. They are visible only on the surfaces of membrane-like structures, and do not appear to follow bedding planes or any axis that might suggest compaction of the sediments.

Close by this fossil is a structure which exhibits the lineated surface features overprinted on characteristic *Pteridinium* morphology (Fig. 6). Two other specimens preserve features of both *Pteridinium* and membrane-like structures superimposed (Fig. 7).

Discussion

Life habit of *Pteridinium*.—Controversy has centred on the life-habit of *Pteridinium*. Jenkins (1985: 338) inferred from the orientations of fossils that *Pteridinium* and *Rangia* from the Nama Group had been deposited in flow events, although he allowed that some blocks may have been transported under “quite gentle” conditions, somewhat preserving a life assemblage. Elsewhere it was suggested that this style of preservation represents organisms that have been deposited in chaotic, often massive, sediment flows composed of fluidised sand (Jenkins 1992), and Narbonne et al. (1997) reported the presence of *Pteridinium* in sandstone beds containing hummocky cross-stratification. The latter study focused on organisms from high in the Schwarzsand Subgroup (Fig. 2).

In contrast, Grazhdankin and Seilacher (2002) identified two distinct taphocoenoses: “winnowed” and “virgin” assemblages. Winnowed assemblages contained organisms which appeared stacked with no signs of over-folding or inter-penetration. Virgin assemblages bore a twisted and over-folded habit, and were characterised as assemblages lacking “any sign of directed stress” (Grazhdankin and Seilacher 2002: 65), with organisms preserved convex-downward. These assemblages are interpreted as un-transported, and taken as evidence of an infaunal habit for *Pteridinium*. Grazhdankin and Seilacher (2002) advocated an infaunal manner of growth for *Pteridinium* in which the organism added new segments while resident within the sediment.

Crimes and Fedonkin (1996: 322) first proposed a mode of growth for *Ernietta* and *Pteridinium* “in which their walls develop as a body of protoplasm that migrates through the pore spaces between the sand grains which would then serve to support the organism”, and this proposal is reiterated by Grazhdankin and Seilacher (2002). Grazhdankin and Seilacher

