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Ediacaran periglacial sedimentary structures

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ABSTRACT

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Ediacaran fossils are sometimes reconstructed as colorful organisms of clear azure seas like tropical lagoons, or as ghostlike forms in deep, dark oceans. Alternatively, they can be envisaged as sessile organisms in frigid soils, to judge from associated Ediacaran periglacial paleosols and tillites. Additional evidence of cool Ediacaran paleoclimate now comes from reinterpretation of two supposed trace fossils: (1) grooves radiating from Ediacaran fossils interpreted as radular feeding traces ("*Kimberichnus*") of supposed molluscs (*Kimberella*), and (2) chains of fossil impressions interpreted as feeding traces ("*Epibaion*") of supposed worms or placozoans (*Yorgia, Dickinsonia*). The grooves are not curved with rounded ends like radular scratches, but with sharp or crudely bifid tips like frost flowers and frost needles extruded from plant debris. Fossil impressions in chains are not sequential feeding stations, but in polygonal arrays, like vagrant lichens and mosses displaced by wind gusts and periglacial frost boils. Thus, neither the taphomorph "*Epibaion*", nor the ice crystal pseudomorphs "*Kimberichnus*" are valid ichnogenera. These newly recognized frost boils, needle ice, frost feathers, frost hair and frost shawls are additions to isotopic and glendonite evidence that the Ediacaran was another period in Earth history when even low paleolatitudes were cool.

Key–words—*Kimberichnus*, *Epibaion*, Periglacial, Vagrant lichens, Frost boils, Needle ice.

