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ARTICLE



Arumberia and other Ediacaran–Cambrian fossils of central Australia

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ABSTRACT

Problematic fossils are described from Late Ediacaran to Early Cambrian red sandstones of the Arumbera Sandstone, Grant Bluff, and Central Mount Stuart Formations in central Australia, within a new systematic classification of Vendobionta. *Arumberia banksi* has been one of the most problematic of Ediacaran fossils, at first considered a fossil and then a sedimentary or organo-sedimentary structure. Our re-examination of the type material and collection of new material reveals misconceptions about its topology: it was a recessive fossil on the bed top, protruding down from the counterpart overlying slab. The concave-up body was 3 mm thick and chambered above a diffuse lower surface, so not a sedimentary structure. Also re-evaluated is the discoid fossil *Hallidaya brueri*, here including “*Skinnera brooksi*” as its upper surface. A new species (*Noffkarkys storaaslii* gen. et sp. nov.) is a multilobed frond with regular, fine, trapezoidal quilts. Three new records of *Trepaswia wardae*, *Dickinsonia costata*, and *Ernietta plateauensis* are reported from the Arumbera and Grant Bluff Formations. Reevaluation of palaeomagnetic and biostratigraphic data suggest an hiatus of 26 million years at the Ediacaran–Cambrian boundary within the Arumbera Formation, but some of this missing time is filled by the Grant Bluff and Central Mount Stuart Formations.

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KEYWORDS

Arumberia; Ediacaran;
Vendobionta; Central
Australia; problematica

Introduction

Arumberia in microcosm, encapsulates a variety of fundamental problems with Ediacaran fossils. Is it a body fossil, a trace fossil, or a microbially induced sedimentary structure? Is it even anything or just another case of pareidolia? What biologically in the modern world is remotely related? *Arumberia* was first proposed as a body fossil of a cnidarian (Glaessner and Walter 1975), but then one of its authors considered it a pseudofossil, a flute cast with a microbial surface fabric (McIlroy and Walter 1997). Bland (1984) considered *Arumberia* a vendobiont allied with *Ernietta* and *Pteridinium*, a view supported by thin section study reported here. Subsequently, *Arumberia* has been retained as a distinctive microbial trace fossil or organo-sedimentary structure (McIlroy et al. 2005; Mapstone and McIlroy 2006; Kumar and Pandey 2008, 2009; Callow et al. 2011a; Liu 2011; Kolesnikov et al. 2012, 2017; Kumar and Ahmad 2014; Parihar et al. 2015; Droser et al. 2017; Nesterovsky et al. 2018), comparable with *Rugulichnus matthewi* (Stimson et al. 2017). These interpretations of *Arumberia* conflate a variety of materials different from its holotype, which is re-examined here, as well as recollected and studied in thin sections and slabs from the type locality. Opinions on the biological affinities and habitats of other Ediacaran quilted fossils (Vendobionta of Seilacher 1992) also remain unsettled (Liu et al. 2015; Retallack 2016a, 2018a, 2019; Evans et al. 2017, 2019a, 2019b; Hoekzema et al. 2017; Dunn et al. 2018; Bobrovskiy et al. 2018; Wood et al. 2019), but will not be addressed in this contribution, which aims to better define the morphology and petrographic structure of *Arumberia* and other fossils in non-calcareous red sandstones of central Australia.

Arumberia is also of interest as one of the few taxa found in both Cambrian and Ediacaran parts of the Arumbera Formation, separated by an apparent regional hiatus (Kirschvink 1978; McIlroy et al. 1997). Along with other boundary-crossing vendobionts, *Arumberia* undermines the severity of latest Ediacaran extinctions

(Wood et al. 2019). *Arumberia* has been suggested as a biostratigraphic marker of Ediacaran–Cambrian boundary beds (Bland 1984).

Geological background

This paper examines fossils from the Arumbera Sandstone of the Amadeus Basin, and the Grant Bluff Formation of the Georgina Basin in central Australia (Figure 1). Measured sections were made of the Arumbera Sandstone at Ross River (Figure 2) and Valley Dam (Figure 3), and of the Grant Bluff and Central Mount Stuart Formations at Central Mount Stuart and Mt Skinner (Figure 4). Fossils of the Arumbera Sandstone were also collected in Jinker Creek, Temple Bar, Ellery Creek, and below Neil Hargrave Lookout (Figure 1). Four members of the Arumbera Formation are recognised: I, red non-calcareous sandstones and siltstones; II, thick red non-calcareous sandstones; III, grey calcareous siltstones and red sandstones; and IV, red non-calcareous sandstones (McIlroy et al. 1997; Mapstone and McIlroy 2006). An alternative nomenclature of Kirschvink (1978) of Arumbera Sandstone (I and II) and then Box Hole (III), and Allua Formations (IV) has been used only by Jenkins et al. (1992), not subsequently (Shaw and Wells 1983; Mapstone and McIlroy 2006). The sequence exposed at Central Mount Stuart follows the mapping of Donnellan (2008), and similar subdivision has been applied to Mt Skinner (Wade 1969; Shaw and Warren 1975). All the fossils described here are in red sandstones and siltstones interpreted as deposits of shallow marine to lagoonal and coastal plain environments by McIlroy et al. (1997) and Mapstone and McIlroy (2006).

The Arumbera Sandstone and Grant Bluff Formation have yielded a variety of body and trace fossils of uncertain geological age (Wade 1969; Glaessner and Walter 1975; Walter et al. 1989; McIlroy and Walter 1997; Mapstone and McIlroy

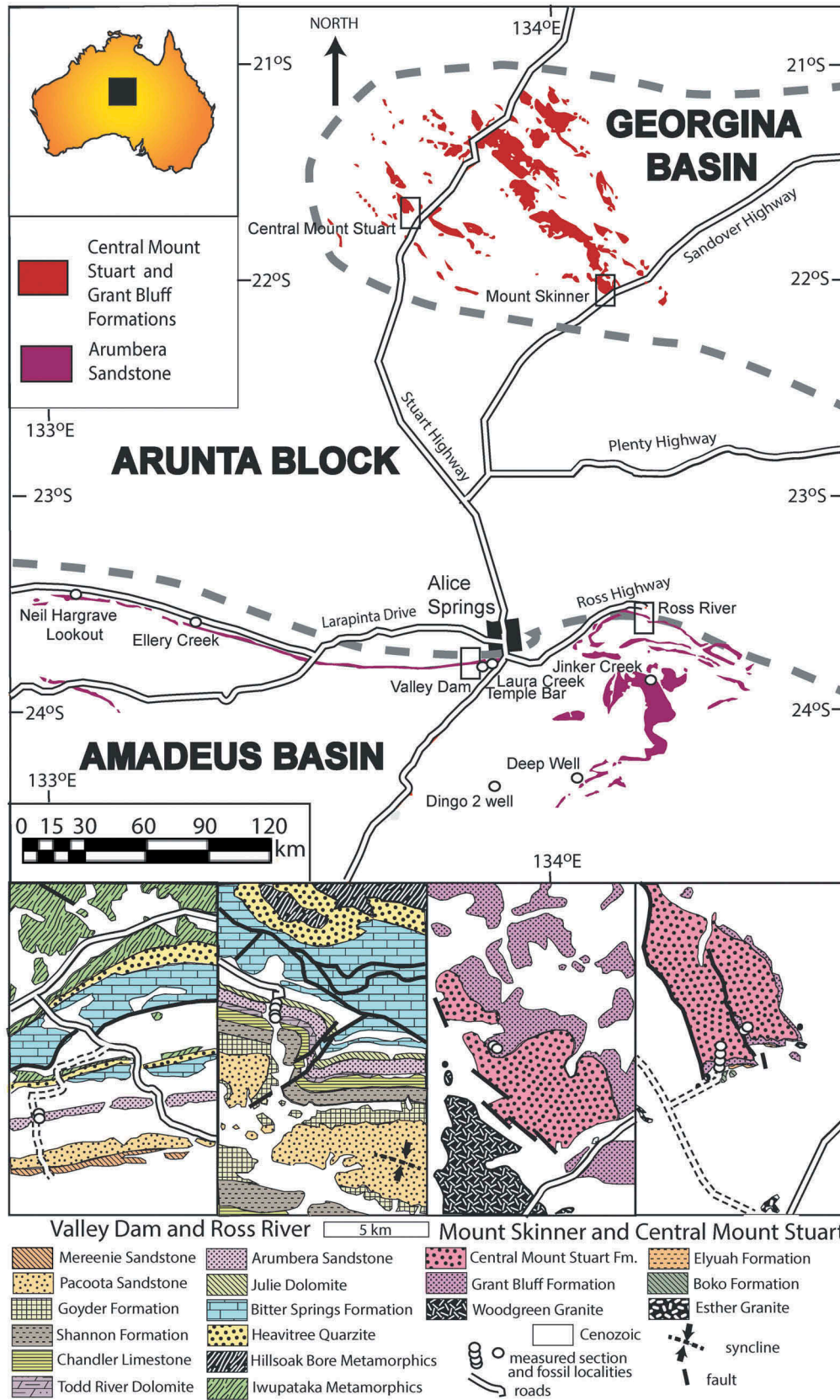


Figure 1. Ediacaran–Cambrian fossil localities in central Australia. Detailed maps are from Shaw and Wells (1983) for Valley Dam and Ross River, Shaw and Warren (1975) for Mount Skinner, and Donellan (2008) for Central Mount Stuart.

2006). The most significant for geological age is *Rusophycus* cf. *R. avalonensis* from Member III of the Arumbera Formation at Laura Creek, Ross River and Valley Dam

(Glaessner 1969, fig. 6B, McIlroy et al. 1997; Mapstone and McIlroy 2006). *Rusophycus* is usually attributed to trilobites, but often precedes the first occurrence of trilobite body

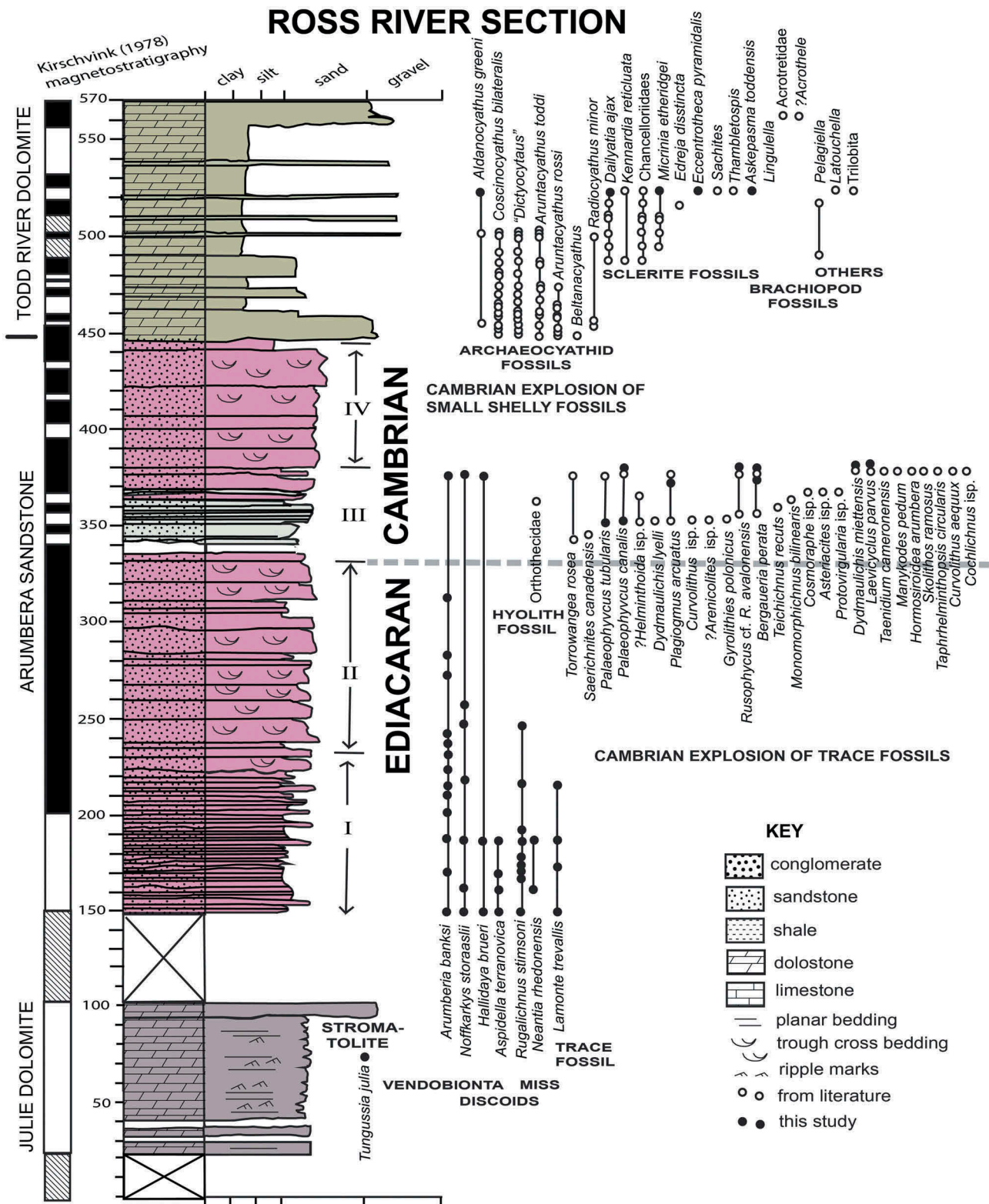


Figure 2. Ediacaran–Cambrian fossils and measured section at Ross River, Northern Territory. Palaeomagnetic stratigraphy is from Kirschvink (1978). Fossil occurrences from literature (open circles) are from Glaessner (1969), Kruse and West (1980), Laurie and Shergold (1985), Laurie (1986), Haines (1991), Kennard (1991), and McLroy et al. (1997).

fossils, and may represent other Early Cambrian soft-bodied arthropods (Wood et al. 2019). Orthothecoid hyoliths in Member III at Ross River are early Cambrian small shelly fossils (Haines 1991). The first actual trilobites in the Ross River section are in the Todd River Dolomite, along with

a diverse assemblage of archaeocyathids and small shelly fossils of late Tommotian to early Atdabanian age within the Early Cambrian (Kruse and West 1980; Laurie and Shergold 1985; Laurie 1986; Kennard 1991). Other limits on age are provided by the Ediacaran stromatolite *Tungussia julia* in the

