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Depositional environment and taphonomy of the 'strings of beads': Mesoproterozoic multicellular fossils in the Bangemall Supergroup, Western Australia

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Enigmatic Mesoproterozoic bedding-plane structures, informally known as 'strings of beads', are common in the Bangemall Supergroup in Western Australia and the Belt Supergroup in North America. The Belt Supergroup structures are formally known as *Horodyskia moniliformis*, and age constraints show that they are more than 350 million years older than similar 1070 Ma structures in the Bangemall Supergroup. Strings of beads in the Bangemall Supergroup have previously been interpreted as fossils of multicellular organisms based on their morphology and on statistical comparisons with a range of organic and inorganic structures. However, details of their depositional environment and taphonomy, which can provide important insights into their origin, are poorly known. This study shows that strings of beads in the Backdoor Formation of the Bangemall Supergroup were deposited in a subtidal marine-shelf environment in association with microbial mats and enigmatic dimple marks. The structures are preserved at the base of fine sandstone beds within shoaling-upward shelfal mudstone and sandstone packages deposited below storm wave-base. Following deposition from suspension, the strings of beads were bound to the sea floor by microbial mats and their associated mucilage, preventing realignment by palaeocurrents. Relationships between the strings of beads and dimple marks in offshore sandstones suggest that the latter may represent holdfasts to which the strings were originally attached.

KEY WORDS: Bangemall Supergroup, fossils, Mesoproterozoic, subtidal laminite, wrinkle marks.

INTRODUCTION

Distinctive bedding-plane structures, resembling strings of beads, were first described from the Belt Supergroup, Montana (Horodyski 1982), and subsequently from the Bangemall Supergroup, Western Australia (Grey & Williams 1990; Grey *et al.* 2002), both of Mesoproterozoic age. These structures are abundant in the Bangemall Supergroup, with over 400 samples (each with several strings) collected from more than 50 sites representing 11 major localities (Figure 1). Despite their abundance, the origin and significance of the strings of beads are highly controversial and remain problematic. This is partly due to the limited understanding of their stratigraphic setting, depositional environment, taphonomy and association with other bedding-plane structures.

These enigmatic structures in the Bangemall Supergroup are preserved on the base of sandstone beds and consist of serially aligned hemispherical impressions (beads) that are commonly connected by a narrow groove (Figure 2a) to form linear subparallel to arcuate, semicircular and irregularly shaped strings (Grey & Williams 1990; Grey *et al.* 2002). Early workers favoured a non-biogenic origin (Horodyski 1982; Fedonkin & Runnegar 1992; Hofmann 1992), although biogenicity was not entirely discounted by Horodyski (1982) and was favoured by Grey and Williams (1990). In contrast, recent studies of the extensive Montana and Western Australian collections support a multicellular origin (Horodyski 1993; Yochelson & Fedonkin 2000; Fedonkin & Yochelson 2002; Grey *et al.* 2002), although consensus as to their origin and biological affinity has not been reached. Interpretation of their biogenicity is based primarily on regular bead spacing in proportion to diameter, morphological evidence for flexibility and tissue differentiation, and statistical dissimilarity to abiogenic structures (Grey & Williams 1990; Fedonkin & Yochelson 2002).

Grey and Williams (1990) interpreted the Bangemall structures as metaphytes (primitive seaweeds) deposited along a strandline, based partly on evidence for linear alignment and associated current scouring in the eastern Bangemall Supergroup. This interpretation was later also accepted by Horodyski (1993) for the Belt Supergroup structures, although Fedonkin *et al.* (1994), Yochelson and Fedonkin (2000), and Fedonkin and Yochelson (2002) interpreted them as colonial metazoans (*Horodyskia moniliformis* Yochelson and Fedonkin). The metazoan interpretation, in which cone-shaped beads up to 1 cm high are connected by a stolon anchored within a muddy substrate, is based largely on the need to explain the lack of current alignment of the structures and the presence of associated current crescents in the Belt Supergroup. This interpretation cannot be applied to the Bangemall Supergroup because the beads are not cone-shaped, and the connecting strand is preserved in concave hyporelief at the sandstone–mudstone interface (Figure 2a).