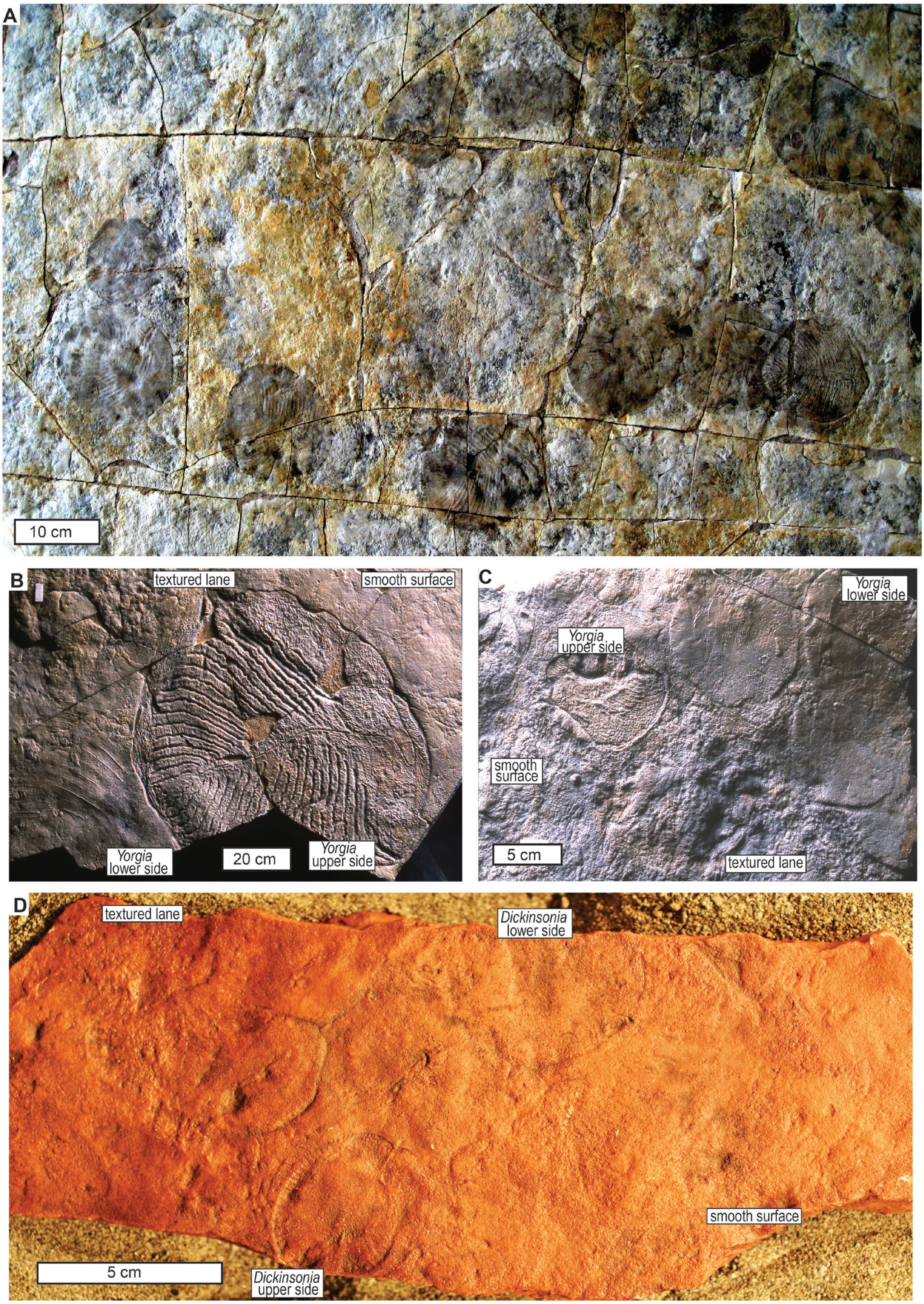
INTRODUCTION

FOSSILS of Ediacaran age have been considered animals and antecedents to the Cambrian explosion of marine invertebrate diversity, and envisaged in gaudy colors and clear blue water of tropical ecosystems (Fedonkin *et al.*, 2007a), or as pale, ghost like denizens of deep, dark waters (Narbonne *et al.*, 2014). In contrast, the discovery of paleosols in host rocks of Ediacaran fossils allows very different interpretations of grey to green creatures living on red to brown soils, and in temperate to frigid paleoclimates (Retallack, 2013b, 2017a). The Gaskiers Glaciation (Retallack, 2013a; Pu *et al.*, 2016) is only one of several glacial advances now documented from the Ediacaran Period (Retallack *et al.*, 2014; Linnemann *et al.*, 2017). This paper documents additional terrestrial periglacial sedimentary structures associated with Ediacaran fossils.

The likely periglacial structures are so distinctive that they have been named as trace fossils with unfortunately interpretative names. Ichnogenus "*Epibaion*", with three species "*E. waggoneris*", "*E axiferus*" and "*E. costatus*", has been regarded as intermittent trails of Ediacaran vendobionts (Ivantsov, 2013), *Yorgia waggoneri*, *Dickinsonia elongata*, and *Dickinsonia costata*, respectively. Ichnospecies "*Kimberichnus teruzzi*" has been interpreted as a scratch–trace of *Kimberella quadrata* (Gehling *et al.*, 2014). "*Epibaion*" has been envisaged as a feeding trail of Ediacaran fossils, such as *Yorgia* and *Dickinsonia*, thought to have moved intermittently like a flatworm or placozoan between patches of marine microbial mat consumed by ciliary abrasion or by osmotrophy (Ivantsov, 2013). "*Kimberichnus*" has been envisaged as molluscan radular scrapes from a long proboscis of *Kimberella* (Gehling *et al.*, 2014). This paper advances alternative hypotheses that "*Epibaion*" and "*Kimberichnus*" are phenomena of vagrant lichens and needle ice, respectively, and provides evidence for periglacial Ediacaran paleoclimate additional to that of other studies (Retallack, 2007; Chumakov, 2009; Vernhet *et al.*, 2012; Tahata *et al.*, 2013; Retallack *et al.*, 2014; Wang *et al.*, 2017).