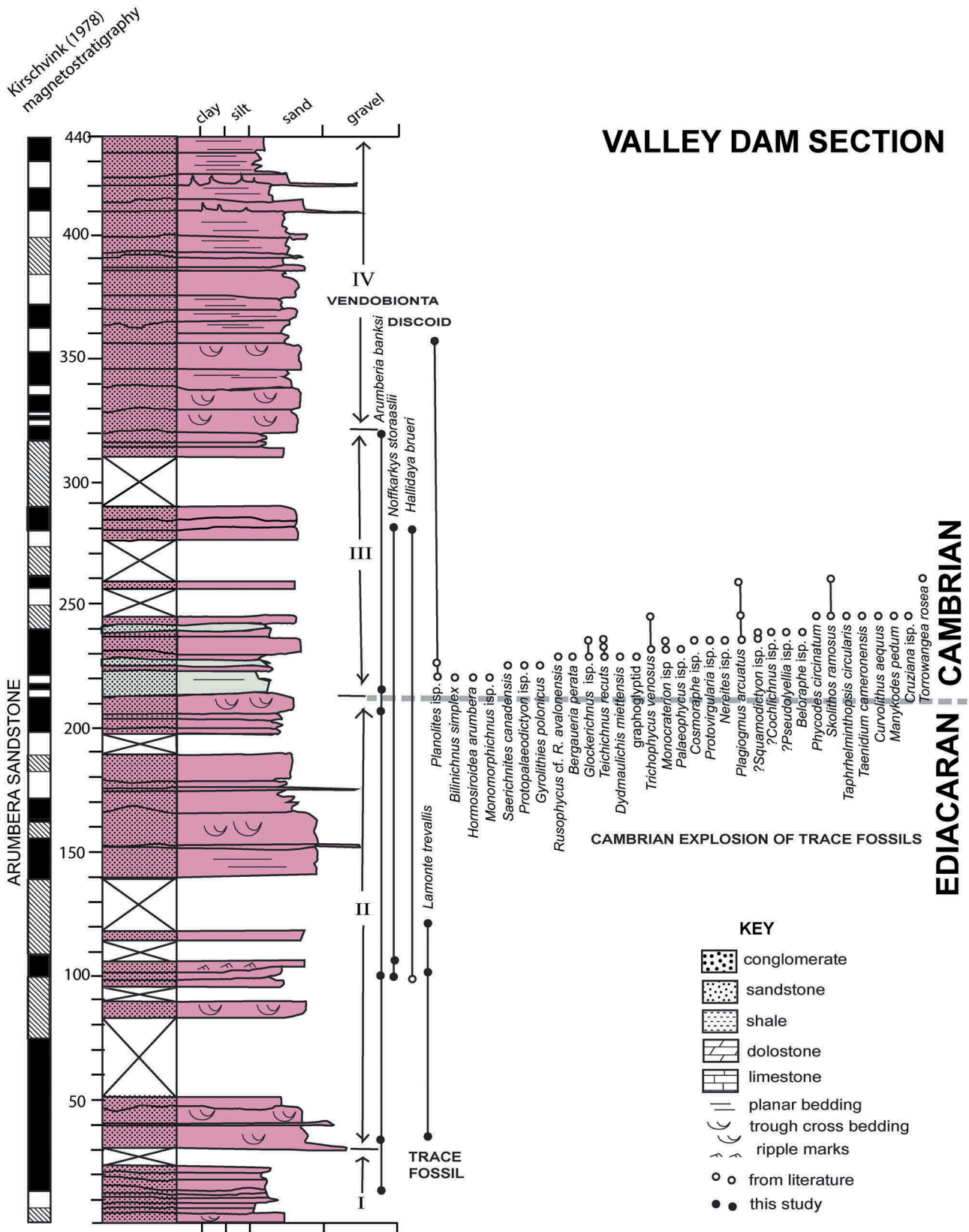


Figure 3. Ediacaran–Cambrian fossils and measured section at Valley Dam, Northern Territory. Fossil occurrences from literature (open circles) are from Kirschvink (1978), and McIlroy et al. (1997).

Julie Dolomite underlying the Arumbera Sandstone, and in the Elkeru Formation underlying the Grant Bluff Formation (Walter et al. 1979; Grey 2005).

Isotopic chemostratigraphy also offers constraints, because a distinct negative carbonate carbon isotopic excursion in the upper Arumbera Sandstone in Dingo Well 2 (Schmid 2017a, 2017b), just

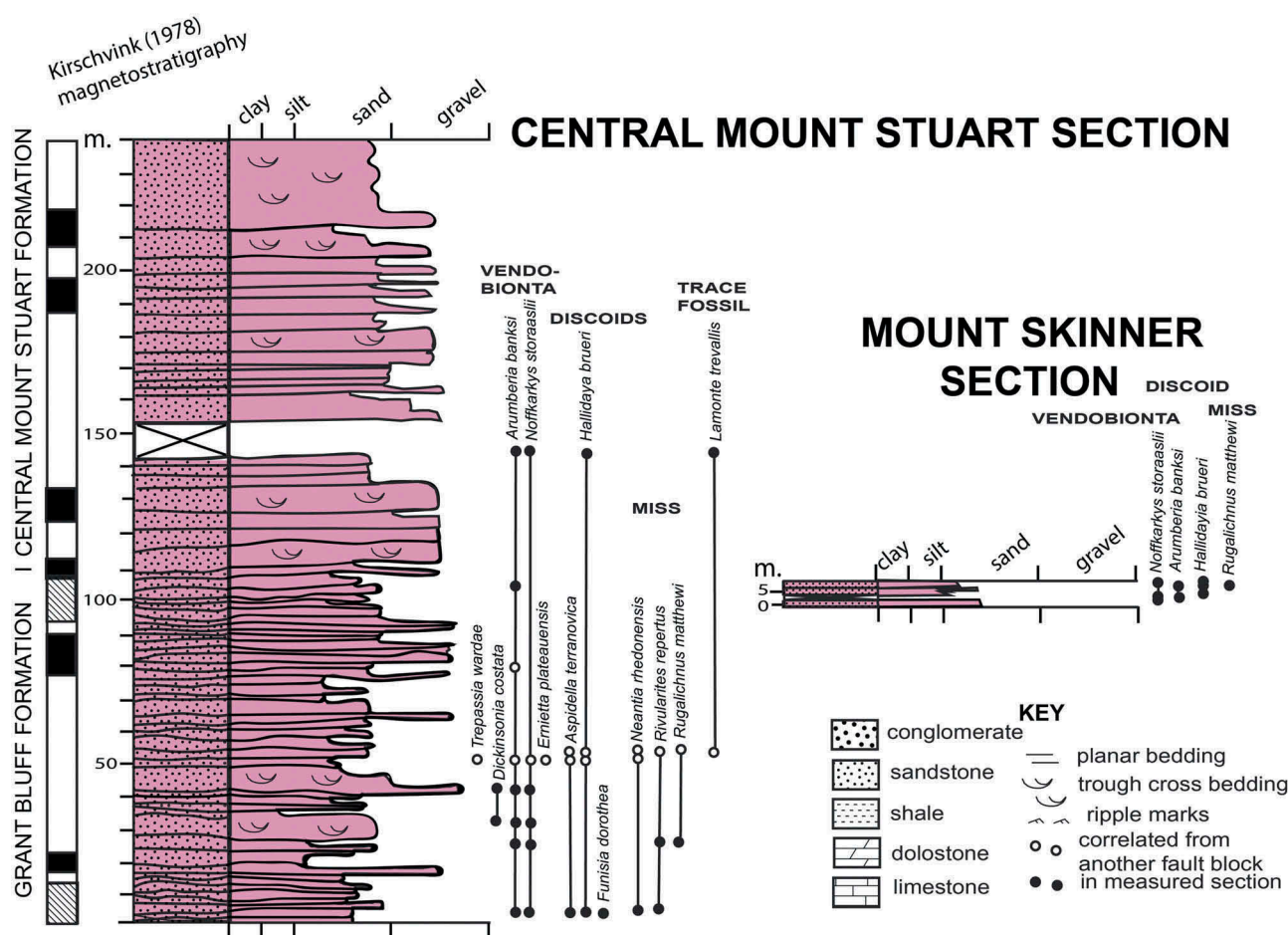


Figure 4. Ediacaran–Cambrian fossils and measured section at Central Mount Stuart, Northern Territory. Open circle fossil occurrences are from the eastern fault block, with lithological correlation back to main measured section.

below the Tommotian–Atdabanian Todd River Dolomite, may be the SCHICE excursion dated at 524 Ma (Peng et al. 2012). A negative excursion in the upper Julie Dolomite (Walter et al. 1995; Calver and Lindsay 1998) may be the Shuram–Wonoka negative isotopic anomaly dated by an age-model assuming constant accumulation rate at ca. 564 Ma (Retallack et al. 2014).

Magnetostratigraphy revealed a profound disconformity between Arumbera Sandstone Members I–II and III–IV, and non-correlation of the Arumbera Sandstone with the Grant Bluff and Central Mount Stuart Formations (Kirschvink 1978). The standard magnetostratigraphy for the Cambrian remains incomplete (Peng et al. 2012), and there are only two magnetostratigraphic studies of Ediacaran rocks for (1) Zimnigory Formation of Russia (Popov et al. 2002) and (2) Wonoka Formation of South Australia (Schmidt and Williams 2010; Retallack et al. 2014; Minguez and Kodama 2017). Meert et al. (2016) indicate a marked change in palaeomagnetic reversal frequency starting at about 550 Ma, with long chrons before, and short chrons after that. The long normal in Arumbera Sandstone I–II at Ross River and Valley Dam may correlate with the long normal at the top of the Wonoka Formation in South Australia, and the sequence of reversals at Central Mount Stuart are less high frequency, and probably younger than those of the Zimnigory Formation of Russia (chrons at 550 Ma in Figure 5). This correlation is still unsatisfactory, but implies an hiatus of 26 million years between Arumbera Sandstone members I–II and

members III–IV. We went to central Australia in the hope of finding a complete Ediacaran–Cambrian boundary sequence as advocated by (Walter et al. 1989), but now accept Kirschvink's (1978) disconformity, in part also because there is no more than 330 m of Ediacaran rock in Central Australia, compared with 3,137 m of Ediacaran rock in South Australia (Retallack et al. 2014).

Materials and methods

This work is the product of three field seasons remeasuring and collecting fossils from the palaeomagnetic sections of Kirschvink (1978) at Valley Dam, Ross River, and Central Mount Stuart (Figure 1). Other localities collected were Jinker Creek, Neil Hargrave Lookout, Temple Bar, and Mt Skinner. Holotype material of *Arumberia banksi* was examined and photographed at Geoscience Australia, Canberra. The Arumbera Sandstone was also examined in core at 616–618 m in Lake Amadeus 5 DDH1 core (from S24.343619° E130.555608° 200 km west of Figure 1) in the Northern Territory Department of Resources Core Facilities in Alice Springs. Most rocks and fossils described here (F-) are curated in the Condon Collection of the Museum of Natural and Cultural History of the University of Oregon, in Eugene, Oregon (online catalogue at paleo.uoregon.edu). Also figured here are holotypes of *Arumberia* from Palaeontological Collections of Geoscience

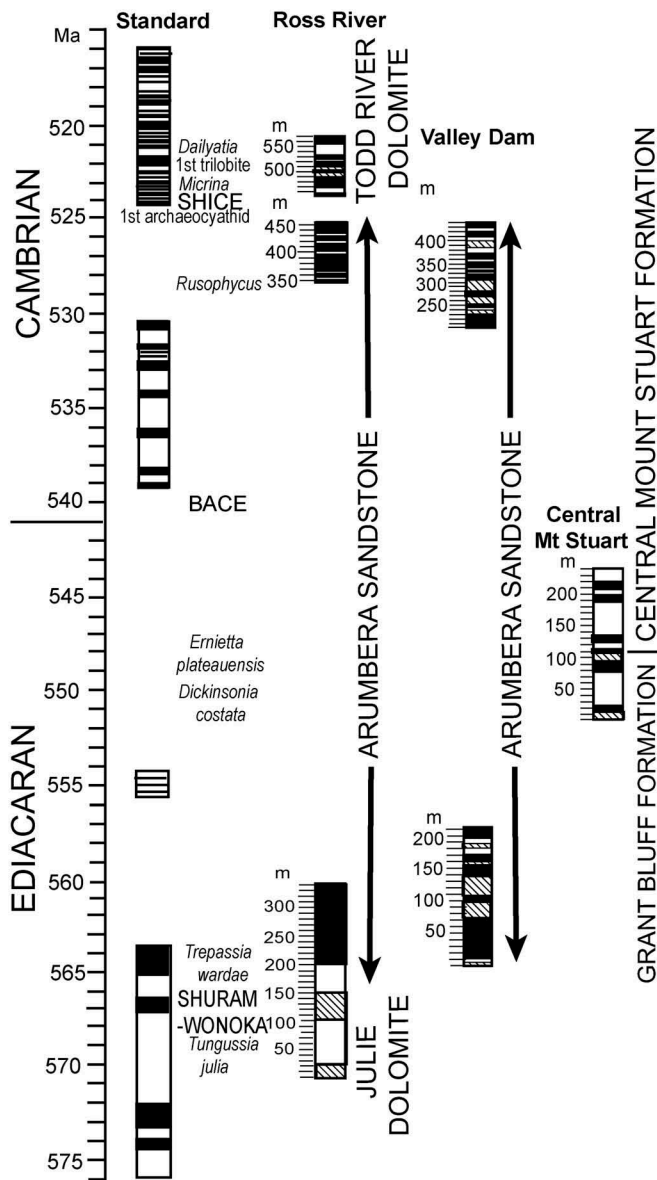


Figure 5. Palaeomagnetic evidence from Kirschvink (1978) for major hiatus in age within the Arumbera Sandstone, and likely late Ediacaran age of Grant Bluff and Central Mount Stuart Formations. Standard Cambrian palaeomagnetic columns are from Peng et al. (2012). Ediacaran radiometrically dated palaeomagnetic stratigraphy is from the Zimnigory Formation of Russia (Popov et al. 2002), and the Wonoka Formation of South Australia (Retallack et al. 2014; Minguez and Kodama 2017). Carbon isotopic profiles of the Arumbera Formation for correlation with global excursions (SHICE and BACE) are from Schmid (2017a, 2017b).

Australia, Canberra (CPC-) and of *Hallidaya* and *Skinnera* from the South Australian Museum, Adelaide (SAM-).

Most of the fossils figured and described here have been named previously using the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 2012), which has different orthography and other traditions than the International Code of Botanical Nomenclature (Turland et al. 2017). The class rank and ordinal subdivision of Vendobionta expands on a classification of Retallack (2016a), based in part on informal clades of Xiao and Laflamme (2009) and Erwin et al. (2011). Past higher taxa of informal or nonordinal rank include Erniettomorpha (Class

of Pflug 1972), Dickinsoniomorpha (informal of Brasier 2004), and Charniomorpha (informal of Antcliffe and Brasier 2007).

Systematic palaeontology

Kingdom and Phylum *Incertae sedis*

Class **Vendobionta** Seilacher, 1992
 Order **Erniettomorpha** Pflug, 1972
 Family **Erniettidae** Pflug, 1972
 Genus ***Arumberia*** Glaessner and Walter, 1975

Type species

Arumberia banksi Glaessner and Walter, 1975

Emended diagnosis

Shallow, concave, ellipsoidal ribbed bodies, with deepest part near one end. Ribs radiating from deepest point back to margin, bifurcating in places, and may incorporate finer ribs. Surface ribs are expression of septae in sedimentary matrix below, extending down to connect chambers between upper wall, middle lamella and lower wall, and above a zone of matrix below disrupted by vertical filaments or walls. Septae alternate at the inflexions of the inner lamellae.