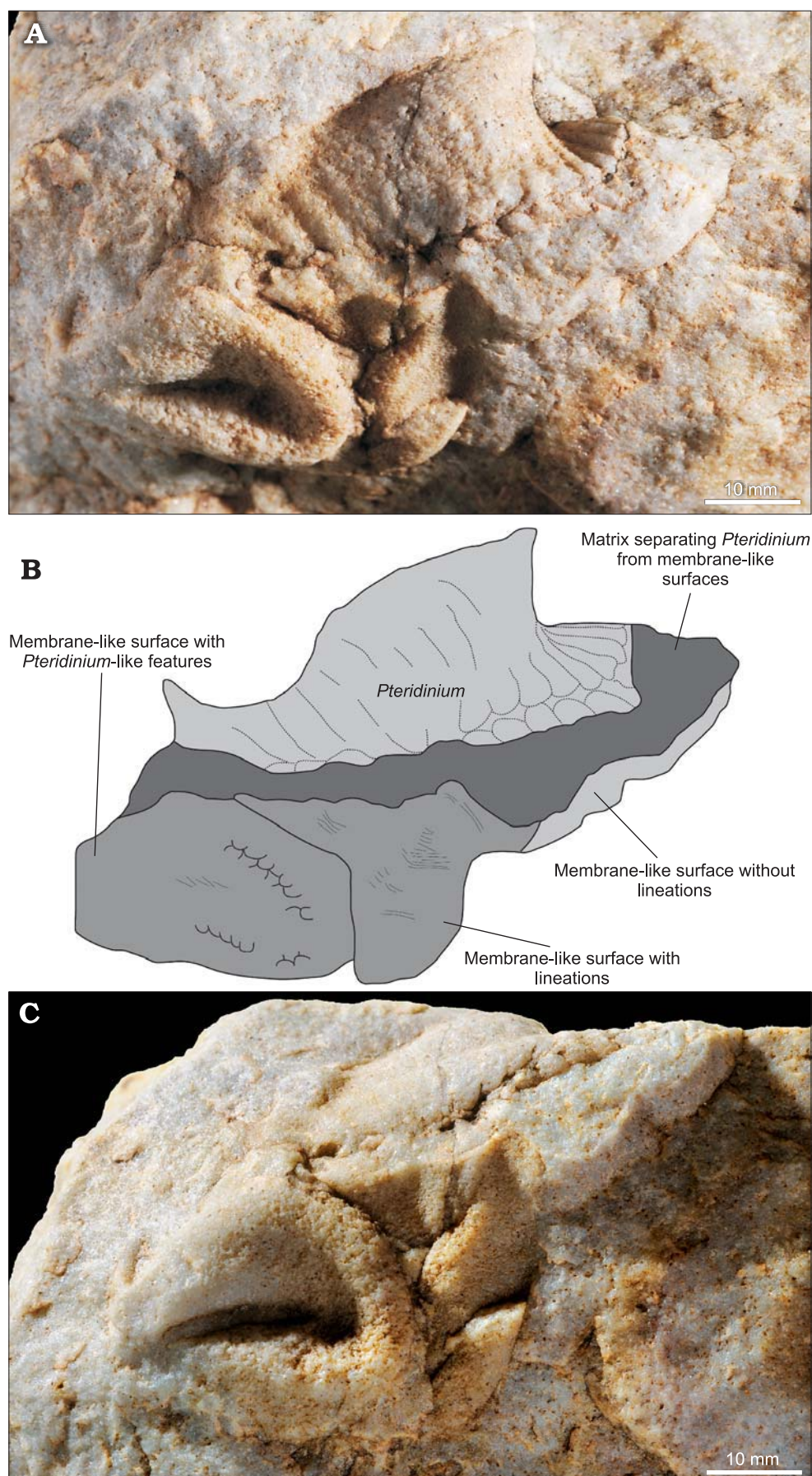


Fig. 6. Membrane-like structures preserved in association with *Pteridinium* fossils. Block number NGS-F-V-174. **A.** Specimen showing the membrane-like surfaces running parallel to a *Pteridinium* specimen. **B.** Map of features. Compare to A and C; note the non-lineated membrane-like surface immediately adjacent to the surface bearing fine parallel lineations. **C.** The same specimen rotated to focus on the membrane-like structure. Note the consistency of lineations.