Evidence for or against alignment or interaction with palaeocurrents is critical to interpreting the origin of the strings of beads and their possible biogenicity, and is integral to the interpretations of Fedonkin and Yochelson (2002). In the western Bangemall Supergroup, strings of beads are generally not aligned despite evidence for relatively high-energy palaeocurrents. This paper describes their relationship to sedimentary facies and other bedding-plane markings (Figs 2b, c) in order to develop a depositional and taphonomic model that can explain this paradox, regardless of their biological affinity.

STRATIGRAPHY AND AGE

The Mesoproterozoic Bangemall Supergroup comprises the basal Edmund Group, overlain by the Collier Group and laterally equivalent Manganese Group (Figure 1) (Martin & Thorne 2004). The strings of beads were first described from the lower Manganese Group (Stag Arrow Formation: Grey & Williams 1990) but are now also known from the lower Collier Group (Backdoor Formation: Grey *et al.* 2002). Fossil localities are distributed over a >500 km strike (Figure 1), and a stratigraphic range of at least 1500 m in the lower Backdoor Formation. The presence of strings of beads in the Stag Arrow and Backdoor Formations has been used to correlate these formations biostratigraphically (Grey *et al.* 2002).

The strings of beads are younger than *ca* 1400 Ma detrital zircons in the lower Backdoor Formation, but older than *ca* 1070 Ma dolerite sills that intrude many levels of the Collier Group (Figure 3) (Martin & Thorne 2004). These sills locally intruded wet, partially consolidated sediment suggesting a depositional age close to 1070 Ma (Martin 2003). In contrast, the Belt Supergroup structures are older than the 1443 ± 7 Ma Purcell Lava (Evans *et al.* 2000), and perhaps as old as 1.5 Ga (Fedonkin & Yochelson 2002). Thus, the Bangemall structures are more than 350 million years younger than *H. moniliformis*.

BEDDING-PLANE STRUCTURES IN THE BACKDOOR FORMATION

Two types of bedding-plane structures are preserved on the soles of sandstone beds in the Backdoor Formation. Type 1 structures are external moulds of convex epichnia preserved in concave hyporelief and include the strings of beads, wrinkle marks and enigmatic dimple marks (Figure 2b). These structures are commonly preserved on the same bedding surface. Veneers of mudstone forming incomplete natural casts attest to their syndepositional