Discussion

The reconstruction by Glaessner and Walter (1975) of *Arumberia* as a fluted tumbler or vase, was clear in describing it as 'mound like on lower surfaces of beds'. Reinterpretation by McIlroy & Walter (1997; McIlroy et al. 2005) as ornamented linguoid ripples, was unclear whether they were ripples (mounds on the upper surfaces of beds) or the flute casts downstream (mounds on the lower surface of beds). Careful examination of the holotype showed that it was not bulging upwards into the overlying bed, but bulging downward into the substrate (Figure 7(b)). This topology is also clear from other examples examined in the field at the type locality. The type material in Canberra (Geoscience Australia CPC14948) has inverse topology to a linguoid ripple mark, which is a positive or ridged feature (Potter and Pettijohn 1963; Baas 1994). It also lacks the anterior conical excavation, flanking anterior separation bubble, pinnate skin friction lines and posterior reattachment plane of flute casts into shaley tops of turbidites (Allen 1968; Allen 1969; Aalto 1995). The type material is a simple scoop with radiating striations and persistent curvature with little clay below or above. *Arumberia* was thus non-resistant in terminology of Wade (1968) for Ediacaran fossils, a concave epirelief (Seilacher 2007) and epichnial groove (Martinsson 1970).

Additional details of the topology of *Arumberia* come from thin sections and slabs cut from specimens oriented in the field, especially fragments traceable back into overlying matrix (Figure 8(e,f)). *Arumberia* has a complex internal structure of chambers defined by ferruginized seams and filaments, which follow external morphology in such a way as to suggest that they were unskeletonized biopolymers. The three-dimensional body plan includes a thick upper wall, impersistent middle lamella, and lower wall, each connected at intervals corresponding to surface seams by orthogonal vertical struts. The chambers are filled with sand grains when the wall structure is disrupted and presumably decayed (Figure 8(b,f)), but with silica when the walls are better preserved (Figure 8(d)). Thus, quilted chambers were partly empty or filled with soft tissue in life. Below this quilted structure, substrate bedding is disrupted by branching and tapering vertical structures to a depth of 8 mm (Figure

8). This disruption is not a laterally folded deformation predicted by a rheological model of Ediacaran preservation, either up into a dome or down into a bowl (Bobrovskiy et al. 2019).

Below that again is horizontal lamination of flat, undisrupted laminae, like the passive fill above the fossil, expected for these thin sections oriented vertical to bedding. The chambers and vertical walls or filaments in haematite are similar to those of other vendobionts (Retallack 2016a, 2018a), but better preservation of these elaborate structures is known from other pyrite-permineralised vendobionts (Retallack 2015a). Thus, it was not a simple microbial mat or microbially induced sedimentary structure, as widely envisaged (McIlroy et al. 2005; Mapstone and McIlroy 2006; Kumar and Pandey 2008, 2009; Callow et al. 2011; Liu 2011; Kolesnikov et al. 2012, 2017; Kumar and Ahmad 2014; Parihar et al. 2015; Droser et al. 2017; Nesterovsky et al. 2018).

Comparison. The topology and internal wall structure of *Arumberia* is most like that of *Ernietta* (Jenkins et al. 1981; Retallack 2016a), but a shallow depression, rather than the deep bag, with zigzag suture of *Ernietta* (Ivantsov et al. 2016). Several genera have been synonymised with *Ernietta* (Elliott et al. 2016), but not the similar and fragmentary *Baikalina* (Fedonkin et al. 2008), *Mashania* (Liu 1981), *Namalia* (Germs 1968), and *Nasepia* (Germs 1973), which also show greater relief than *Arumberia*. This chambered wall structure is also comparable with thin sections of the Chinese Ediacaran fossil *Yangtziramus zhangi* (Xiao et al. 2005; Shen et al. 2009), Namibian *Pteridinium simplex* (Jenkins 1992; Grazhdankin and Seilacher 2002), and South Australian *Dickinsonia costata* (Retallack 2016a), as well as North American Silurian *Rutgersella* (Retallack 2015a), and Devonian *Protonympha* (Retallack 2018b).

***Arumberia banksi* Glaessner and Walter, 1975** (Figures 6(a–c), 7(a–c), and 8)

1856 ‘ripple marks (with thin mud coating?)’ Salter, p. 250, Fig. 2, pl. IV, fig. 5–6.

1857 ‘surf ripple on current marks’ Salter, p.201, pl. V, fig. 8–9.

1975 *Arumberia banksi* Glaessner and Walter, p.61, figs. 1–4.

1980 *Arumberia banksi*; Becker, p.481, fig. 2.

1981 *Arumberia banksi*; Liu, p.74, pl.1, figs 3a,b, pls 2c, 4.

1984 *Arumberia banksi*; Bland, fig.1a–b, 2a.

1984 *Arumberia banksi*; Glaessner, p.73, fig. 2.9.

1997 ‘Arumberia’; McIlroy and Walter, p. 79–80, figs. 1–3.

1985 *Arumberia banksi*; Becker, p. 127, pl. 5, fig. 5.

2007 *Arumberia*; Jenkins and Nedin, p. 197, fig. 1.

2008 *Arumberia banksi*; Kumar and Pandey, p.88, pl. II, Fig. 4a–d.

2011a ‘Arumberia’; Callow et al., p.182, fig.6.

2012 *Arumberia banksi*; Kolesnikov et al. p.1235, Fig. 3 upper left only, fig 4 right hand panels only.

2012 *Arumberia banksi*; Sharma et al., p.412, fig.5a–b.

2013a ‘Arumberia’; Liu et al., p.100, fig. 2a

2014 *Arumberia banksi*; Sharma and Mathur p.628, Fig. 2b–g.

2016 ‘Arumberia fabric’; Davies et al. fig. 1T.

Holotype

CPC 14948 in Palaeontological Collections, Geoscience Australia, Canberra, from upper Member II of the Arumberia Sandstone at Valley Dam (207 m in Figure 3).

Emended diagnosis

Shallow, concave, ellipsoidal bodies, with deepest part near one end. Ribs, expressed as grooves in cast, radiating from the deepest point back to margin, bifurcating in places, and with intervening

finer ribs. Body size ranges from 34 to 159 mm long and 31 to 124 mm wide. Ribs are spaced at 1.5 to 3.0 mm in mid-length of body.

Description

The type material of *Arumberia banksi* described here consists of discrete bodies with seams marking their edges, even when clustered in groups (Figures 6(a,b) and 7(a,c)). Isolated individuals also have been found on large slabs in the field (half specimen sectioned from overhang in Figure 8(a)). These groups also show a high degree of common orientation, with the deepest point at the same end. While such multiples are striking, most of the examples collected for this study were isolated individuals. The main ribs are those most marked in relief, but there are finer ribs between, which branch from them (Figures 6(a,b) and 7(a)). These finer ribs gain in strength in the outward radiation of ribs to become major ribs themselves.

Comparison

The strict view of *Arumberia banksi* as discrete fossils comparable with erniettomorphs, advocated here, and by Glaessner and Walter (1975) and Bland (1984), implies that a variety of extensive microbial fabrics named as other species of *Arumberia* can no longer be regarded as congeneric (Table 1). Microbially induced sedimentary structures are very different in thin section, simple laminae with limited crenulation and doming (Retallack 2016a), unlike the poorly preserved double walls with septae of *Arumberia* (Figure 8). Microbial fabrics are better assigned to species of the ichnogenera *Neantia*, *Eoclathrus*, and *Rugalichnus* (Häntzschel 1975; Seilacher 2007; Stimson et al. 2017). The only conspecific specimens accepted here are listed above in synonymy, but this leaves uncertain a number of unillustrated specimens listed by Bland (1984), and Kumar and Pandey (2008).

Measurements

The type specimen (Figures 6(b) and 7(a)) is 98 mm wide and 110 mm long, the width between grooves at mid-length of this and another like it on the same slab is 2.2 ± 0.4 mm (standard deviation for $n = 48$, range = 1.5–3.0 mm). All complete specimens available ($n = 11$) were 50 ± 16 mm wide ($r = 31$ –62) and 60 ± 21 mm long ($r = 34$ –83 mm). The holotype is the largest of these complete specimens, but there are wider incomplete specimens ($r = 31$ –124 mm), and their length can be estimated by linear extrapolation as 159 mm (Figure 9(a)).

Distribution

Arumberia banksi was also found in the Ediacaran Arumberia Sandstone at Neil Hargrave Lookout and Ross River (Figure 2), and in the Ediacaran Grant Bluff Formation at both Central Mount Stuart and Mt Skinner (Figure 4). Other Ediacaran localities for *Arumberia banksi* accepted here are the Bonney Sandstone in Brachina Gorge, South Australia (Bland 1984; Jenkins and Nedin 2007), Cape Ballard Formation near St Johns, Newfoundland (Bland 1984), Maihar Sandstone near Kudra, India (Kumar and Pandey 2008), Sonia Sandstone near Jodhpur, India (Sharma and Mathur 2014), Chernyi Kamen Formation on the Us’va River, Russia (Kolesnikov et al. 2012), Zigan Formation on the Zigan River, Russia (Kolesnikov et al. 2012), Zigan Formation on the Askyn River, Russia (Becker 1980), Ust Sylvitsa Formation on Koiva River, Russia (Becker 1985), Moshakov Formation near Artyugino, Siberia (Liu et al. 2013a), Synalds Formation near Church Stretton, England (Salter 1856, 1857; Bland 1984; Callow et al. 2011a), Mashan Group near Jixi, China (Liu 1981; McCall 2006). *Arumberia banksi* has also been found in the Cambrian–Ordovician Port Lazo Formation of Brehec France (Bland 1984; Davies et al. 2016).

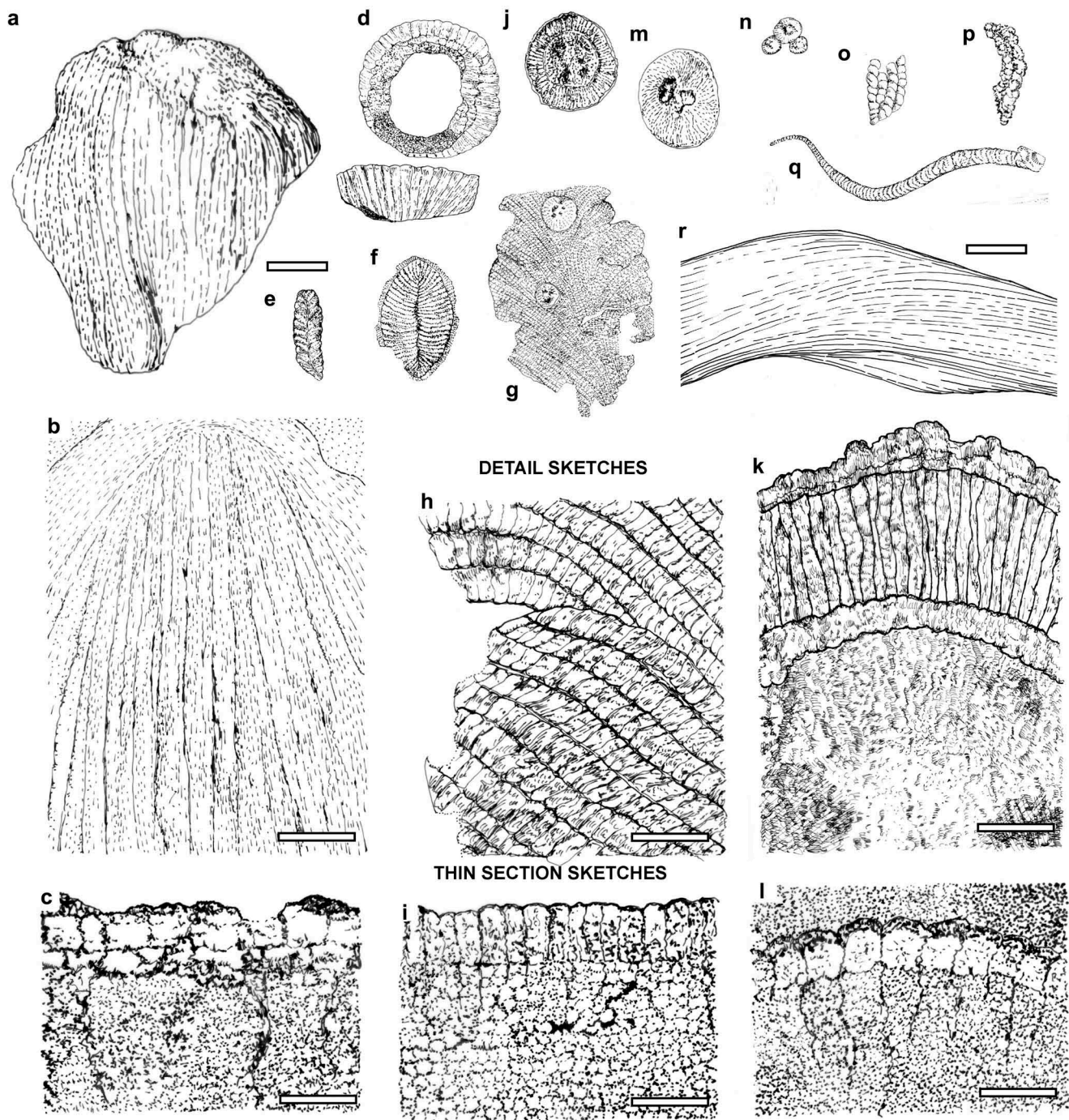


Figure 6. Summary interpretive sketches of key Ediacaran–Cambrian species of the Arumbera Sandstone and Central Mount Stuart beds, with quilt details, and thin section petrography: (a–c), *Arumberia banksi*: (a), CPC14950; (b), CPC14958; (c), F117272; (d), *Ernietta plateauensis*, F125435; (e), *Trepassia wardae*, F125895; (f), *Dickinsonia costata*: (g–i), *Noffkarkys storaaslii*; (g), F125437; (h), F125437; (i), F117258; (j–m), *Hallidaya brueri*: (j), F117275; (k), F117261; (l), F117261; (n), *Aspidella terranova*, F117270; (o), *Funisia dorothea*, F119659; (p), *Archaeonassa fossulata*, F117276; (q), *Lamonte trevallis*, F125469; (r), *Neantia rhodonensis*, F125457. Scale bars 20 mm for (a, d–g, j, m–r), and 5 mm for (b, c, h, i), and (k, l).

Affinities

Arumberia had an inner and outer wall connected by orthogonal septae and was concave up in the sediment like *Ernietta*, so can also be regarded as an erniettomorph vendobiont (Seilacher 1992; Erwin et al. 2011). Chambered organisation and disruption of the substrate below are also evidence against a sedimentary structure, with or without a mantling microbial mat (McIlroy and Walter 1997; McIlroy et al. 2005). As Kolesnikov et al. (2017) make clear from

excavation of modern microbial mats which they consider comparable with *Arumberia*, the internal structure of a mat is laminated and does not disrupt bedding (Retallack 2012), not chambered and disrupted like *Arumberia* (Figure 8). This does not help with biological affinities because *Ernietta* itself is an extinct problematicum without clear modern relatives (Ivantsov et al. 2016). Cnidarian, stem metazoan, or lichen are possibilities (Glaessner and Walter 1975; Retallack 1994; Hoyal Cuthill et al. 2018).