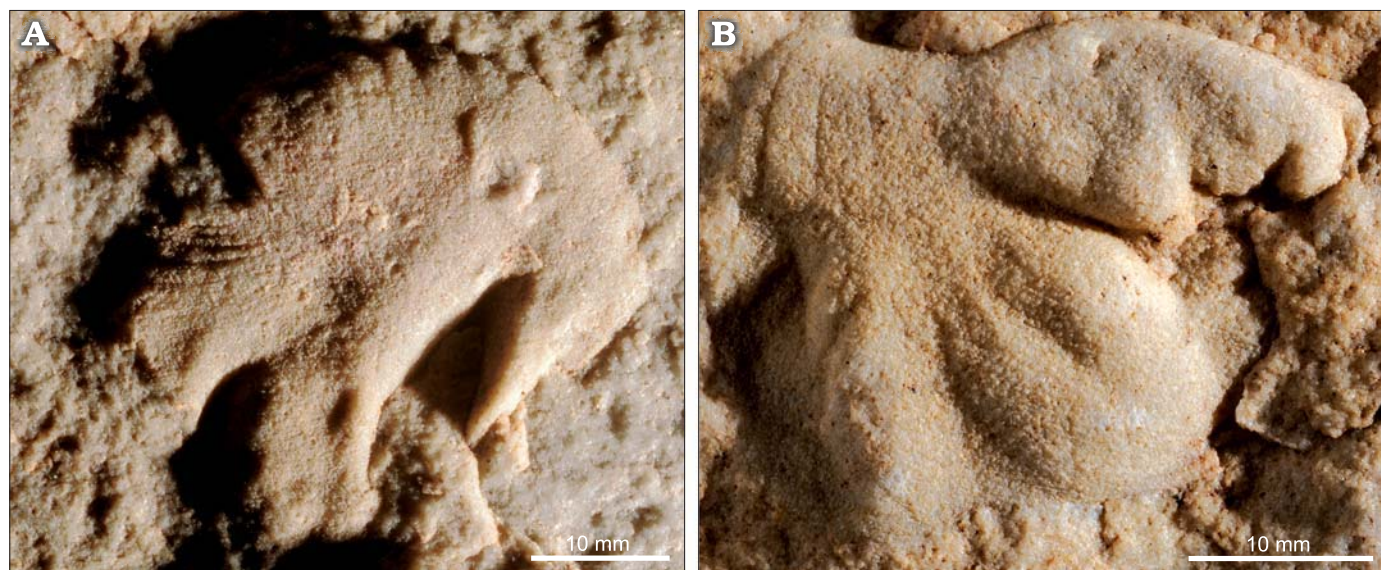


Fig. 7. Membrane-like structures preserved in association with *Pteridinium* fossils. **A.** Block number NGS-F-V-172, note the pattern resembling a repeated series of segments around the outer edge of the specimen (towards the top of the photograph). **B.** A membrane-like structure on block NGS-F-V-166, note the larger structures resembling *Pteridinium* segments in the upper left of the figure.

lacher (2002) reported individual fossils crossing past one another in such a striking manner that they were convinced these individuals had penetrated neighbouring specimens during growth. They argued that *Pteridinium* grew by invading the surrounding sediment, even intersecting and cutting through other individual *Pteridinium*.

We suggest there are reasons to doubt the sediment pervasion model in general. In order for such organisms to grow by sediment pervasion as described by Crimes and Fedonkin (1996), one would expect displacement either of the substrate or of the organism's body wall. Both *Pteridinium* and *Ernietta* have body walls with well-defined shapes that are strikingly consistent across specimens, and are clearly not controlled by the sand grains which preserve them. Examination of *Pteridinium* fossils from the Kliphoek Member turns up no trace of the sediment displacement one would expect for an organism growing by sediment pervasion.

Additionally, "virgin" assemblages (sensu Grazhdankin and Seilacher 2002) are identified here immediately above scour-and-fill structures and dish structures within the Kliphoek Member (Figs. 3, 4). Dish structures are typically taken to indicate rapid deposition leading to the dewatering of saturated sediments (e.g., Lowe 1975; Boggs 2006). The presence of *Pteridinium* fossils above the dish structures is compelling evidence for the transport of these fossils as a component of sand flows, in line with the observations of Jenkins (1992) and Narbonne et al. (1997). *Pteridinium* fossils are associated with laminar beds of sandstone indicating deposition during brief high-energy events.

The *Pteridinium* fossils reported here show little sign of a preferred directional orientation within beds, but this does not necessarily weigh against their deposition as a component of sand flows. Gastaldo (2004) reported no correlation

between palaeocurrent direction and the orientation of fossil logs in flood events, and the apparently flexible nature of *Pteridinium*, as well as the lack of unequivocally complete specimens, may complicate predictions of their behaviour as a component of flows.