MATERIALS AND METHODS

In addition to re–examination of museum specimens of "*Epibaon*" and "*Kimberichnus*" in the Paleontological Institute in Moscow and the South Australian Museum in Adelaide, this research included compilation of two comparative data sets. One compilation was measurements of the diameter of fossil circlets of "*Epibaon*", and of modern frost boils of varied substrate grain size (Table 1). A second compilation was


A
10 cm
B
textured lane
smooth surface
Yorgia lower side
20 cm
Yorgia upper side
C
Yorgia lower side
Yorgia upper side
smooth surface
5 cm
textured lane
D
textured lane
Dickinsonia lower side
smooth surface
5 cm
Dickinsonia upper side

measurements of width and length of scratches of two variants (needle and wedge) of "*Kimberichnus*", and of molluscan radular scratches, frost needles and frost flowers (Table 2). Most measurements were taken from digital images with included scales, but fieldwork in South Australia included measurement of sections and cliff to create panels true to scale (Retallack, 2012a).

RE–EXAMINATION OF "*EPIBAION*"

Original description as feeding traces

Remarkable large slabs from the *Yorgia* bed of the Erga beds of the Mezen Formation, at the Zimnie Gory Locality near the Russian White Sea, showed in addition to negative hyporeliefs of the dickinsoniomorph *Yorgia waggoneri* (Fig. 1B, C), chains of less distinct positive hyporeliefs of comparable shape and size (Fig. 1A). Similar arcuate chains of fossils have also been discovered in the Ediacara Member of the Rawnsley Quartzite in South Australia (Retallack, 2007; Evans *et al.*, 2019a), again with deep negative hyporeliefs of *Dickinsonia costata*, but also indistinct positive hyporeliefs (Fig. 1D). In both cases, the fossils are on the base of the sandy bed overlying the original living surface. These remains were interpreted by Ivantsov & Malakhovskyaya (2002) as resting or feeding traces of the underside of motile organisms, broadly comparable with trilobite feeding traces, such as *Rusophycus* (Fig. 2). The indistinct fossils were given an ichnotaxonomic name "*Epibaion*", with species based on associated species of *Yorgia* and *Dickinsonia* body fossils (Ivantsov, 2013). Faint impressions of "*Epibaon*" have also been characterized as "footprints" of *Dickinsonia* (Evans *et al.*, 2019a, b), and as faint impressions of undersides of individuals moved by currents (McIlroy *et al.*, 2009). *Rusophycus* does not show chains of fossils and has deep scrapes from limbs unlike "*Epibaion*", which thus was envisaged to have had a different feeding mode of dorsal osmotrophy or mucociliary feeding on algal mats of the sea floor at intermittent feeding stations (Ivantsov, 2013). Comparable feeding has also been envisaged for a placozoan interpretation of *Dickinsonia* (Sperling & Vinther, 2010).

Problems with feeding trace interpretation

Re–examination of "*Epibaion*" from the Flinders Ranges of Australia and White Sea Coasts of Russia (Fig. 1) confirmed four features noted during the original description (Ivantsov & Malakhovskyaya, 2002), but incompatible with interpretation as trace fossils.

Fig. 2—*Rusophycus latus* from the underside of a bed in the Early Ordovician (Tremadocian), Pacoota Sandstone in Roe Creek, Northern Territory, as an example of an undoubted feeding trace. Ornamental stone from courtyard of Geological Survey of Northern Territory, Core Facility, Alice Springs. The Australian coin to right for scale is 29 mm in diameter.

First, the lanes supposedly reworked by the fossils were originally topographically lower with "old elephant skin texture", but adjacent areas on the same slabs beyond the lanes were smooth and higher (Fig. 1A, D). As noted by Ivantsov & Malakhovskyaya (2002, p.618), "These traces occur on a common bedding surface that includes two different areas. The surface of the first area is flattened, whereas that of the second area is hummocky and complicated with different folds. Body impressions and traces of Proarticulata representatives occur only at the surface of the second area. The contact between areas with different surface patterns is sharp: the hummocky surface is slightly lower compared to the flattened one, and its margins are downwarped and submerged several centimeters into sediments grading into jointing surfaces. Short linear and star–shaped folds on the hummocky surface can be deep." Old elephant skin has been taken as a microbial texture, and thus potential food, and the smooth areas were considered eroded just before cover by sandstone (Ivantsov & Malakhovskyaya, 2002). However, feeding in well–defined lanes to expose underlying sediment should create the opposite effect: smooth lanes but microbially textured fabrics in unaffected domes beyond.