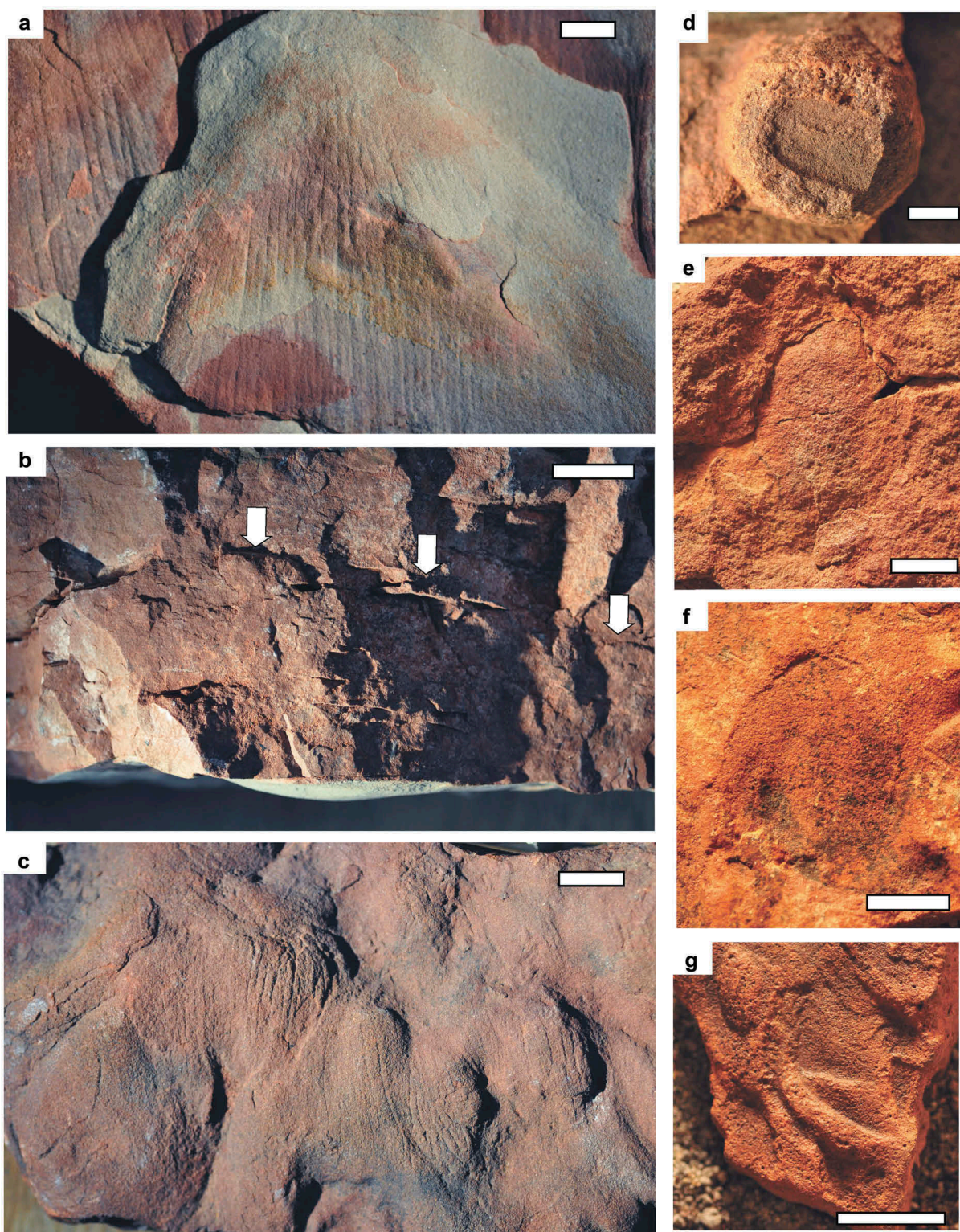


Figure 7. Erniettomorphs (*Arumberia* and *Ernietta*), Dickinsoniomorph (*Dickinsonia*) and Charniomorph (*Trepassia*) from the Ediacaran–Cambrian Arumbera Sandstone and Grant Bluff Formation: (a, b), holotype of *Arumberia banksi*, including side view of holotype slab with bedding plane truncations by scour (arrows in (b)) indicating *Arumberia* are mounds at the base of beds (curve in (b)); c, *Arumberia banksi*; (d), *Ernietta plateauensis* viewed from below; (e, f), *Dickinsonia costata*; (g), *Trepassia wardae*; (a–c), from Arumbera Sandstone at Valley Dam, (d–g) from Grant Bluff Formation at Central Mount Stuart. Specimens in the Palaeontological Collections of Geoscience Australia are CPC14948 (a, b), CPC14950 (c), and in the Condon Collection of the Museum of Natural and Cultural History of the University of Oregon are F125435 (d), F119667 (e), F125471 (f) and F125895 (g). Scale bars all 10 mm.

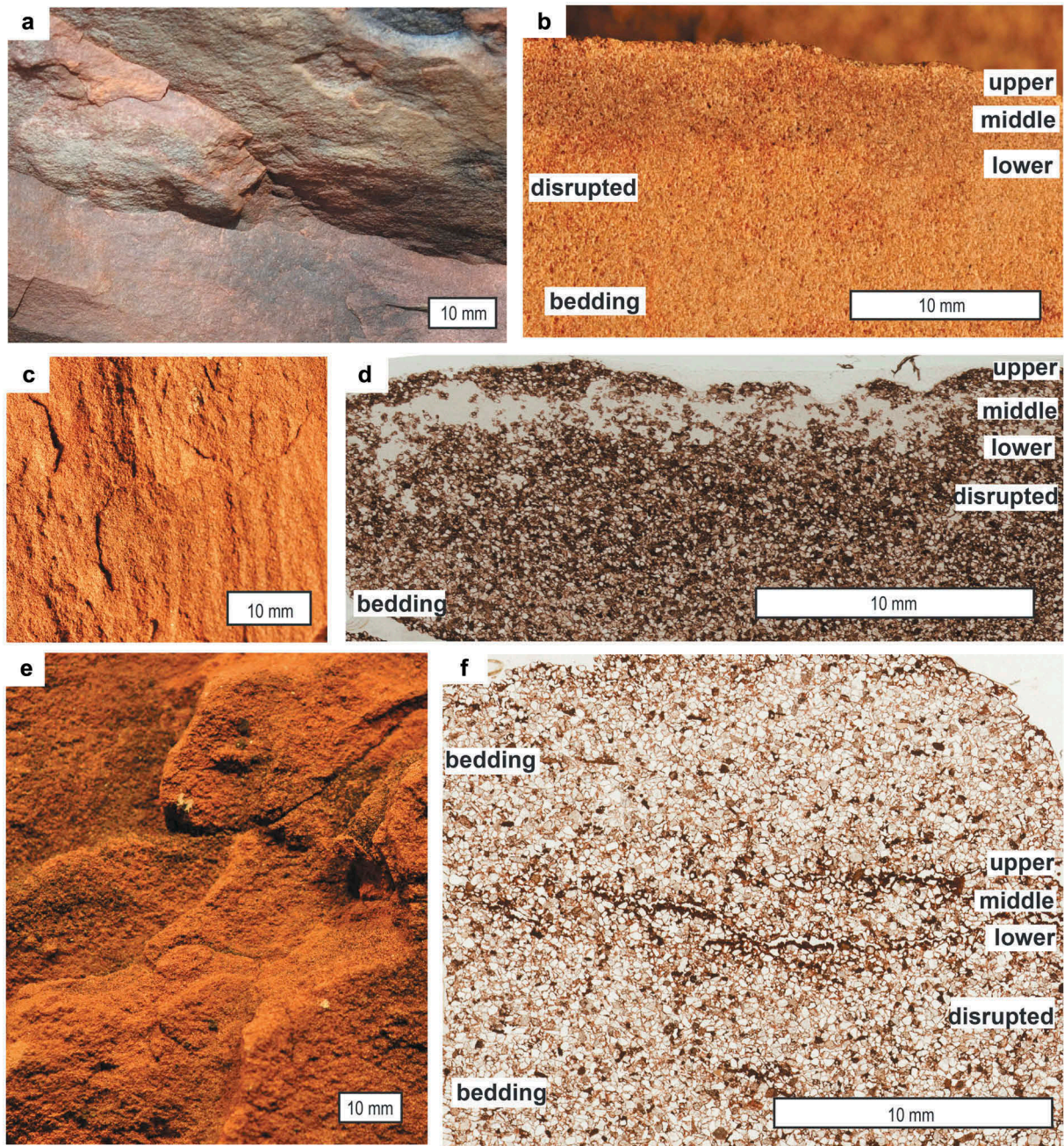


Figure 8. Polished slab (b) and thin sections (d, f) of figured specimens *Arumberia banksi*: (a, b), from base of bed in field at 207 m in measured section of Arumberia Sandstone near Valley Dam; (c, d), from Grant Bluff Formation at Mount Skinner; (e, f), from Arumberia Sandstone at Valley Dam: (e) shows *Arumberia* in upper left corner disappearing under cover rock lower right. Specimens and thin sections from the upper edge of each illustrated specimen are in the Condon Collection of the Museum of Natural and Cultural History of the University of Oregon as R4271 (b), F117272 (c, d) and F117256 (e, f). Scale bars are 10 mm. Dotted white lines are planes of cutting thin sections.

Ernietta plateauensis Pflug, 1966
(Figures 6(d) and 7(d))

Comments

Only one specimen was found (F125435) in the middle Grant Bluff Formation of the eastern fault block at Central Mount Stuart (Figure 1). The specimen cuts down across the bedding into the underlying strata, and is filled with sediment as is

common for this species (Ivantsov et al. 2016). Characteristic of this species is the double wall structure of an inner and outer wall connected by orthogonal, radial seams corresponding to the external pleating (Retallack 2016a). The lowest surface is broken, and so does not show the zig-zag suture which would be more diagnostic, but a geniculation near the top of the specimen (transverse groove in upper Figure 7(d)) is another feature of moderately large *Ernietta* (Jenkins et al. 1981; Elliott et al. 2016).

Table 1. Records of *Arumberia* not accepted here as congeneric and better referred to ichnotaxa such as *Rugalichnus*, *Neantia*, or *Eoclathrus*.

Taxon	References	Formation	Age
<i>Arumberia vindhyanensis</i>	Kumar and Pandey (2008)	Maihar Sandstone	Ediacaran
<i>Arumberia banksi</i>	Kumar and Pandey (2009)	Jodpur Sandstone	Ediacaran
<i>Arumberia vindhyanensis</i>	Kolesnikov et al. (2012)	Chernyi Kamen Fn.	Ediacaran
<i>Arumberia usvaensis</i>	Kolesnikov et al. (2012)	Chernyi Kamen Fn.	Ediacaran
<i>Arumberia multykensis</i>	Kolesnikov et al. (2012)	Chernyi Kamen Fn.	Ediacaran
<i>Arumberia ollii</i>	Kolesnikov et al. (2012)	Chernyi Kamen Fn.	Ediacaran
<i>Arumberia beckeri</i>	Kolesnikov et al. (2012)	Chernyi Kamen Fn.	Ediacaran
Arumberiomorph	Kolesnikov et al. (2017)	Tidal flat	Modern
<i>Arumberia banksi</i>	Parihar et al. (2015)	Girbhakar Sandst.	Ediacaran
'Arumberia'	Liu (2011)	Synalds Formation	Ediacaran
'Arumberia'	Callow et al. (2011b)	Diabag Formation	Mesoproterozoic
cf <i>Arumberia</i>	Callow and Brasier (2009)	Drook Formation	Ediacaran
<i>Arumberia</i> type structure	Arrouy et al. (2016)	Cerro Negro Form.	Ediacaran

Ernietta plateauensis has been recently re-evaluated with much new material (Ivantsov et al. 2016), and comprehensive taxonomic revision (Elliott et al. 2016).

Measurements

With ellipse long diameter of 44 mm and short diameter 41 mm, and depth into substrate of 23 mm, this specimen (F125435) is slightly smaller than the population described by Ivantsov et al. (2016) but larger than common small examples (Retallack 2016a).

Comparison

Elliott et al. (2016) synonymised several genera with *Ernietta*, but not *Baikalina* (with more strongly radiating ribs: Fedonkin et al. 2008), *Mashania* (elongate like *Pteridinium*: Liu 1981; McCall 2006), *Namalia* (with conical rather than bulbous base: Germs 1968), or *Kuibisia* (also with conical base: Ivantsov et al. 2016). Discovery of variously oriented *Ernietta plateauensis* with preserved distal fans means that it is a senior synonym of *Nasepia* (Germs 1973). The zigzag suture in the base and zigzag ferruginised internal lamella meeting alternating septae of *Ernietta* (Elliott et al. 2016) are both similar to *Dickinsonia* (Retallack 2016a), but that genus is flat with zigzag suture uppermost.

Distribution

Ernietta plateauensis is best known from the Ediacaran Kliphoeck and Aar Member of the Dabis Formation in Namibia (Jenkins et al. 1981; Ivantsov et al. 2016; Elliott et al. 2016), but has also been found stratigraphically lower in the Kanies Member of the Dabis Formation (Condon collection specimen F120819), and stratigraphically much higher, just below the Cambrian boundary, in the Feldshuhorn Member of the Urusis Formation in Namibia (Darroch et al. 2015). It is also known from the late Ediacaran lower Wood Canyon Formation in California and Nevada (Smith et al. 2017).

Affinities

The biological affinities of *Ernietta* are problematic: cnidarian, stem metazoan, or lichen are possibilities (Glaessner and Walter 1975; Retallack 1994; Hoyal Cuthill et al. 2018).

Order **Dickinsoniomorpha** Retallack, 2016a
Family **Dickinsoniidae** Harrington and Moore, 1956

Dickinsonia costata Sprigg, 1947
(Figures 6(f) and 7(e,f))

Comments

This well-known Ediacaran fossil is represented by five poorly preserved specimens from the Grant Bluff Formation at Central Mount Stuart, and in the Arumbera Sandstone at Jinker and Ellery Creeks. Four of them show narrow lateral segments connected by a zigzag suture down the middle, and are negative hyporeliefs (the most common taphomorph or resistant fossils of Wade 1968). One of the specimens (Figures 6(f) and 7(f)) shows a narrow lateral margin, which has been interpreted as a trace of body shrinkage (Runnegar 1982) or as a hypothallus (Retallack 2007). This specimen also shows cross-wrinkled segments on the upper left side (Figure 7(f)), as in other deformed specimens of this species (Evans et al. 2019a). One specimen, however, is a low-relief positive epirelief (Figure 7(e)) in which segments are more finely divided, less deeply incised, and not zigzagging across the midline, as is typical of what Evans et al. (2019a) speculatively call 'footprints'. We agree that these are impressions of the lower surface, and the more common negative hyporeliefs are impressions of the upper surface of the same species (Evans et al. 2019a). None of these specimens was thin sectioned, but thin sections of South Australian specimens (Retallack 2016a) show a thick upper and thin lower ferruginised wall with middle lamella, joined at inflexions by vertical septae, as in *Arumberia* (Figure 8), *Ernietta* (Retallack 2016a), and *Rutgersella* (Retallack 2015a). The thick upper wall was evidently the surface showing greater relief of segments curling around the edges, but the thin lower walls had less relief of segments radiating out to the edges.