Transport as a factor in *Pteridinium* taphonomy appears to be the norm, rather than the exception. Grazhdankin (2004) constrained the occurrence of *Onegia* (a close relative and possible conspecific of *Pteridinium*) in the White Sea to planar-laminated sandstone representing inundates in a distributary mouth-bar environment. The South Australian Ediacara Member is known for the preservation of Ediacaran biota on microbial mat surfaces (Gehling 2000, Droser et al. 2006), however, where *Pteridinium* occurs it is not preserved with these surfaces, but rather as a component of massive quartzite elsewhere in the stratigraphy (Jim Gehling, personal communication 2010 and see Jenkins et al. 1983; Gehling 1999). South Australian and Schwarzsand (Narbonne et al. 1997) specimens of *Pteridinium* are interpreted as deposited at or below storm wave base, in contrast with the shallower depositional environment seen here. Gibson et al. (1984) and Gibson and Teeter (2001) also report *Pteridinium* specimens from the deeper water palaeoenvironmental setting of the Carolina Slate Belt. However, all interpret *Pteridinium* fossils as having been transported.

Structural composition of *Pteridinium*.—Besides casting doubt upon the sediment pervasion model, these observations have further implications for the interpretation of the material construction of *Pteridinium*. Most *Pteridinium* fossils show no signs of physical destruction of the basic body plan, even though twisting and folding are common (e.g., Jenkins 1986, 1992). *Pteridinium* fossils can be observed with specimens twisted 180 degrees along their axis.

There are no broken edges known, and where the extent of a preserved fossil is delimited, it grades into undifferentiated sandstone rather than preserving any potentially broken edge.

Dzik (1999) suggested that a “collagenous fabric” may well have been present in *Ernietta*, a similar organism also known from the Kliphoek Member. He suggested that only a proteinaceous composition could explain the apparently elastic nature of the body wall, as well as its strength and flexibility. It must be noted that there is much less evidence for elasticity in *Pteridinium*, as the apparent inflation of parts of the body that Dzik (1999) observes in *Ernietta* is not so common in *Pteridinium* fossils. However, a collagenous construction would explain the twisted yet unbroken nature of many specimens. Yet another possible candidate for the tough structural component in *Pteridinium* is cellulose, such as occurs in extant urochordates. Cellulose-based tissues in urochordates are known to vary widely in mechanical properties, and can form tough protective tunics in benthic tunicates (e.g., Hirose et al. 1999).

Membrane-like structures.—Membranous surfaces and sacs in the Neoproterozoic are documented elsewhere in the literature. Here we regard “membrane-like structures” as discrete, three-dimensionally warped surfaces preserved in moulded sandstone, which do not form bedding surfaces (e.g., Fig. 5). The presence of these surfaces in association with identifiable taxa have led authors to suggest that some such surfaces represent epidermal coverings of some Ediacaran taxa. Pflüg (1970) reported amorphous organic structures associated with *Pteridinium*, explaining them as an aspect of *Pteridinium* anatomy he called the “lamella basalis”, but interpreted by Grazhdankin and Seilacher (2002) as unrelated bedding surfaces. Germs (1973) described an “epidermis”-like covering on a specimen of the Ediacaran *Rangia* found in a coarse orthoquartzite in the lower Schwarstrand Subgroup (overlying the Kuibis Subgroup). With reference to the same specimen, Grazhdankin and Seilacher (2005) reconstructed *Rangia* as a set of fronds enveloped by a “mucous-supported sheath” (see Germs 1973: fig. 1E; Grazhdankin and Seilacher 2005: figs. 2, 7). Recently, two species of rangeomorph from Newfoundland, *Avalofractus abaculus* and *Beothukis mistakensis*, have been reported to possess a “structureless sheath” partly enclosing the lowermost branches of the organism (Narbonne et al. 2009). Narbonne et al. (2009) discussed the presence of sheaths in many rangeomorph fossils preserved in a fine-grained turbidite from the Trepassey Formation of Spaniard’s Bay. Unlike the Schwarstrand *Rangia* specimen, the Spaniard’s Bay material definitively records organisms in erect life position, increasing the likelihood that these sheaths represent original features of the anatomy of living organisms. Narbonne et al. (2009) noted that while these various sheaths may represent taphonomic artifacts, their presence across two distinct facies in the Trepassey Formation and the Nama Group makes this less likely.