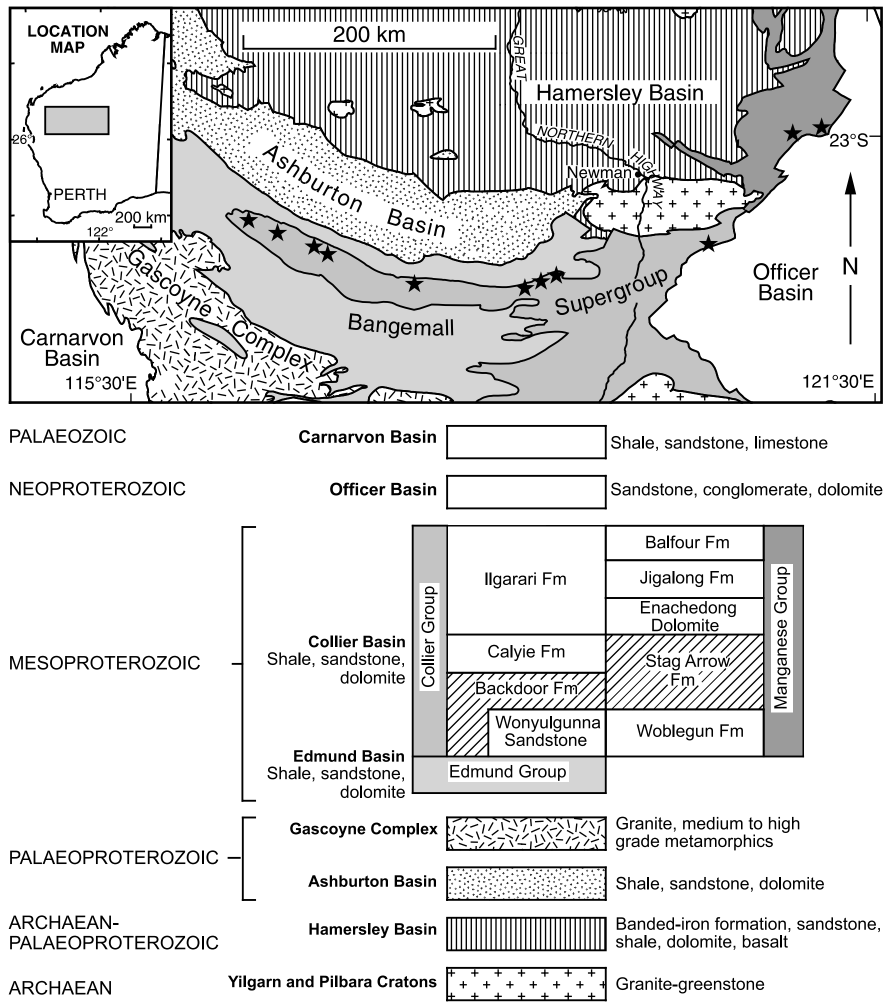

Figure 1 Regional geological setting and distribution of the major string-of-beads fossil localities (stars) in the Bangemall Supergroup (grey shading). The Bangemall Supergroup comprises the Edmund Group (*ca* 1465 Ma), overlain by the Collier and coeval Manganese Groups (*ca* 1070 Ma). Each group overlies a basal regional unconformity. Correlation between the Backdoor and Stag Arrow Formations (cross-hatching) is also shown. Modified after Grey *et al.* (2002).