Measurements

The five specimens found (Figure 9(b)) average 22 ± 5 (15–31) mm wide and 35 ± 6 (28–43) mm long. Segment spacing on specimen F125471 is 1.7 ± 0.4 (1.2–2.5) mm ($n = 17$).

Comparison

In size and segment spacing, the central Australian examples resemble *Dickinsonia costata* from the Ediacara Member of the Rawnsley Quartzite in South Australia (Figure 9(b)). In contrast, *Dickinsonia tenuis* is more elongate with narrower segments (Retallack 2007). *Dickinsonia lissa* is narrow and elongate, and *D.* (formerly *Vendomia*) *meneri* is tiny (4 mm long) with a large segment at one end (Wade 1972; Fedonkin 1985; Ivantsov 2007), variously interpreted as a head or holdfast (Retallack 2016b). *Dickinsonia rex* is a name applied to specimens more than 1 m long and may be extremely old individuals of *D. costata*, considering documented indeterminate growth (Retallack 2007).

Distribution

Dickinsonia costata is best known from the Ediacaran Ediacara Member of the Rawnsley Quartzite throughout the Flinders Ranges and outlying Ediacara Hills and Nilpena, South Australia (Retallack 2007, 2013a; Reid et al. 2018). This species is also found

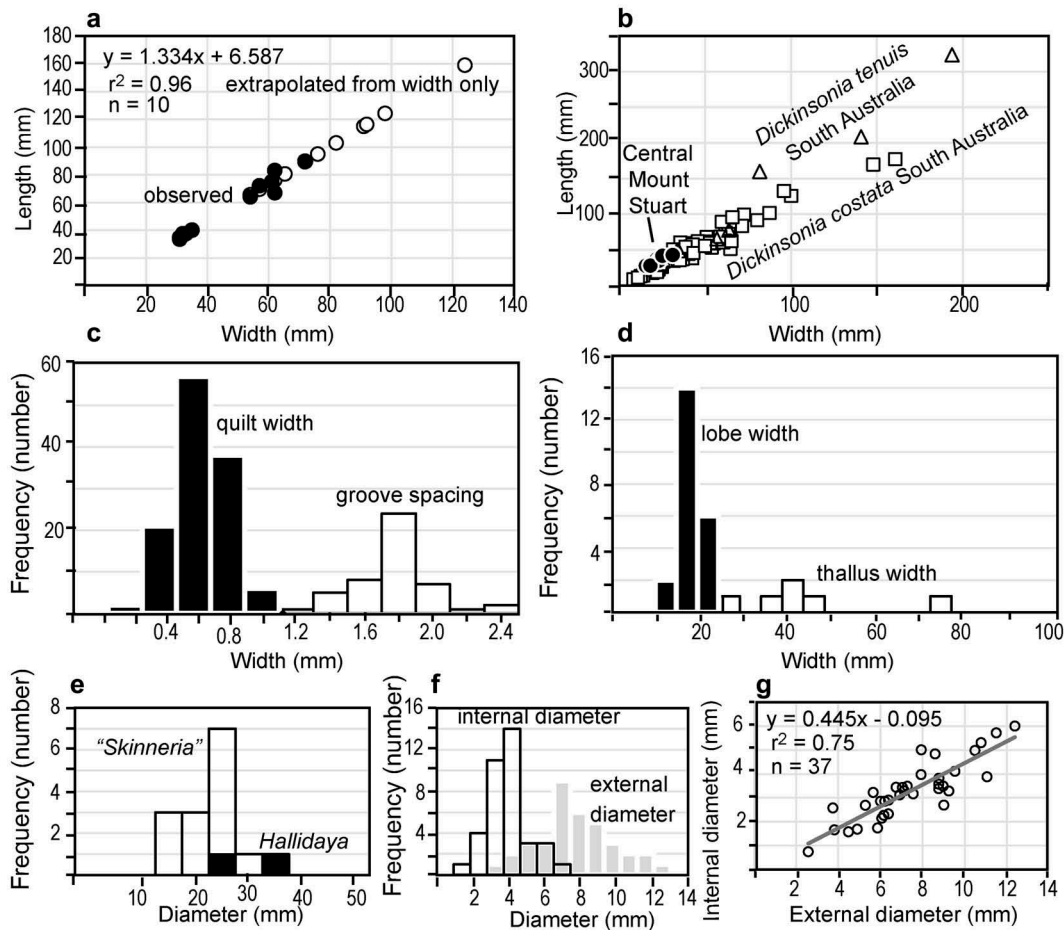


Figure 9. Size distributions of fossils from the Cambrian–Ediacaran Arumbera Sandstone, Grant Bluff and Central Mount Stuart Formations: (a), the relationship between length and width of complete specimens (closed symbols) of *Arumberia banksi*, compared with length of incomplete specimens (open symbols); (b), length and width of *Dickinsonia costata* (closed symbols) from central Mount Stuart compared with two species (open symbols) from the Ediacara Member of the Rawnsley Quartzite in South Australia (after Retallack 2007); (c, d), quilt and groove spacing, and lobe and thallus width of *Noffkarkys storaaslii* gen. et sp. nov.; (e), internal and external diameters of *Aspidella terranova*.

in the Ediacaran Ust Pinega and Zimnigory Formations of Russia, and the Ediacaran Mogilev Formation of Ukraine (Fedonkin 1985).

Affinities

Dickinsonia has proven to be a palaeontological Rorschach test envisaged as (1) lichenised glomeromycotan fungus (Retallack 1994, 2007, 2015b), (2) xenophyophoran protist (Zhuravlev 1993; Seilacher et al. 2005), (3) stem metazoan between sponges and cnidarians (Brasier 2004, Hoekzema et al. 2017; Evans et al. 2017; Dunn et al. 2018), (4) cnidarian sea jelly (Sprigg 1947; Harrington and Moore 1956), (5) cnidarian anemone (Valentine 1992), (6) polychaete worm (Wade 1972; Runnegar 1982), (7) annelid worm (Conway Morris 1979; Evans et al. 2019a), (8) turbellarian flatworm (Termier & Termier 1968, Fedonkin 1981), or (9) placozoan (Sperling and Vinther 2010). Cholesterol isolated from *Dickinsonia* was regarded by Bobrovskiy et al. (2018) as evidence for animals, but C²⁷ cholesterol is also found in the fungal phylum Glomeromycota (Weete et al. 2010) and red algal family Rhodophyceae (Idler et al. 1968), both independently known from Ediacaran and geologically older rocks (Yuan et al. 2005, Retallack 2015b; Gold et al. 2018). The green algal biomarker stigmaterol was also found in *Dickinsonia* and the stigmaterol:cholesterol ratio declines in progressively larger and older specimens (Bobrovskiy

et al. 2018). This observation may be explained as fungal control of symbiotic green algae, or declining algal fouling of an animal with age (Retallack 2018a). Supposed flip-tracks (*‘Epibaion’*) of *Dickinsonia* (Ivantsov and Malakhovskaya 2002), called ‘footprints’ by Evans et al. (2019a), may be taphomorphs displaced by frost boils (Retallack 2016b). Overturned and lacerated edges of *Dickinsonia* taken as evidence of motility (Evans et al. 2015, 2019b), may instead be a testament to the strength of attachment to the substrate of the rest of the fossil (Retallack 2017).

Order **Charniomorpha** Shu, 2006
Family **Charniidae** Glaessner, 1979

Trepassia wardae Narbonne et al., 2009
(Figures 6(e) and 7(g)).

- 1969 *Rangea* cf. *longa*; Glaessner, p.391, fig. 9A.
- 1970 *Rangea* cf. *longa*; Wade p.101.
- 2003 *Charnia wardi*; Narbonne & Gehling, p.30, figs. 2A–D, 3.
- 2005 *Charnia wardi*; Narbonne, p.428 fig. 2g.
- 2007 *Charnia wardi*; Laflamme et al., p.253, figs.5a–h.
- 2007 *Charnia wardi*; Narbonne et al., p.60, fig.81.
- 2008 *Charnia wardi*; Laflamme & Narbonne, fig.3.6–3.8.
- 2009 *Charnia wardi*; Brasier & Antcliffe, fig. 15.

- 2009 *Trepassia wardae*; Narbonne et al., p.515, Fig.10.
 2012 *Trepassia wardae*; Liu et al. p. 398, fig.2a, fig.4c-d.
 2012 *Trepassia wardae*; Brasier et al., p.1112, fig.4D.
 2013b *Trepassia wardae*; Liu et al., p.24, fig.1a
 2013 Charniomorph; Bowers, p.96, fig.10
 2015 *Trepassia wardae*; Liu et al., p.1362, fig.2M

Comments

The best specimen known from the Arumbera Sandstone was illustrated and described by Glaessner (1969), and the descriptions below are largely based on it. Only a single poorly preserved small frond was found during this work (Figures 6(e) and 7(g)). Similarly it is unipolar, with two rows of irregularly spaced primary branches arranged along a central axis, and with moderate inflation of first-order branches. First-order branches are subparallel, but second and third-order branches are irregular, subparallel to radiate. There is a groove below the specimen that flares at the base (Figures 6(e) and 7(g)), but it is not a positive feature like other stalks and holdfasts of Ediacaran fronds (Laflamme et al. 2004).

Measurements

The single specimen found in the Grant Bluff Formation is 14 mm long and 4 mm wide, and its 18 primary branches are spaced at 1.4 ± 0.2 (1.2–1.8) mm, like assumed juvenile fronds (Liu et al. 2012). The other specimen from the Arumbera Sandstone illustrated by Glaessner (1969) is about 20 mm wide, and also small for specimens of *Trepassia wardae* (Narbonne and Gehling 2003).

Comparison

Trepassia wardae is most like *Beothukis mistakensis* (Brasier and Antcliffe 2009, Liu et al. 2016). *Trepassia* has both the primary and secondary branches attached directly to the central stalk, but *Beothukis* has only primary branches attached to the stalk. Also, *Trepassia* has single-sided secondary and tertiary branches, which are double sided in *Beothukis*. Thus, *Trepassia* has a gridded appearance, but *Beothukis* is like a crazy quilt. Both *Beothukis* and *Trepassia* have a narrow stalk, and often lack a rounded holdfast at one end (Brasier and Antcliffe 2009; Laflamme et al. 2012, 2018; Liu et al. 2016). *Trepassia* has a simple two-dimensional quilting pattern and lacks the prominent holdfast and wide tapering stalk of other Ediacaran fronds such as *Charniodiscus* and *Rangea*. A useful key to Ediacaran fronds is provided by Brasier et al. (2012).

Distribution

In Ediacaran sequences of Newfoundland, *Trepassia wardae* is long ranging from the Drook, Briscal, Mistaken Point, and Trepassey Formations of the Avalon Peninsula from Pigeon Cove north to Spaniards Bay (Liu et al. 2012). The single specimen reported here from the Grant Bluff Formation on central Mount Stuart (Figure 7(e)) is very similar to another ('*Rangea cf. longa*' of Glaessner 1969, Wade 1970) found at the base of the Arumbera Sandstone near Deep Well Homestead, 80 km southeast of Alice Springs (Figure 1). The 'charniomorph' figured by Bowers (2013) may be another example in the Ediacaran Bradgate Formation of Charnwood Forest, England.

Affinities

Ediacaran frond shaped fossils have traditionally been interpreted as sea pens (Glaessner 1985), but growth series and lack of free polyps falsify that idea (Seilacher 1992; Antcliffe and Brasier 2007, 2008). Ediacaran fronds may have been lichenised glomeromycotan fungi (Retallack 1994, 2016a, 2016c), or stem metazoans (Brasier et al. 2012; Hoyal Cuthill et al. 2018).

Genus *Noffkarkys* gen. nov. (Figures 6(g–i) and 10)

Type species

Noffkarkys storaaslii sp. nov.

Diagnosis

Lobed, elongate frond, with distinctive quilt pattern of trapezoids, each 1–2 mm long, convex upward; trapezoids form files, bounded by grooves radiating upward and outward from the midline to curve into lateral lobes; lateral lobes rounded and partly overlapping; compaction resistant with relief 3–5 mm; frond with broad wrinkles concentric with margins, like growth rugae.

Derivation

After Nora Noffke, in honour of her research on microbially induced sedimentary structures, and Greek *αρκυς* (feminine noun) meaning net.

Comparisons. Of the variety of Ediacaran frond-like fossils (Brasier and Antcliffe 2009; Brasier et al. 2012), *Noffkarkys* is most like *Bradgatia linfordensis* and *Beothukis mistakensis*, but unlike them has little indication of a strongly differentiated central thread or stalk. Instead *Noffkarkys* has radiating grooves connected by transverse quilts and forms a lobate radiating surface. *Kempia huronense* Bain (1927) is also a system of larger (3–4 mm) meshes, but lacks radial grooves, and has less regular growth increments. Also, lacking radial grooves is the finely quilted *Kuckaraukia multituberculata* (Razumovskiy et al. 2015), which is a simple discoid rather than a spreading frond. Another similar fossil from the Late Ordovician (Katian), Kope Formation of Kentucky has been called informally 'Godzillus', although that name is preoccupied by the orthographic variant *Gozillius robustus*, a remipede crustacean (Hoeneman et al. 2013), but it lacks differentiation between radiating grooves and finer meshes of *Noffkarkys*, with meshes forming parallel chains (Meyer et al. 2016). The dichotomising lobate thalloid structure of *Noffkarkys* and its complex quilting are also distinct from any known microbially influenced sedimentary structure (Noffke 2010).

Noffkarkys storaaslii sp. nov. (Figures 6(g–i) and 10)

- 1857 'rippled surface'; Salter, p.201, pl.5, fig.7.
 1969 pattern between *Hallidaya brueri* and 'minute fossils'; Wade, p.356, pl.68, fig.1d, pl.69, fig.7.
 2013c grid pattern on 'cast of pyrite sun'; Retallack, p. 259, fig. 2D.
 2014 '*Rameshia rampurensis*'; Kumar and Ahmad, p.358, fig.5B-C, non Kumar and Pandey (2008).

Holotype

Specimen F125437 (Figures 6(g,h) and 10(a)) from the Ediacaran Grant Bluff Formation in the eastern fault block of Central Mount Stuart (Figures 1 and 4).

Diagnosis

Noffkarkys frond obovate to elongate, with lateral partly overlapping lobes: frond 10–80 mm wide, with lobes 10–20 mm wide; radiating grooves spaced 1–3 mm apart and filled with files of quilts 0.2–1.4 mm wide defined by short oblique grooves; relief of 3–5 mm from growth rugae and curvature of lateral lobes.