We have reported here that certain of the membrane-like structures discovered in the Nama Group bear distinctive parallel lineations. Fine-scale lineations are not unknown among the Ediacaran biota. Weaver et al. (2008) reported on a “sac-like structure” from North Carolina that features “intersecting sets of sub-parallel to fanned-out grooves” of 0.2–0.6 mm width, on the same scale as the lineations observed here. However, the lineations we report on do not fan out dendritically as in the North Carolina specimen. Narbonne et al. (1997: 959) reported “faint mm-scale transverse markings” on specimens of *Swartpuntia germsi* from the Schwarstrand Subgroup (see Fig. 2). The markings present on *Swartpuntia* are generally of a slightly greater width (0.5–1 mm) than the lineations described here, are less consistent in their size and less continuous over the surface of the fossil. At present it is not clear what relationship these markings have to the anatomy of *Swartpuntia* (e.g., whether they are surficial, a reflection of underlying structure, or an artifact of chance grain alignment), but a connection with membrane-like structures cannot be ruled out. Similar lineations to those discussed here are present on *Ventogyrus chistyakovi* from the White Sea area of Russia (Ivantsov and Grazhdankin 1997). The spaces between lineations in *Ventogyrus* appear to vary in width more profoundly than in the specimens presented here, but Ivantsov and Grazhdankin (1997) propose that they are related to a membrane representing a second body surface distinct from the diagnostic structure of *Ventogyrus*, inviting parallels with the specimens studied here (see below). It must also be noted that *Ventogyrus* and *Pteridinium* display some similarity in preserved features, such as the presence of parallel chambers in alternating symmetry on either side of a median line, and a tri-radiate body structure (see also Dzik 2003). *Protechiuris edmondsi* (Glaessner 1979), known from a single specimen from the Nama Group, is reported to bear faint parallel markings comparable to those described here. These markings are not well characterised in the literature, but it may be that *Protechiuris* reflects similar membrane-like structures.

Lineations in the specimens reported here may be related to an original texture on a biologically controlled surface (either a microbial mat or a macroscopic organism). It must be noted that lineations are present on the same scale as the grain size for the quartzite they are preserved in, but as they are limited to discrete areas, and are not present across non-membrane-like surfaces in the same rock, it is unlikely that they represent artifacts of the grain size. If they represent an original biological texture, then they are at the limit of resolution afforded by the quartzite.

The most striking manifestation of these lineations is when they are preserved on a membrane-like surface immediately adjacent to a *Pteridinium* fossil. The same specimen preserves lineations and *Pteridinium* segments super-imposed on each other (Figs. 6, 7). These and other specimens clearly illustrate an association between *Pteridinium* and some membrane-like structures. Given this association, two broad interpretations are plausible:

(1) The membrane-like structures represent parts of some biological structure caught up by chance with particular *Pteridinium* fossils. As discussed above, the presence of characteristic beds of *Pteridinium* immediately above scour-and-fill structures and dish structures establishes that many *Pteridinium* fossils in the Nama Group were deposited as a component of mass flow events. Therefore, it is highly unlikely that the fossils described here were preserved in their original life position, and the chance association of *Pteridinium* with membrane-like structures is a distinct possibility.

At least some of the membrane-like structures reported here may represent fragments of a microbial mat, producing structures similar to microbial sand chips as defined by Pflüger and Gresse (1996). These are intraclasts formed by the cohesiveness of microbially-bound sand in the presence of microbial mats. Sarkar et al. (2004: fig. 3a) illustrate deformed sand clasts from the Lower Bhander Sandstone of India (ca 0.6Ga) that strongly resemble certain of our membrane-like structures. They describe the “flexible bondage between the non-cohesive sand grains”, and interpret it as a result of the presence of microbes.