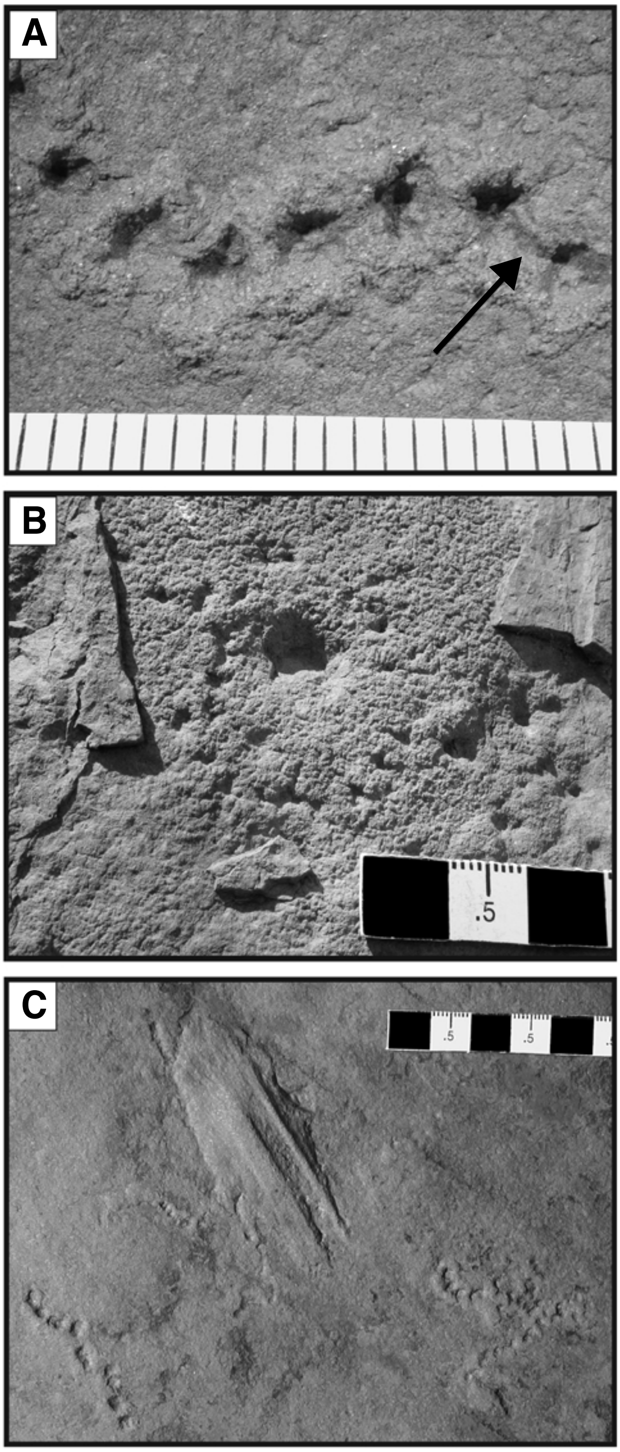

Figure 2 (a) Part of a string of beads showing details of bead morphology, a symmetrical sandstone ridge, and the connecting strand (arrowed): 1 mm scale divisions; MGA coordinates 541350E, 7350360N. (b) Association between strings of beads, dimple marks and wrinkle marks in concave hyporelief. Note the coiled string of beads radiating from the large conical dimple mark, and the veneer of underlying mudstone forming a natural cast: scale is 31 mm long; MGA coordinates 549790E, 7345950N. (c) Bounce cast (convex hyporelief) and strings of beads (concave hyporelief) on the base of a sandstone bed. Palaeocurrent direction towards the top. Note the lack of consistent bead alignment or presence of current crescents: scale is 54 mm long; MGA coordinates 541350E, 7350360N.

origin, and potentially provide evidence of their 3-D structure. The degree of weathering and bedding-plane fissility has hindered the finding of part-and-counterpart specimens. Type 2 structures are convex hypichnia representing casts of erosional features such as flute and tool marks that are irregularly distributed on individual beds, and rarely found in association with Type 1 structures (Figure 2c). Strings of beads and associated Type 1 structures are most abundant on thin sandstone beds and Type 2 on thick beds. The abundance of Type 1 structures appears to be inversely proportional to bed thickness.

FACIES ASSOCIATIONS OF THE BACKDOOR FORMATION

The Backdoor Formation consists of up to 1700 m of laminated mudstone with minor sandstone interbeds deposited in outer shelf or prodelta to distal delta-front environments that grade upward into delta-front and delta-top deposits of the overlying Calyie Formation (Martin & Thorne 2004). The thinly to thickly bedded quartz sandstones show upward thickening and coarsening trends

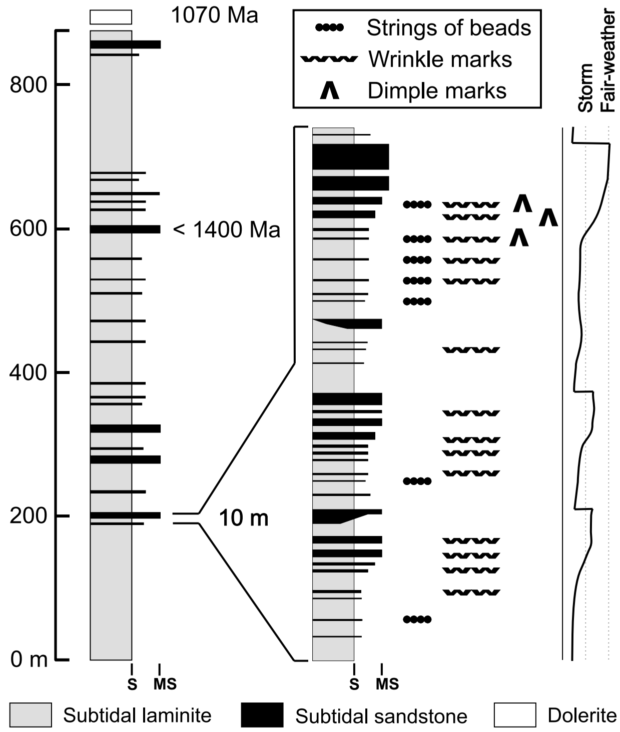

Figure 3 Measured stratigraphic sections in the lower Backdoor Formation on Irregully Creek (23°36′16″S, 116°37′00″E, westernmost locality in Figure 1). Age constraints are provided by SHRIMP U–Pb dating of zircons in dolerite sills and sandstone (Wingate 2002; Martin & Thorne 2004). Detailed section shows the typical stratigraphic distribution, facies associations, and variations in depositional environment with respect to storm and fair-weather wave-base of Type 1 bedding-plane markings in the Backdoor Formation. Grainsize ranges from silt (s) to medium sand (ms). Wedge-shaped sandstone beds indicate the presence of erosional scours. The lower two-thirds of the Backdoor Formation consists of similar bead-bearing intervals, separated by thicker units dominated by subtidal laminite.