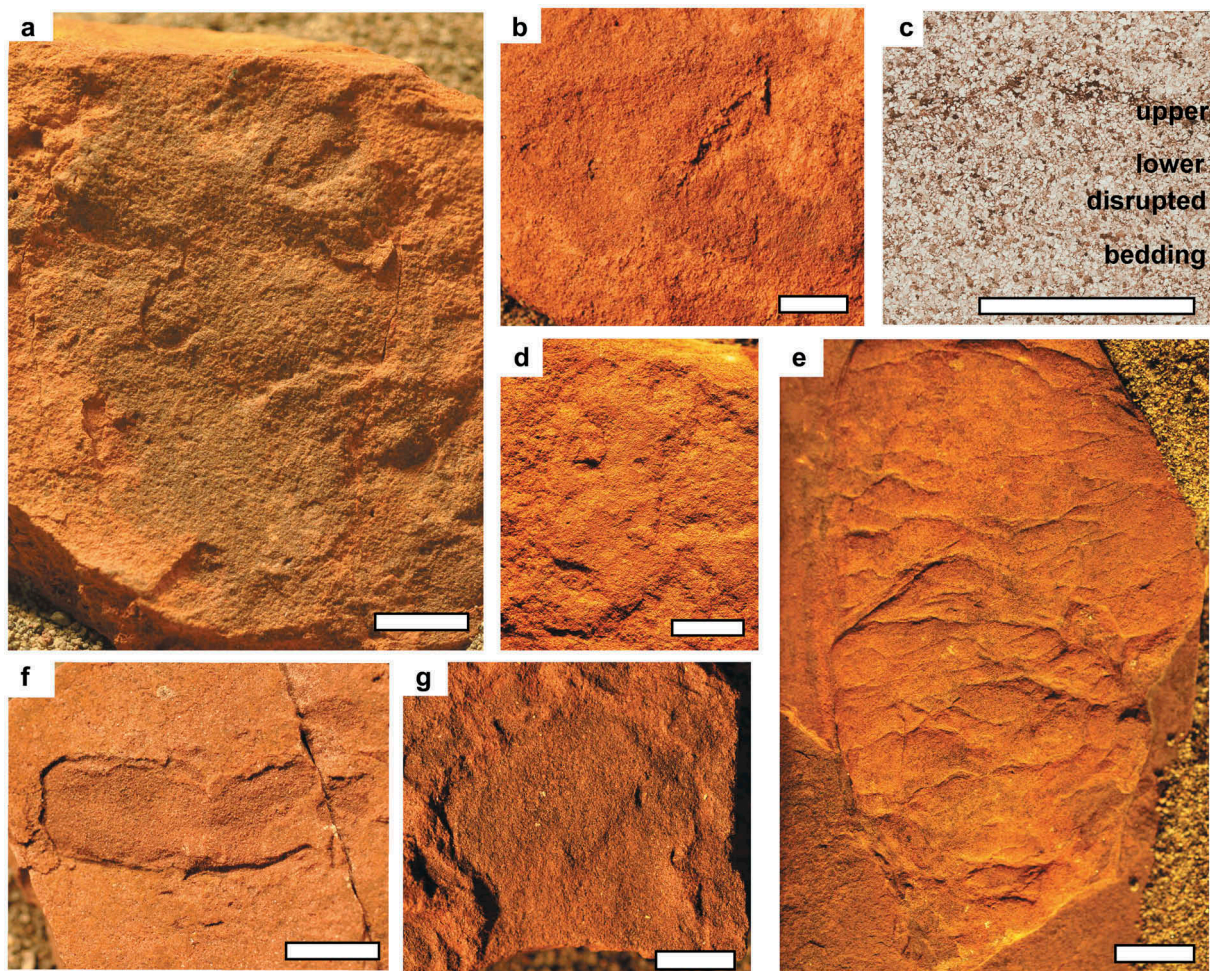


Figure 10. Thalloid fossils. *Noffkarkys storaaslii* gen. et sp. nov. from the Cambrian–Ediacaran Arumbera Sandstone and Grant Bluff Formation: (a), holotype from Grant Bluff Formation at Central Mount Stuart, (b, c), specimen under cover bed to right with thin section from Arumbera Sandstone at Valley Dam; (d, e), from Arumbera Sandstone at Ross River, (f), from Arumbera Formation at Valley Dam; (g), from Grant Bluff Formation at Central Mount Stuart. Specimens and thin sections in the Condon Collection of the Museum of Natural and Cultural History of the University of Oregon are F125437 (a), F117259 (b, c), F125472 (d), F125463 (e), F117263 (f), and F117265 (g). Scale bars are 10 mm.

Derivation

The epithet is after Mark Storaasli, who discovered comparable fossils in Montana (Retallack 2013c).

Description

These fossils are preserved as convex epireliefs (Seilacher 2007) or epichnial ridges (Martinsson 1970) and are thus resistant in the Ediacaran taphonomic terminology of Wade (1968). They undulate on the slab to be mostly above, but in places below the general level of the substrate. The most distinctive feature of *Noffkarkys storaaslii* is a mesh of fine, flat-crested quilts (Figures 6(h) and 10(b)), that are particularly clear and convex-upward shape in thin section (Figures 6(i) and 10(c)). Quilts are also defined and aligned by radial grooves (Figure 6(i)). Margins are irregular lobate, slightly inflated. Some specimens show overlap of lobes with one lobe above the other. Regardless of the size of the lobes or overall thallus, quilts, rings, and grooves retain the same size and spacing.

Thin sections of *Noffkarkys storaaslii* reveal 4 distinct layers of ferruginised organic matter (Figures 6(i) and 10(c)), from the top downwards; (1) thick opaque upper wall bulging upward at quilts, (2) open interwall space with vertical septae below surface grooves between quilts, (3) thin discontinuous lower wall, and (4) thick zone of tangles and vertically branching filaments or walls above

undisturbed horizontal bedding. Again, this vertically disrupted zone is not a soft-sediment deformation predicted by a rheological model for fossil preservation of Bobrovskiy et al. (2019). This is a comparable wall structure to that of *Arumberia* (Figure 8(b,d,e)), *Ernietta* (Elliott et al. 2016, Retallack 2016a) and *Rutgersella* (Retallack 2015a), which have a middle lamella between the upper and lower wall, and septae meeting inflections in the middle lamella. In *Noffkarkys* the vertical septae corresponding to surface grooves extend between upper and lower walls.

Measurements

The holotype specimen is a nearly complete thallus 66.5 mm long and 39.6 mm wide, with 7 complete terminal lobes 12.9 ± 0 , 6 mm (12.3–14.0) mm wide. Widths between main 47 radial grooves are 1.7 ± 0.2 (1.1–2.4) mm, and widths of 123 individual quilts are 0.5 ± 0.2 (0.2–0.9) mm (Figure 9(c)). Another 20 specimens from the Arumbera and Grant Bluff Formations have thallus widths 408 ± 17 (13–72) mm and 43 lobes with width 14 ± 3 (9–25) mm (Figure 9(c)).

Distribution

Noffkarkys storaaslii is a common fossil in the Ediacaran to Cambrian Arumbera Sandstone (Jinker Creek, Ross River, Valley Dam), and Ediacaran Grant Bluff Formation (Central Mount Stuart

and Mt Skinner). The same species from the Ediacaran Synalids Formation near Church Stretton, England (Salter 1857; Bland 1984) is confirmed by specimens in the Condon Collection (F116163-5). Also confirmed by our collections (F116818-21, F116826-8) is *Noffkarkys storaaslii* from the early Cambrian lower Flathead Sandstone near Fishtrap Lake Montana (Retallack 2013c). Included are fossils of '*Rameshia rampurensis*' from the Jodhpur Sandstone near Jodhpur India (Kumar and Ahmad 2014), not considered conspecific with '*R. rampurensis*' Kumar and Pandey (2008).

Affinities

Quilted Ediacaran frond fossils have been compared with seaweeds (Ford 1958), lichenised glomeromycotan fungi (Retallack 1994, 2015b, 2016a), xenophyophore foraminifera (Seilacher et al. 2005), and stem metazoans between sponges and cnidarians (Brasier et al. 2012; Hoyal Cuthill et al. 2018).

Order *Aspidellomorpha* Retallack, 2016a Family *Aspidellidae* fam. nov.

Diagnosis

Discoid fossils with radial symmetry, concentric growth rings, and small areas of quilting in a differentiated central region, preserved as negative hyporeliefs: quilting also revealed by vertical septae in thin section.

Comments

Synonymy of virtually all Ediacaran discoid fossils with *Aspidella terranovica* by Gehling et al. (2000) not only made them unrecognisable but also introduced confusion by interpreting them all as holdfasts of frond-like fossils (MacGabhann 2007). Thus, *Aspidella* is sometimes used as a taxon for holdfasts, often without either stalk or frond (Tarhan et al. 2015; Bykova et al. 2017), which could be any one of many genera in the Order Rangeomorpha (Brasier et al. 2012; Retallack 2016a). At its type localities near St Johns and Ferryland in Newfoundland (Billings 1872), *Aspidella* is not a holdfast, because specimens oriented by collection in place have axes tapering down into the rock rather than up and out of the bed, and most lack axes, but have remnants of quilting in a central area (Retallack 2016a). The revised diagnosis provided here is based on observations of paratypic material from Ferryland and St Johns studied in thin section (Retallack 2016a). The family Aspidellidae is thus proposed to include *Aspidella* and *Hallidaya* as a segregate of segmented and resistant fossils, removed from the majority of Ediacaran discoid fossils, such as *Beltanelliformis* and *Cyclomedusa*, which are non-resistant, convex hyporeliefs, without evidence of internal chambering in thin section or quilting at the surface.

Aspidella terranovica Billings, 1872 (Figures 6(n) and 11(c))

- 1872 *Aspidella terranovica* Billings, p.467, fig.14.
1923 *Aspidella*-like markings; Clark, p.482, fig.2.
1975 *Aspidella terranovica*; Häntzschel, p.W170, Fig.102-2a-c.
1987 *Vendella larine*; Gureev, p.36, fig.13.
2000 *Aspidella terranovica*; Gehling et al. *partim*, p.432, text-figs. 4–5, 6A–D, J–K, 8–9.
2005 *Medusinites* aff. *asteroides*; McIlroy et al., p.449, fig.6b,7a-b.
2006 *Aspidella terranovica*; Mapstone & McIlroy, p.131, Fig.4d-j.
2008 *Aspidella terranovica*; Boyce & Reynolds, p.56, pl.1 F,5,6B.
2009 *Aspidella* sp.; Kumar and Pandey, 2009, p.176, pl.2, fig a-e

- 2009 *Aspidella terranovica*: Retallack, p.358, figs.3B-F, 4B-C
2013a *Medusinites* aff. *asteroides*; Liu et al., p.100, fig. 2b.
2013 *Aspidella terranovica*; Menon et al., p.496, fig.2.
2013 *Aspidella terranovica*; Gehling & Droser, p.449, fig.2E.
2016 *Aspidella*; Darroch et al., p.201, figs.3–4
2016a *Aspidella terranovica*; Retallack, p.6, fig 3E, 6.
2016 *Aspidella terranovica*; Buatois & Mángano, p.28, fig.2.1, 2.3a.
2016 *Aspidella*-plexus; Arrouy et al., p.2, figs.2,5.
2019 discoidal structures; Inglez et al., p.323, fig.3C-D.
2017 *Aspidella terranovica*; Minicucci, p.58, fig.2

Revised diagnosis

Circular to ovate structures up to 4 cm in diameter, with differentiated central and peripheral areas each with distinctive quilting. Central area with 3–5 trapezoidal quilts, sometimes obliquely tilted, in contrast with radial quilts from central circle to margin. Body is thick, with parts both above and below substrate. A thick carbonaceous upper wall contrasts with a thin lower carbonaceous wall, sometimes with tubular extensions into the substrate.

Comments

Unlike type material of *Aspidella terranovica* (Retallack 2016a), these central Australian specimens are in red sandstone rather than grey shale, but they do share with the type material a central circle, divided obliquely into two or more segments by deep grooves (Figures 6(n) and 11(f)). Oriented thin sections of paratypic material from Newfoundland, show that *Aspidella* maintained a thickness of 0.2–0.5 mm even in highly compactible shales, and had thick upper versus thin lower opaque carbonaceous wall (Retallack 2016a). This and the quilting observed in the centre are unlike holdfasts of frond fossils (Tarhan et al. 2015; Bykova et al. 2017), and the non-resistant preservation of most Ediacaran discoid fossils (Wade 1968; MacGabhann 2007), but more like other vendobionts (Seilacher 1992; Retallack 2016a).

Comparisons

Two other species, *Aspidella costata* and *A. hatyspytia* are both larger (10–74 mm) diameter with wider (8–11 mm) ribs than *A. terranovica* (Vodanjuk 1989).

Measurements

The 37 specimens available had external diameter of 7.3 ± 2.3 (3–12) mm and internal diameter of 3.3 ± 1.2 (1–6) mm (Figure 9(f)). This ratio is maintained with growth (Figure 9(g)).

Distribution

Aspidella terranovica has been previously reported from the Arumbera Sandstone of central Australia (McIlroy et al. 2005; Mapstone and McIlroy 2006), and has a long range in Ediacaran rocks (Drook, Briscal, Mistaken Point, Trepassey, and Renew Head Formations) in Newfoundland (Billings 1872, Häntzschel 1975; Gehling et al. 2000; Boyce and Reynolds 2008; Liu et al. 2012; Menon et al. 2013; Buatois and Mángano 2016; Retallack 2016a). It has also been found in the following Ediacaran formations: Cambridge Argillite near Boston Massachusetts (Clark 1923: specimens in Condon collection F114496-9), Cerro Negro Formation near Salta, Argentina (Arrouy et al. 2016; Inglez et al. 2019), Moshakov Formation near Artyugino, Siberia (Liu et al. 2013a), Jodhpur Sandstone near Jodhpur, India (Kumar and Pandey 2009), Schwarzrand Subgroup near Zebra River, Namibia (Darroch et al. 2016), and Ediacara Member of the Rawnsley