Second, broad domal areas between crowded lanes of slightly overlapping "*Epibaon*" have fewer fossils, with only one or two *Parvancorina* and *Dickinsonia* an order of

←

Fig. 1—Putative Ediacaran trace fossils of animal movement all on undersides of beds and interpreted here as frost boils. (A−C), "*Epibaon waggoneris*" putative trace of *Yorgia waggoneri* (B), here interpreted as inner and external moulds of *Yorgia waggoneri*. (D), "*Epibaion costatus*", putative traces of *Dickinsonia costata*, here interpreted as inner and external moulds of *Dickinsonia costata*. Specimen numbers are 44–686 KP (A, C) in Arkhangelsk Regional Museum and specimen 3993–5024 (B) in the Paleontological Institute Moscow from Yorgia bed, Erga beds, Mezen Formation, Zimnie Gory Locality, and P14359 in South Australian Museum from Ediacara Member of Rawnsley Quartzite in Ediacara Hills (D). Photos are courtesy of Aleksey Nagovitsin and Wikimedia (A, C) and Dima Grazhdankin (B).

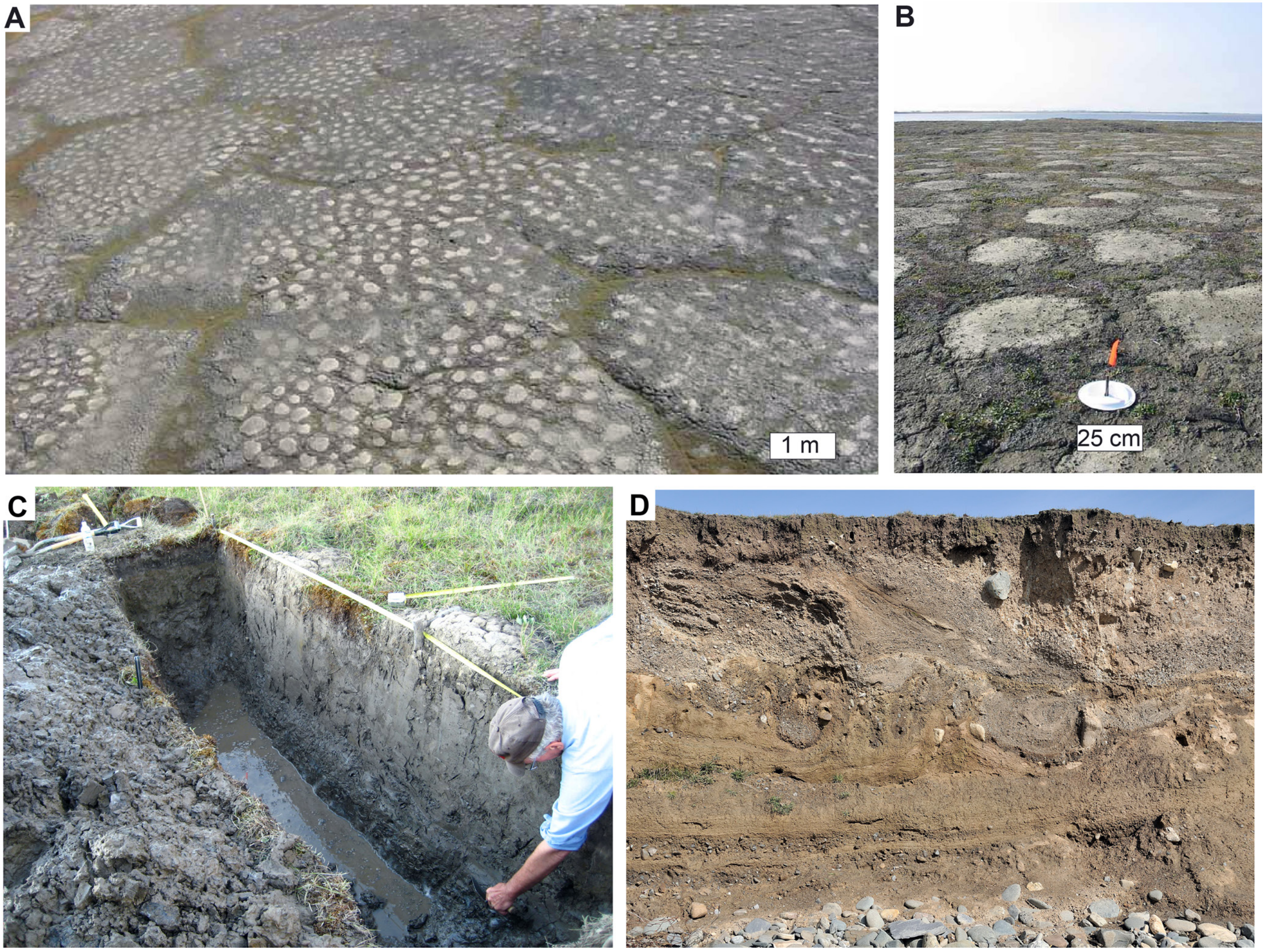


Fig. 3—Modern (A−C) and Quaternary (D) periglacial frost boils and patterned ground. (A–B), Aerial and ground view of sandy loam soil on Howe Island, Alaska (Walker *et al.*, 2011). (C), Glaciolacustrine shales and frost boils near Galbraith Lake, Alaska (Brown & Krieg 1983). (D), 4–m–thick section of Quaternary (late Devensian) till, Tonfanau Beach, Wales (TON4 of Patton & Hambrey, 2009). Photographs by and with permission of D.A. Walker and Alaska Geobotany Center, University of Alaska, Fairbanks (A–B), Nick Bonney (C) and John S. Mason (D).