(Figure 3). These trends are tens of metres thick and record an upward increase in compositional maturity, size of bedforms and associated internal structures, and evidence for both current- and wave-reworking. Palaeocurrent indicators and rare synsedimentary slump folds in the Backdoor Formation suggest a palaeoslope to the southwest.

Laminated mudstone association

The bulk of the Backdoor Formation consists of dark-grey to maroon and olive-green weathered fissile mudstone with millimetre to sub-millimetre scale plane-parallel lamination. The normally graded laminae consist of coarse to fine quartz silt with disseminated iron oxides in a sericite–chlorite matrix. Cubic hematite pseudomorphs after pyrite are commonly concentrated in specific laminae, or disseminated through thicker beds. Hummocky and wavy-laminated mudstone is also present, particularly towards the tops of upward thickening and coarsening trends.

Thinly bedded sandstone association

Thin sandstones (10–100 mm) are tabular to broadly lenticular bedded, very fine to medium grained, and well sorted. They are massive or planar laminated, and locally ripple cross-laminated. Grading is not common, even in thin-section. Many beds consist of a thin, planar-laminated base overlain by a tangential cross-lamination set with 1–2 cm-high linguoid ripple marks on the upper surface. Erosional features are limited to rare large-scale scours (Figure 3) and Type 2 bedding-plane structures (mainly groove, bounce and prod casts). Type 1 structures are common and dominated by strings of beads and wrinkle marks (Figure 3). Tabular mudstone intraclasts are locally preserved on planar bed tops. Thin sandstones are interbedded with medium to very thick beds of planar laminated mudstone.

Thickly bedded sandstone association

Thick sandstones (0.1–0.5 m) are fine to very coarse grained, with minor granule pebble conglomerate lags and tabular mudstone intraclasts. Beds are mainly tabular to lenticular with hummocky to rippled tops, and are seldom >0.5 m thick. Thick sandstones are massive, planar laminated, or normally graded at the base and ripple cross-laminated and wavy bedded at the top, with localised large-scale trough cross-stratification up to 2 m wide and 0.3 m deep. They are also commonly amalgamated, or interbedded with thin beds of planar to hummocky laminated mudstone. Basal surfaces are conformable to erosional, and characterised by Type 2 bedding-plane structures (mainly groove and bounce casts and rare flute casts). Type 1 structures are dominated by wrinkle and dimple marks, with rare short strings of beads.

Depositional environments

The fine, normally graded lamination and general lack of current structures in the laminated mudstone association indicate deposition from suspension, below storm wave-base, as subtidal laminites. Localised hummocky and wavy lamination provides evidence of reworking close to wave-base, particularly in association with thickly bedded sandstones.

Planar lamination in fine sandstones is a reliable indicator of laminar flow, high current velocity and bed shear stress, tractional transport in a viscous sublayer of concentrated grains, and deposition in the transition and plane-bed stages of the upper flow regime (Middleton & Southard 1978; Allen & Leeder 1980; Allen 1984). Peak flow velocities in the Backdoor Formation were probably in the order of 20–100 cm/s, with the rapid gradation to ripple cross-lamination in-phase with surface bedforms reflecting flow deceleration and increased turbulence. The stability of ripple over dune bedforms further indicates that the bed grainsize ($\geq$0.25 mm) is less than the thickness of the viscous sublayer (Allen & Leeder 1980).

The consistent relationship between planar and ripple-laminated sets, especially in thin beds, suggests that most sandstones were deposited by decelerating traction currents. Massive beds, particularly those with mudstone intraclasts, were deposited by higher density sediment gravity flows. Thickly bedded sandstones were deposited under conditions of high turbulence and current velocity, with significant scouring, and some beds may be the product of multiple flows. Thinly bedded sandstones were deposited below storm wave-base, whereas thick-bedded sandstones were deposited between storm and fair-weather wave-base (Figure 3). Stacking patterns in the Backdoor Formation therefore record progradation of subtidal deposits, punctuated by storm events, with wave reworking at the top.