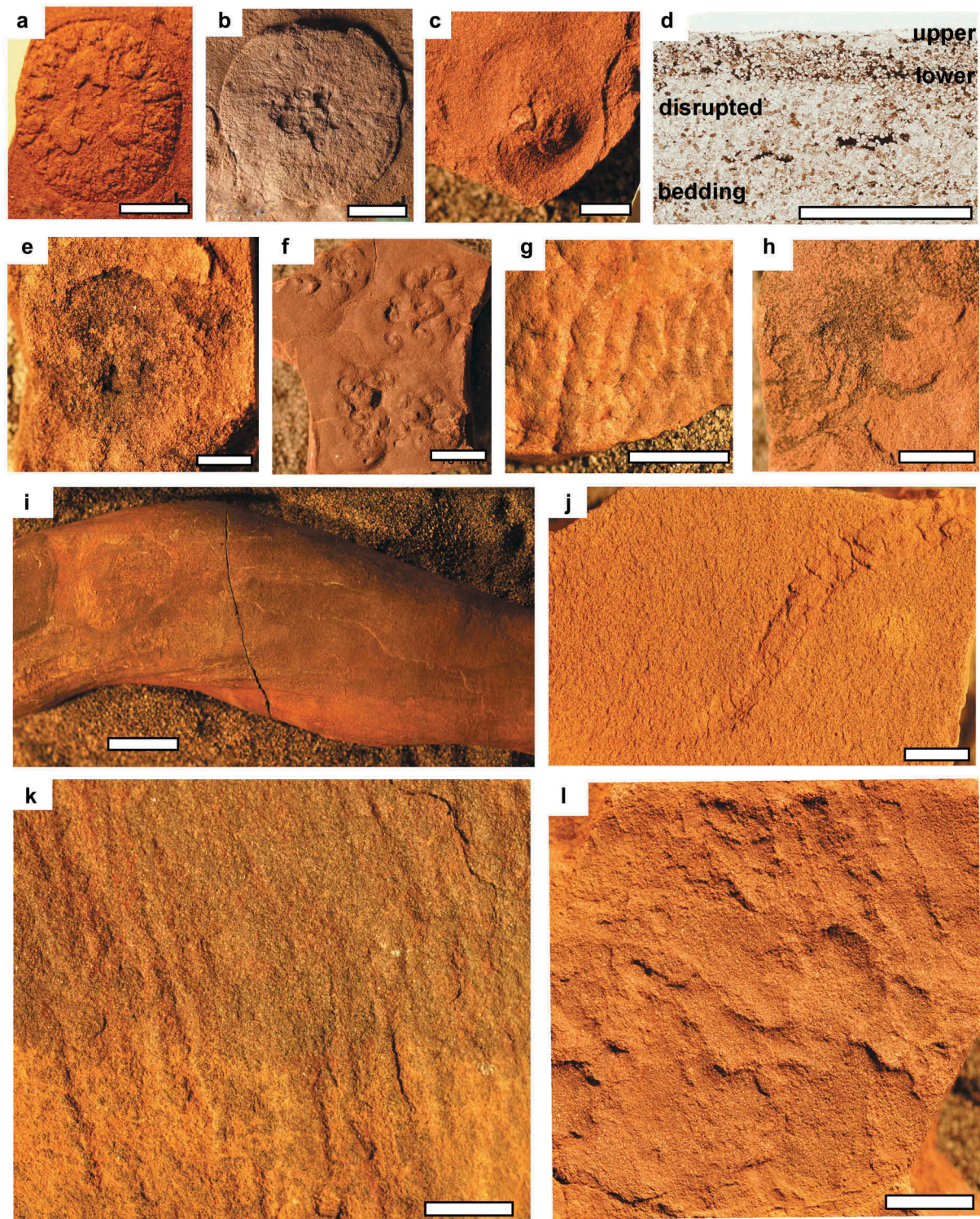


Figure 11. Discoïd and trace fossils from the Cambrian-Ediacaran Arumbera Sandstone and Grant Bluff Formations: (a-e), *Hallidaya brueri*, (f), *Aspidella terranovica*; (g), *Funisia dorothea*; (h), *Archaeonassa fossulata*, (i), *Neantia rhodonensis*; (j), *Lamonte trevallisi*, (k), *Rugalichnus matthewi*, and (l), *Rivularites repertus*, from Grant Bluff Formation at Mt Skinner (a, b, e, f), and Central Mount Stuart (g, k), and from Arumbera Sandstone at Valley Dam (c, d), and Ross River (i, j, l). Holotypes in South Australian Museum are SAM16473 (a) = “*Skinnera brooksi*” holotype, and SAM16464a (b) = *Hallidaya brueri* holotype. Specimens and thin sections in the Condon Collection of the Museum of Natural and Cultural History of the University of Oregon are F117261 (c), F117258 (d), F125275 (e), F125270 (f), F119659 (g), F117276 (h), F117275 (i), F125464 (j), F125436 (k) and F115740 (l). Scale bars are 10 mm.

Quartzite at Nilpena in South Australia (Gehling & Droser 2013). *Aspidella terranovica* has also been recorded from the Cambrian-Ordovician Grindstone Range Sandstone of South Australia (Retallack 2009).

Affinities

Aspidella has been considered a pseudofossil, such as a gas escape structure, spall mark, or nodule (Häntzschel 1975; Boyce and Reynolds 2008). It has also been considered

a microbial colony (Grazhdankin and Gerdes 2007), lichenised fungus (Retallack 2016a), cnidarian polyp (Menon et al. 2013), chiton (Billings 1872), and crustacean (Dawson 1897).

Hallidaya brueri Wade, 1969
(Figures 6(j–m) and 11(a–e))

1969 *Hallidaya brueri* Wade, p.356, pl.68, pl.69, figs 1–5,
1969 *Skinnera brooksi* Wade, p.361, pl.69, figs. 8–12.
2013a *Hallidaya brueri*; Retallack, p.91, fig.2a

Revised diagnosis

Body disc-shaped with high relief and central near-spherical bodies flanked by a rim of radiating ribs. Upper surface preserved as concave hypichnion with three central spherical bodies branching outward to connect with broad radiating depressions. Lower surface preserved as convex hypichnion with up to nine central bodies and fine ribs dichotomising towards the margin. Thick upper and thin lower organic wall in thin section are united by closely spaced vertical septae.

Comments

Hallidaya and ‘*Skinnera*’ are found in the same beds, within the same size range (Figure 9(e)), and have similar fundamental organization of central spherical bodies and radial ribs. New collections revealed a continuum of intermediate forms. Like recently recognised upper and lower views of *Dickinsonia* (Evans et al. 2019a), ‘*Skinnera*’ is here interpreted as an upper view preserved as concave hyporeliefs with coarse quilting extending to and around the margins, but *Hallidaya* as a lower view preserved as concave hyporeliefs with fine quilting radiating to the margin. The central bodies in ‘*Skinnera*’ are large and number only three, but there are up to nine smaller ones in *Hallidaya*, which also has finer radiating and dichotomising ribs on the flange, and perhaps beyond. Our collection includes fossils intermediate in morphology between ‘*Skinnera*’ and *Hallidaya*: with central bodies and marginal flange smaller than ‘*Skinnera*’ and larger than *Hallidaya* (Figure 11(c, e)).

Thin sections of *Hallidaya* also reveal differences between what is here interpreted as upper and lower sides: the body was thick (3 mm), with a thick ferruginised upper wall connected by vertical septae to a thin lower wall, above a substrate disrupted by branching filaments or walls, and then undisturbed horizontal bedding planes below that (Figure 11(d)). This is a similar petrographic structure to that of paratypic specimens of *Aspidella terranova*, and very different from that of non-resistant, easily compacted discoid fossils such as *Nemiana* (Retallack 2016a). The upper surface (‘*Skinnera*’) may also have been effaced and encrusted by processes not affecting the lower surface against the substrate (*Hallidaya*), as noticed for Ediacaran *Ivesheadia* (Liu et al. 2011). *Hallidaya* has priority over ‘*Skinnera*’ by virtue of first mention by Wade (1969).

Comparisons

The upper side of *Hallidaya* (‘*Skinnera*’ of Wade 1969), may be a junior synonym of *Rugoconites enigmaticus*, and they do occur together (Retallack 2013a), but the folds in *R. enigmaticus* are much coarser (Glaessner and Wade 1966; Fedonkin et al. 2008). *Hallidaya* is a complex discoid impression with distinctly different central and marginal portions, unlike problematic discoid fossils reviewed by MacGabhann (2007), and Razumovskiy et al. (2015). Pits in the central area of *Hallidaya* have a threefold symmetry (Hall et al. 2018), but it is not as marked or extended as branching ribs, as in *Albumares*, *Anfesta*, *Arkarua*, *Armillifera*, *Marsonia*, *Persimedesites*, and *Tribrachidium* (Fedonkin et al. 2008; Kumar

and Ahmad 2012, ‘Triradialomorpha’ of Erwin et al. 2011). *Conomedusites lobatus* is also similar but seems to have a fourfold symmetry (Glaessner and Wade 1966). *Bonata septata* and *Tiernavia tiernae* have much greater relief and larger central bodies so that the radially striated marginal zone is almost vertical to bedding, like a fluted cup crammed with touching spheres (Fedonkin et al. 1983, 2008). *Kaisalia mensae* also has a margin of radially diverging ribs, but *Kaisalia* has central area with glide plane symmetry of six tubular features with a zigzag junction down the middle (Fedonkin 1985; Fedonkin et al. 2008).

Measurements

This study includes 16 specimens with diameter 21.6 ± 6.5 (10–35) mm, and only two of them (25 and 35 mm diameter) were finely lined like the original concept of *Hallidaya* (Figure 9(e)). Wade (1969) had 49 specimens of *Hallidaya* with size range 5–50 mm, and 26 specimens of ‘*Skinnera*’ with diameter 4–32 mm. Unlike many other vendobiont fossils, *Hallidaya* has a normal distribution (Figure 9(e)), perhaps indicating determinate growth (Retallack 2007).

Affinities

Hallidaya was at first considered a sea jelly (Wade 1969), although more strongly impressed in the centre than margins, where cnidarian muscle masses are located (Seilacher 1992). Discoid fossils have been interpreted as microbial colonies (Steiner and Reitner 2001; Grazhdankin and Gerdes 2007), but these are mostly preserved as convex hyporeliefs with no body thickness (Retallack 2016a). Simple concentrically banded examples do have the general appearance of microbial cultures on agar medium. Complex radial and infolded patterns also can be found in modern bacterial colonies (Ben-Jacob et al. 1994; Shapiro 1998), but not structures differentiated into central and marginal zones like *Hallidaya* and *Tiernavia* (Fedonkin et al. 1983). Finally, discoids have been compared with lichenised fungi and fungal fruiting bodies (Retallack 1994; Peterson et al. 2003), because of peculiarities of their sessile growth, decay without marginal collapse, and compaction-resistance.

Funisia dorothea Droser and Gehling, 2008
(Figures 6(o) and 11(g))

2008 *Funisia dorothea* Droser and Gehling, p.1661, Fig. 1.
2012 *Funisia dorothea*; Gehling and Droser, p.242, fig.7B.
2013 *Funisia dorothea*; Gehling and Droser, p.449, fig.2E.
2018 *Funisia dorothea*; Gehling et al., p.215, Fig.1C.
2019 *Funisia dorothea*; Droser et al., p.142, Fig.8B.

Comments

Funisia dorothea is a hypichnial ridge (Martinsson 1970), and thus a non-resistant fossil (Wade 1968) of spherical-flattened spheroids, which are arranged in chains, which sometimes dichotomise. Each unit in the chain is distinctly spherical (Figures 6(o) and 11(g)), and twice the size of the trapezoidal quilts of *Noffkarkys* (Figures 6(g,h) and 10). Like the type material from South Australia, the single specimen here from Central Mount Stuart has many crowded individuals on a slab.

Comparisons

Nemiana is also a non-resistant Ediacaran fossil (Retallack 2016a), but *Nemiana* balls are randomly arranged rather than in chains like *Funisia*.

Measurements

Widths of 42 of the subspherical units are 3.7 ± 0.6 (2.6–5.1) mm, small for the range (2–12 mm) observed by Droser and Gehling (2008).

Distribution

Funisia dorothea is only otherwise known from the Ediacaran Ediacara Member of the Rawnsley Quartzite in South Australia (Droser and Gehling 2008).

Affinities

Droser and Gehling (2008) reconstruct *Funisia dorothea* as an erect branching structure similar to the modern seaweed *Hormosira*. They also speculated about ‘dispersed propagation by the production of spats ... almost ubiquitously the result of sexual reproduction’, and thus propose that it was a stem metazoan between sponges and cnidarians. It was easily compressed, a feature shared with non-resistant Ediacaran discoids attributed to microbial colonies (Grazhdankin and Gerdes 2007). It may have lived flat to the substrate in the position in which it is found, and thus like *Nemiana* could be extremely compressed bodies or only the trace imprint of the original body.

Systematic ichnology

Ichnotaxa are traces of activity of organisms, usually with imprecise indication of the trace maker (Seilacher 2007). *Lamonte* is a good example, an Ediacaran trail and shallow burrow (Meyer et al. 2014), but with little indication of exactly what kind of creature made it (Chen et al. 2013). Similarly, the great variety of Ediacaran discoid fossils such as *Nemiana* and *Cyclomedusa* are preserved as positive hyporeliefs, either as a resting trace of the organism, or a collapsed remnant of the non-resistant body (Wade 1968). *Nemiana* may be a fossil of a lake ball of the type now produced by the cyanobacterium *Nostoc* (Retallack 2016a). *Cyclomedusa* may also be a fossil microbial colony (Grazhdankin and Gerdes 2007). In both cases preservation in sandstone precludes exact identification in microbial taxonomy. Similarly, microbially influenced sedimentary structures (MISS of Noffke 2010) reveal little about the microbes involved. The informal classification of Davies et al. (2016) is not used here, because the names are interpretive, and confusingly include both abiotic as well as biotic structures, so is best suited for sedimentological studies. This paper follows conventional ichnotaxonomy based on holotypes and comparison of forms (Stimson et al. 2017). The ichnotaxonomic approach implies biogenicity, but names once considered biogenic such as ‘*Kinneyia*’, can later be demonstrated to be invalid and abiogenic pseudofossils (Häntzschel 1975; Stimson et al. 2017). Higher taxonomy and interpretation of trace fossils are problematic (Seilacher 2007), and species below are listed here in alphabetical order.

Archaeonassa fossulata Fenton and Fenton, 1937 (Figures 6(p) and 11(h))

- 1937 *Archaeonassa fossulata* Fenton & Fenton, p.455, pl.1, fig. 1.
 1997 *Archaeonassa fossulata*; Yochelson and Fedonkin, p.1214, figs. 1,2,4–7.
 1997 *Archaeonassa fossulata*; Johnson et al., p.31, fig.7A
 2002 *Archaeonassa fossulata*; Buatois & Mángano, p.78, fig.7A
 2003 *Archaeonassa fossulata*; Melchor, p.24, fig.4A.
 2005 *Archaeonassa fossulata*; Mángano et al., p.645, fig.2A-B.
 2005 *Archaeonassa* sp.; Jensen et al., p.24, fig.3.
 2005 *Archaeonassa fossulata*; Aceñolaza & Aceñolaza, p.75, fig.7B.
 2007 *Archaeonassa fossulata*; Pazos et al., p.141, fig.3A
 2012 *Archaeonassa fossulata*; Buatois & Mángano, p.17, fig.1C.
 2012 *Archaeonassa fossulata*; Hofmann et al., p.937, fig.7.1
 2013 *Archaeonassa fossulata*; Mángano et al., p.8, fig.11A-B
 2016 *Archaeonassa fossulata*; Buatois & Mángano, p.40, fig.2, 8g-h.

- 2016 *Archaeonassa* cf. *fossulata*; Demircan & Uchman, p.88, figs 4A-B,
 2016 *Archaeonassa* sp.; Arrouy et al., p.5, fig.4D
 2016 *Archaeonassa fossulata*; Carvalho et al., p.48, fig.6.
 2017 *Archaeonassa fossulata*; Luo et al., p.11, fig.4A.

Comments

These are, horizontal shallow burrows and trails with distinctive wide lumpy levees of displaced sediment forming irregular mounds alongside a central depression.

Comparison

Other Ediacaran tubular fossils, *Somatohelix sinuosis* (Sappenfield et al. 2011), *Helminthoidites tenuis* (Buatois and Mángano 2016; Droser et al. 2017; Gehling et al. 2018), and *Archaeichnium* sp. (Droser et al. 2017) are more deeply impressed and lack lateral levees.

Measurements

The central trail measured at 25 points averages 1.4 ± 0.5 (0.7–2.5) mm wide and the levees measured at 25 points are 2.4 ± 0.6 (1.7–3.5) mm wide.