magnitude smaller than the other fossils on the same slab (Fig. 1A, D). If the smaller fossils of *Dickinsonia* were comparable with the larger ones in feeding on microbial mats it is puzzling that they are not in supposed grazing lanes with "ungrazed" patches, but on untextured areas presumably lacking food. Furthermore, the smaller fossils would have been swept away if the domes had been eroded as proposed by Ivantsov & Malakhovskyaya (2002).

Third, "*Epibaon*" impressions were considered oriented with long axes subparallel as if heading in the same direction (Ivantsov & Malakhovskyaya, 2002), but their orientation is scattered and some are orthogonal to others (Fig. 1A top right). Another way of looking at this orientation is that they are not moving in the same direction, but had their long axes displaced orthogonal to radial expansion of the smooth areas, or were randomly nudged along. Other "*Epibaon*" traces are also randomly oriented (McIlroy *et al.*, 2009; Evans *et al.*, 2019a, b).

Fourth, the body fossils *Dickinsonia* (Fig. 1D), and *Yorgia* (Fig. 1B, C) protruded from the sedimentary surface, so are deep holes in the overlying bed, but "*Epibaion*" had low relief domes with visible segmentation on the overlying bed (Fig. 1), so were shallow holes on the original sedimentary surface (Evans *et al.*, 2019a, b). In all cases the low relief fossils have internal seams unsmudged or blurred by any motion (Fig. 1B-D). While microbial mats could theoretically resist or overgrow smudging, the particular "old elephant skin" of the lanes has high enough relief to make that explanation untenable. "*Epibaion*" is more like remnants of poorly preserved lower structures rather than superficial imprints or feeding traces of a moving organism (Evans *et al.*, 2019a, b). It has long been clear from measurements of *Dickinsonia* that it did not decay by bloating and twisting, but by deflating