STRINGS OF BEADS AND ASSOCIATED STRUCTURES

Strings of beads

There is little evidence in the Backdoor Formation for regular alignment of the strings of beads, or linear chevron-shaped markings attributed to current scouring (cf. Grey & Williams 1990 figure 10), despite the high current velocity required for deposition of the overlying sandstone. Linear subparallel strings of beads are rare, and are usually found on very thin, planar beds, unrelated to other bedding-plane structures. Narrow (<1 mm) ridges, representing depressions in epirelief, are commonly preserved around the beads (Figure 2a), but are not related to measured palaeocurrent directions. These ridges are developed as partial or complete haloes around the beads, and do not taper in a preferred direction.

The beads are therefore interpreted to have been originally immovable rigid structures that resisted deformation and displaced sand during compaction (Grey & Williams 1990). Their morphology is a result of external moulding followed by varying degrees of compaction prior to decomposition. The morphology of the ridges associated with the beads is not consistent with them being current crescents (Allen 1984). Neither are they current shadows or scour-remnant ridges (Allen 1984), which are positive features in epirelief. An interpretation for the strings of beads similar to that of Fedonkin and Yochelson (2002) is therefore not plausible.

Wrinkle marks

Wrinkle marks are by far the most common bedding-plane structures in the Backdoor Formation and indicate the likely presence of other Type 1 structures. They are present on both thinly and thickly bedded subtidal sandstones, deposited from below storm wave-base to fair-weather wave-base (Figure 3). Wrinkle marks cover large areas and are generally not modified by palaeocurrents. In high-energy environments they are associated with thick beds, Type 2 structures, and have a patchy distribution. In these settings, the wrinkled surface is locally dragged into chevron folds bounded by longitudinal grooves subparallel to palaeocurrents in the overlying sandstone (Figure 4a). These folds are important indicators of syndepositional deformation of a cohesive veneer by either moving objects or tractional shear beneath currents (cf. Seilacher 1999 figure 2a). In epirelief, the wrinkles would comprise sub-millimetre- to millimetre-scale reticulate ridges and pinnacles, which in hyporelief resemble the crudely wrinkled texture of elephant skin (cf. Fedonkin 1992; Runnegar & Fedonkin 1992; Gehling 1999; Steiner & Reitner 2001; Fedonkin & Yochelson 2002). The mudstone substrate is thinly planar laminated, and separated from the overlying sandstone by <1 mm of cryptocrystalline mica with disseminated quartz grains and wavy–crinkly opaque lamination (Figure 4b).

Wrinkle marks are commonly interpreted as fossilised traces of microbial mats (Seilacher *et al.* 1985; Narbonne & Aitken 1990; Hagadorn & Bottjer 1997; Gehling 1999; Schieber 1999; Seilacher 1999; Gerdes *et al.* 2000; Steiner & Reitner 2001; Fedonkin & Yochelson 2002). Because the preservation potential of fossilised *in situ* microbial mat is low, this interpretation relies on the identification of features of likely microbial origin. A microbial origin for wrinkle marks in the Backdoor Formation is supported by their external morphology, deformation of a cohesive veneer, wavy–crinkly lamination, and mica enrichment beneath wrinkled surfaces.

Dimple marks

A previously undescribed Type 1 structure consists of discrete, randomly distributed conical, stellate, irregular or elongate moulds (5–20 mm across) preserved in negative hyporelief. In epirelief, they would be up to 5 mm high. Dimple marks are found only on wrinkled bedding surfaces, beneath thick sandstone beds deposited between storm and fair-weather wave-base, and are usually associated with disaggregated beads and very short strings. In rare cases, a string of beads appears to be attached to the structure (Figure 2b). The internal ornament of the moulds is similar to adjacent wrinkle marks, suggesting that the dimples were originally convex epichnia covered by microbial mats. There are no related obstacle scours or evidence for rupturing or thrusting of the wrinkled veneer over the dimples. Most dimples are preserved as natural moulds, with rare veneers of the mudstone cast (Figure 2b).

These structures bear a superficial resemblance to *Pseudorhizostomites howchini* Sprigg 1949 that is attributed to gas-bubble escape (Runnegar & Fedonkin 1992 figure 7.5.5.D). Indeed, they may represent moulds of gas bubbles formed beneath microbial mats, but this interpretation would require early cementation that is not consistent with the interpreted displacement of sand around rigid beads, and their preservation as natural moulds rather than secondary cavity fills (fenestrae). Dimple marks also bear a striking resemblance to some of the 'dumbbell structures' of Fedonkin *et al.* (1994 figure 10) that were interpreted as possible biogenic structures, but considered more likely due to compaction and dewatering.