Distribution

This is a common Ediacaran trace fossil from the Ediacara Member of the Rawnsley Quartzite in South Australia (Buatois and Mángano 2012, 2016), and Cerro Negro and Puncoviscana Formations near Salta, Argentina (Aceñolaza and Aceñolaza 2005; Arrouy et al. 2016), but ranges throughout the geological record (Fenton and Fenton 1937; Yochelson and Fedonkin 1997; Johnson et al. 1997; Buatois and Mángano 2002; Melchor 2003; Mángano et al. 2005, 2013; Pazos et al. 2007; Hofmann et al. 2012; Carvalho et al. 2016; Demircan and Uchman 2016; Luo et al. 2019) and can still be recognised among modern traces (Baucon and Felletti 2013; Schatz et al. 2013).

Affinities

Originally regarded as trails of snails (Fenton and Fenton 1937; Buckman 1994; Baucon and Felletti 2013), other possibilities are slug-like molluscs (Jensen 2003), short-bodied arthropods (Yochelson and Fedonkin 1997), flatworms and cerianthid anemones (Demircan and Uchman 2016), and polychaetes (Schatz et al. 2013).

Lamonte trevallisi Meyer et al., 2014 (Figures 6(q) and 11(j))

- 1981 *Planolites montanus*; Jenkins et al., p.203.
 1989 *Planolites ballandus*; Walter et al., p.239, fig.10D,F.
 1992 *Planolites montanus*; Jenkins et al., p.407, fig.5a-b
 1992 *Palaeophycus tubularis*; Jenkins et al., p.407, fig. 5c.
 2013 Unnamed bilaterian trace fossils; Chen et al., figs.2–3,5–6, 8.
 2013b Unnamed bilaterian trace fossils; Retallack, p.383.
 2014 *Lamonte trevallisi*; Meyer et al., p.67, figs 3–8
 2016 tubular fossil; Buatois & Mángano, p.44, figs.2,11.

Comments

Lamonte trevallisi is ‘characterized by horizontal tunnels connected with short vertical burrows and surface trails’ (Meyer et al. 2014), preserved as both a hypichnial ridge or epichnial groove, or a full form (exichnion of Martinsson 1970). One end may be narrow and the other end with a wider bulb or turn-around, separated by about 8–10 cm of more parallel-sided burrow (Chen et al. 2013). It is distinctive in showing arcuate ridges that are convex in the direction of the narrow end, and also beaded levees. Our specimens are

not in grey silty limestone with carbonaceous partings like the type material of *Lamonte* (Chen et al. 2013; Meyer et al. 2014), but in red siltstone with ferruginised partings, like comparable trace fossils from the Arumbera, Central Mount Stuart, and Grant Bluff Formations previously described by Jenkins et al. (1981, Jenkins 1992) and Walter et al. (1989).

Comparison

These tubular trace fossils are unusually short in length and tapered, unlike almost all other tubular trace fossils such as *Archaeonasssa* (see above) which generally run off even large slabs without change in diameter. *Myxomitodes stirlingensis* also has this unusual tapering morphology but has much smaller trails with more pronounced levees (Bengtson et al. 2007).

Measurements

Six complete specimens were 52 ± 15 (33–67) mm long, with minimum width of 2.0 ± 0.6 (1–3) mm. Seven showed maximum widths of 4.9 ± 1.2 (4–7) mm, and five showed a terminal bulb 9.6 ± 9.3 (4–16) mm in diameter. These compare well with diameters of 3–8 mm for the specimens of Chen et al. (2013) and Meyer et al. (2014).

Distribution

In addition to Ediacaran portions of the Arumbera, Central Mount Stuart and Grant Bluff Formations at Valley Dam (Figure 3), Central Mount Stuart (Figure 4) and Neil Hargrave Lookout, documented here, *Lamonte trevallisi* is known from the Ediacaran Shibantan Member of the Dengying Formation in the Yangtze Gorges area of China (Chen et al. 2013; Meyer et al. 2014).

Affinities

Lamonte trevallisi has been considered a trace of a worm-like metazoan (Chen et al. 2013; Meyer et al. 2014), and of the slug (grex) stage of a cellular slime mould, assembling, moving and sporulating from a terminal bulb (Retallack 2013c).

Neantia rhedonensis Lebesconte, 1887 (Figures 6(r) and 11(i))

- 1887 *Neantia Rhedonensis*, Lebesconte, p. 786.
- 1891 *Neantia Rhedonensis*, Lebesconte, p. 202, fig. 2.
- 1975 *Neantia rhedonensis*, Häntschel, 1975
- 2007 '*Neantia*', Seilacher, p. 166, pl.58.
- 2018 *Neantia rhedonensis*, Néraudeau, et al., p.514. Fig.4,5.
- 2018 *Neantia*, Gougeon et al., p.15–16, figs 3,5.

Comments

This elongate fossil with microbial surface texture (MISS of Noffke 2010) is ellipsoidal in cross-section wrapped around sediment infill, unlike other specimens which are elongate two-dimensional skeins of microbially textured rock surfaces.

Comparison

Four species of *Neantia* were proposed by Lebesconte (1887), including *N. reticulata* (occasional wider and rounded bumps between the fine lineations), *N. verrucosa* (abundant bumps in rows between lineations), and *N. deformata* (patchwork of bumpy areas connected by seams). *Neantia rhedonensis* has fine lineations only, with only hints of cross struts.

Measurements

Two specimens were 52 and 72 mm wide, and the longer one was in excess of 244 mm long.

Distribution

Originally recognised from the Brioverian (Ediacaran–Cambrian) of Normandy and Brittany (Lebesconte 1887, 1887), and recorded also from the Cambrian of India (Seilacher 2007), this species was found in the Arumbera Sandstone at Ross River (Figure 2) and Valley Dam (Figure 3), and Grant Bluff Formation at Central Mount Stuart (Figure 4). This ichnospecies is probably very widespread but seldom recognised.

Affinities

Neantia rhedonensis is similar to skeins of cyanobacterial mats seen in modern dried ponds and creeks (Retallack 2012), and the three-dimensional shape of the one figured here (Figures 6(r) and 11(i)) is like a microbial mat rollup (Beraldi-Campesi and Garcia-Pichel 2011). This rollup form is evidence against Cloud's (1968) opinion that *Neantia* was a ripple mark. Seilacher (2007) illustrates an example under a carbonaceous film which he interprets as a microbial mat. Lebesconte (1887) considered it was a colonial animal, perhaps hydroid or cnidarian.

Rivularites repertus Fliche, 1906 (Figure 11(l))

- 1906 *Rivularites repertus* Fliche, p. 46, pl. III, fig. 4.
- 1991 'old-elephant-skin texture'; Fedonkin in Runnegar & Fedonkin, figs 7.5.2B, 7.5.7F.
- 1999 'elephant skin bed-surface texture'; Gehling p.44, fig.3A–B.
- 2000 'dimpled sandstone surface'; Gehling p.76, figs.7d,h.
- 2000 'elephant skin' texture'; Gehling et al., pl.I, figs 1, 5.
- 2008 'elephant skin' structure'; Fedonkin et al. p.110, fig.187.

Comments

Irregularly cracked, rumpled, sutured, and pustulose surfaces of many Ediacaran slabs are widely and aptly called 'old elephant skin', but a formal name of Fliche (1906) is available to characterise this as an ichnogenus. Because the holotype is no longer available the nature and validity of this ichnospecies deserve further attention (Stimson et al. 2017).

Comparisons

Other MISS ichnotaxa such as *Neantia*, *Eoclathrus*, *Rameshia*, and *Rugalichnus* (Häntzschel 1975; Kumar and Pandey 2008; Stimson et al. 2017), all have flexuous, undulating or regularly striated textures, but *Rivularites* has sharp disruptions and cracking.

Distribution

This microbial ichnogenus has been mainly reported from the classic Ediacaran Zimnigory Formation in Russia and Ediacara Member of the Rawnley Quarzite in South Australia (Gehling 2000; Gehling et al. 2000).

Affinities

Comparable modern textures are known from biological soil crusts, and although microbial mats can be torn and disrupted by water-plant growth and grazing, disrupted microbial mats show flakes, rollups, and draped skeins (Noffke 2010), unlike the compact and

complex cracking and healing of *Rivularites repertus* (Retallack 2012).

Rugalichnus matthewi Stimson et al., 2017
(Figure 11(k))

Comments

A complete synonymy and description of *Rugalichnus matthewi* by Stimson et al. (2017) justifies the need for this ichnotaxon for what have widely been reported as wrinkle marks, and also as ‘*Kinneyia simulans*’, although that name is based on undulose joint structures in limestone. *Rugalichnus* in contrast is shale or silt wrinkled like the central layer of corrugated cardboard. These are extensive corrugated surfaces that have in the past been referred to *Arumberia* (Kumar and Pandey 2009; Kolesnikov et al. 2012), but our re-examination of type material of *Arumberia* here shows that it is a discrete and smaller fossil.

Comparisons

Both linear undulations and short sausage-like undulations are included within *Rugalichnus matthewi*, but the short mounds may be better referred to *Eoclathrus* (Häntzschel 1975). *Neantia* is a comparable form with finer linear undulations and cross struts (Gougeon et al. 2018; Neraudeau et al. 2018).

Distribution

Structures identifiable as *Rugalichnus matthewi* have previously been illustrated from the Arumbera Sandstone (Mapstone and McIlroy 2006, fig. 3a, f-g). Similar wrinkle marks range in age from Archaean (3.2 Ga) to modern (Noffke et al. 2006).

Affinities

Modern examples of *Rugalichnus* on tidal flats are generally attributed to cyanobacterial mats, with considerable debate about whether it is a structure of surface or shallow subsurface microbial activity (Noffke 2010).

Ediacaran biostratigraphy

Reconstructions of the newly discovered internal structure of *Arumberia*, *Noffkarkys*, and *Hallidaya* are presented in Figure 12, emphasising similarities in their prostrate habit and internal wall structures. The two views of *Hallidaya* are of the upper effaced to rugulose surface to the right and the lower radially striated surface to the left. All three are assigned to Vendobionta of Seilacher (1992) because of their compaction resistant and chambered structure, although the exact biological affinities of Vendobionta remain controversial (Bobrovskiy et al. 2018, Retallack 2018a; Wood et al. 2019).

The assemblage of *Arumberia*, *Noffkarkys*, and *Hallidaya* described here was a widespread community during both Ediacaran and Cambrian. In addition to Arumbera Sandstone and Central Mount Stuart and Grant Bluff Formations of central Australia, redbeds with *Arumberia* are known from 9 regions: (1) Cryogenian or Ediacaran, Maihar Sandstone, near Maihar and Kroh, India (Kumar and Pandey 2008); (2) late Ediacaran, Bonney Sandstone, Brachina Gorge, Flinders Ranges, South Australia (Bland 1984; Jenkins and Nedin 2007); (3) late Ediacaran Ust Sylvitsa, Chernyi Kamen and Zigan Formations of the Ural Mountains, Russia (Becker 1980, 1985; Bland 1984; Kolesnikov et al. 2012); (4) Ediacaran Moshakov Formation near Artyugino, east Siberia (Liu et al. 2013a); (5) Neoproterozoic, Gibbett Hill Formation of Newfoundland, Canada (Bland 1984); (6) late Ediacaran or Early Cambrian, Synalds, Lightspout, and Bridges Formations near Church Stretton, England

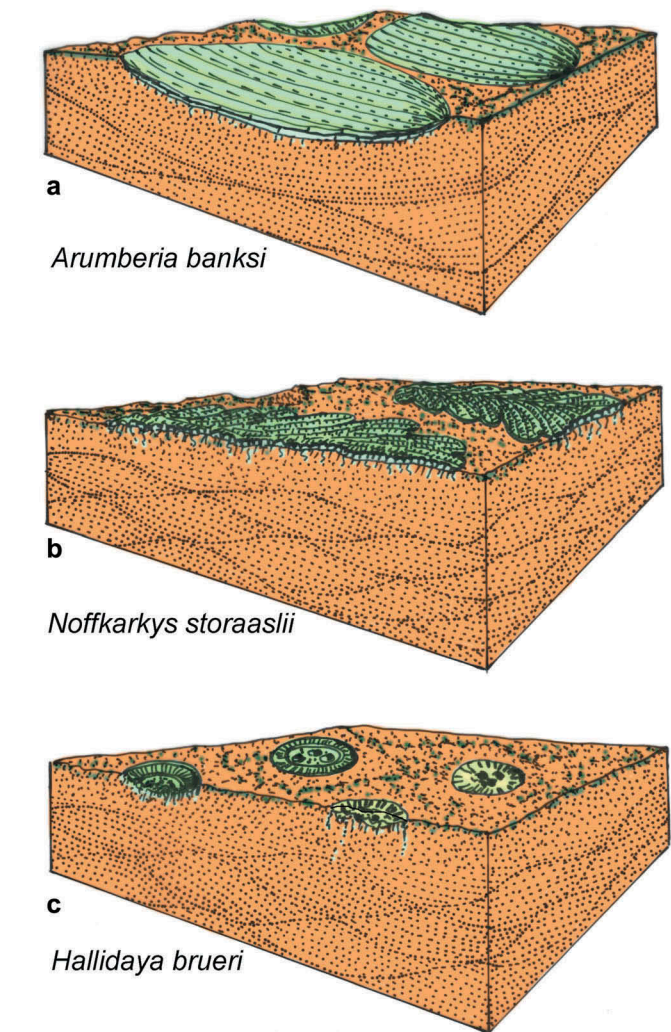


Figure 12. Reconstructions of life position in matrix of *Arumberia banksi* (a), *Noffkarkys storaaslii* gen et sp. nov (b), and *Hallidaya brueri* (c).

(Bland 1984; McIlroy et al. 2005); (7) Early Cambrian, Billy Creek Formation, Flinders Ranges, South Australia (Bland 1984, Retallack 2009); (8) late Ediacaran or early Ordovician, Rozel Conglomerate on the British Channel island of Jersey (Bland 1984; Went 2005); and (9) late Cambrian or early Ordovician Pluorivo Formation near Erquy and Bréhec, France (Bland 1984). An additional three localities for *Arumberia* in Namibia, China and Sweden are uncertain as to identity of the fossils or the facies in which they were found (Bland 1984). Unfortunately, the biostratigraphic significance of *Arumberia* is diminished by discovery that this assemblage was long ranging from Middle Ediacaran (564 Ma) to early Cambrian (527 Ma).

Conclusions

Problematic trace and body fossils are described from Late Ediacaran to Early Cambrian red siltstones of the Arumbera Sandstone, Grant Bluff, and Central Mount Stuart Formations in central Australia. Re-examination of the type material and collection of new material of *Arumberia banksi* reveals that it was a recessive fossil on the bed top, protruding from the counterpart overlying slab, and attached firmly to the substrate by a chambered and diffuse lower surface. Also, re-evaluated was the discoid fossil *Hallidaya brueri*, now redefined to include ‘*Skinnera brooksi*’ as its upper surface. A new frond taxon (*Noffkarkys storaaslii* gen. et sp.

nov.) has distinctive fine, trapezoidal quilts. Three new records for the Arumbera Sandstone and Grant Bluff Formation are *Trepassia wardae*, *Dickinsonia costata*, and *Ernietta plateauensis*. Palaeomagnetic data suggest an hiatus of 26 million years in central Australia at the Ediacaran–Cambrian boundary which is within the Arumbera Formation. Some of this missing time is filled by the Grant Bluff and Central Mount Stuart Formations at Mt Skinner and Central Mount Stuart.

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