Another possibility is that membrane-like structures associated with *Pteridinium* represent rangeomorph sheaths that have become disassociated from the original organism (perhaps in the normal progress of ontogenetic development), such as the enclosing “epidermis” reported from specimens of *Rangaea* in Nama Group sediments (Germs 1973; Grazhdankin and Seilacher 2005) and from the Yorga Formation in Russia (Grazhdankin and Seilacher 2005). *Pteridinium* is known to occur in close association with *Rangaea* (e.g., see Grazhdankin and Seilacher 2005: fig. 1). *Rangaea* is rare and much smaller than *Pteridinium*. It is not as common in *Pteridinium*-bearing quartzite from the Nama Group as the membrane-like structures are. During the 2009 expedition, only one *Rangaea* specimen was unambiguously identified in the immediate vicinity of *Pteridinium* fossils.

(2) The second class of possibilities is that the membrane-like structures could represent a previously unreported aspect of the anatomy (or decomposition) of *Pteridinium*, potentially enclosing the structures traditionally recognised as diagnostic of the species. The membrane-like structures could represent states of decay for *Pteridinium*, where some degree of bacterial replacement of soft tissue has occurred. Superimposition of membrane-like surfaces with *Pteridinium* features may represent a transitional step in the decomposition and colonisation of an organism with microbial activity. However, we would not expect tissues damaged by decomposition to survive the flow events leading to the deposition of *Pteridinium* fossils. There is no evidence within these specimens for *Pteridinium* bearing signs of the physical destruction expected of decaying organisms, such as broken *Pteridinium* anatomy.

If the rangeomorph sheaths reported from Newfoundland (Narbonne et al. 2009) represent genuine anatomical features, then similar (even homologous) features may well exist in *Pteridinium*. Intriguing lines of inquiry have been pur-

sued into the exact nature of organisms from the White Sea such as *Ventogyrus* and *Vendoconularia triradiata* (Ivantsov and Fedonkin 2002; Dzik 2003), both of which are suspected to represent internal anatomical structures surrounded by exterior body walls, potentially similar to the membrane-like structures associated with *Pteridinium*. *Pteridinium* fossils lacking the membrane-like structures may have had them torn away during a high energy burial. Alternately, the membrane-like structures may be more prone to decomposition and physical destruction than the rest of the body, rotting away quickly after death and therefore failing to be preserved in most cases.

Whether or not the membrane-like structures were associated with *Pteridinium* in life, they appear to be composed of a more deformable material than the *Pteridinium* fossils. Some have features of both the membrane-like structures and of standard *Pteridinium* anatomy (see above). The most straightforward interpretation is that the surface containing the lineations observed on some membrane-like structures lies on a *Pteridinium* fossil so that both sets of features are preserved on the one surface. This implies that the membrane is quite thin and flexible, thin enough that both the *Pteridinium* features and the membrane features are over and under-printed upon each other. Microbial mats are known to vary in “transparency”, defined as the degree to which biomat surfaces preserve the details of underlying sediments (Noffke 2000). This “transparent” preservation has also been inferred for macroscopic fossils such as *Inaria karli* (Gehling 1988) from South Australia, where “internal resistant structures” are suspected to be overprinted upon a more delicate outer surface. And Dzik (2002) has suggested that surface details of some Kuibis Quartzite fossils were, in fact, internal structures over which an organism’s outer surface had collapsed.

Conclusion

It is apparent that most *Pteridinium* fossils in the Nama Group are a component of sand flow events, and these organisms can no longer be regarded as representing in situ material. In addition, there is an undeniable association between *Pteridinium* and some membrane-like structures. Due to the high energy deposition of the fossils, it cannot be absolutely determined whether these represent genuine parts of *Pteridinium* anatomy, or unrelated organic material caught up by chance alongside *Pteridinium*.

Further work on the anatomy and depositional conditions associated with *Pteridinium* may elucidate further details, and lead to an understanding of the nature of this association.

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