DISCUSSION

Any interpretation of the origin of the strings of beads in the Backdoor Formation must account for their (i) preservation as concave hypichnia; (ii) variable morphology; (iii) general absence of current alignment, current crescents, or current scours; (iv) relationships with coeval microbial mats and dimple marks; and (v) consistent facies associations (Figure 3). Preservation in concave hyporelief indicates that they are not tool marks and they do not appear

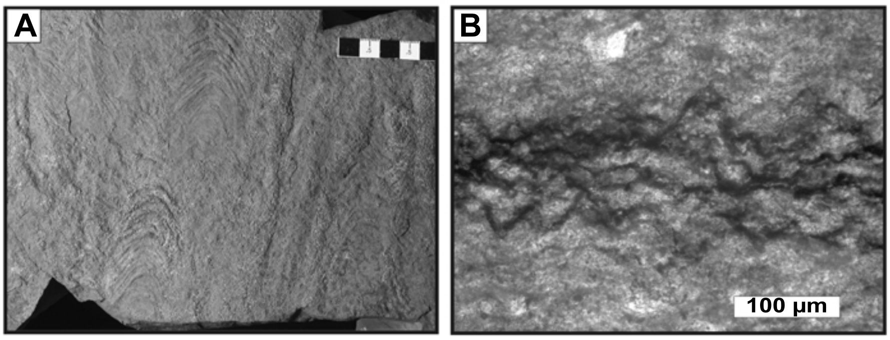

Figure 4 (a) Wrinkled veneer (elephant-skin texture) dragged into chevron folds bounded by linear groove-casts. Ripple cross-lamination in the overlying sandstone indicates a palaeocurrent direction from top to bottom: scale is 50 mm long; MGA coordinates 460740E, 7389270N. (b) Photomicrograph of wavy–crinkly lamination in cryptocrystalline mica with 'floating' quartz silt grains; MGA coordinates. 517720E, 7358810N; Geological Survey of Western Australia (GSWA) thin-section no. 156570.

to have acted as tools prior to sandstone deposition (cf. Horodyski 1982; Haines 1997). Their style of preservation at sandstone–mudstone interfaces suggests that they were flexible biogenic structures. In addition, the strong facies-dependent association with microbial mats (Figure 3) and lack of alignment by upper flow regime palaeocurrents suggests that they were firmly bound to the substrate prior to burial.

In upper flow regime conditions, an unstable muddy substrate would be eroded and the strings of beads either entrained, or realigned in association with the formation of obstacle scours and current shadows. Preservation of the beads can therefore be attributed to the stabilising effects of microbial mats (Noffke *et al.* 2001), combined with high grain concentrations and suppressed turbulence within upper-stage plane-beds (Allen & Leeder 1980). In addition to stabilising the substrate by trapping and binding, microbial mats also reduce bed roughness and frictional forces at the sediment–water interface (Noffke *et al.* 2001), thereby reducing turbulence. The most significant implication is that microbial mats and their associated mucilage were important in binding the strings of beads in a manner similar to the 'death mask' model proposed for Ediacaran fossils (Gehling 1999). In cases where wrinkle marks are not preserved, microbial films may have played a similar role (cf. Gerdes *et al.* 2000). Further indirect evidence of this binding effect is provided by the absence of current-reworked beads in ripple troughs on sandstone bed tops. The cohesive strength of a microbially bound interface may have also contributed to the enhanced displacement of sand around the beads during compaction, and account for the narrow haloes preserved in convex hyporelief (Figure 2a).

The facies relationships of Type 1 bedding-plane structures indicate that dimple marks were formed close to fair-weather wave-base, and may represent holdfasts to which the strings of beads were attached. Although the origin and significance of the dimple marks require further work, this interpretation suggests that most of the strings of beads in the Backdoor Formation are not in growth position, but were transported offshore where they settled from suspension onto extensive microbial mats that extended to depths below storm wave-base. These relationships also suggest that the exceptional preservation of the strings of beads is primarily due to rapid burial by fine sand deposited by storm currents, followed by compaction and formation of a natural mould prior to decomposition.

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