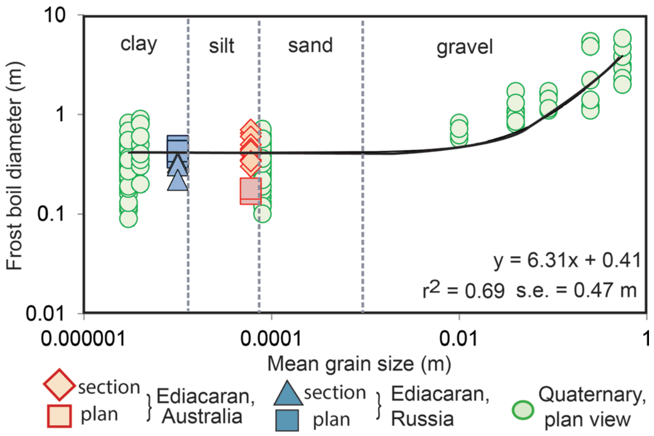


Fig. 4—Variation of size of Quaternary frost boils with mean grain size of soil for comparison with Ediacaran putative frost boils in slabs from Russia (44–686 KP in Arkhangelsk Regional Museum from Yorgia bed, Erga Formation, Zimnie Gory Locality, Russia, n = 4) and Australia (P14359 in South Australian Museum from Ediacara Member of Rawnsley Quartzite in Ediacara Hills, n = 2). The Australian Ediacaran frost boils in plan are illustrated in Fig. 1D and in section in Fig. 5A. Quaternary frost boil data (n = 187) is from Kessler & Werner (2003), Overduin and Kane (2006), Valcárcel–Díaz *et al.* (2006), Vopata *et al.* (2006), Boike *et al.* (2007), and Walker *et al.* (2011).

in thickness while maintaining the same ribbing and outline (Retallack, 2007).

New hypothesis as vagrant lichens

An alternative hypothesis explored here is that "*Epibaion*" slabs represent vagrant lichens or "glacier mice" ("jökla–mýs"), moved by wind on ground ice (Pérez, 1994, 2020; Coulson & Midgeley, 2012; Dickson & Johnson, 2014; Hotaling *et al.*, 2020). Thawing of frozen bases of polsters of moss or lichen allow intermittent lateral movement by gusts of wind. This explanation explains linear arrays of what appear like "footprints" of *Dickinsonia* (Evans *et al.*, 2019a). Other *Yorgia* and *Dickinsonia* are arrayed in rings which may have resulted from radial displacement by frost boils (Fig. 3), also known as frost scars, mud boils, mud circles, mud hummocks, and unsorted polygonal patterned ground (Boike *et al.*, 2008). Such structures explain displacement of both living and dead, partly decomposed organisms, before recolonization by a much younger (smaller) cohort (Fig. 1). Faint imprints of "*Epibaion*" overlap slightly, whereas other specimens of presumed living and sessile *Dickinsonia* show allelopathic reaction rims (Retallack, 2007).

Frost boil refers to patches of soil heaved by ground ice like a skin abscess, rather than boiling temperatures. Such soil cracking and doming displaces growth of lichens and plants to polygonal surrounding troughs (Brown & Krieg 1983; Walker *et al.*, 2011). Many frost boils are much larger than the Ediacaran slabs (Fig. 1), but of appropriate size for the modal grain size of Ediacaran fossils, which was 6 ϕ (16 µm) for both the Ediacara Member (Retallack, 2012b) and Erga beds (Ivantsov, 2013; Retallack, 2020). A compilation of data on the size of Quaternary frost boils (Kessler & Werner 2003; Overduin & Kane, 2006; Valcárcel–Díaz *et al.*, 2006; Vopata *et al.*, 2006; Boike *et al.*, 2008; Walker *et al.*, 2011) shows that frost boils on gravel are an order of magnitude larger than those of silty and clayey soils, which scale well with the Ediacaran fossils (Fig. 4). Smaller frost boils are also found in colder climates than larger frost boils, and on land surfaces that are geologically younger (Walker *et al.*, 2011). Circles rather than stripes are found in topographic gradients of less than 2° (Kessler & Werner, 2003).

Good exposures of the Ediacara Member in the Flinders Ranges of South Australia (Fig. 5A, B) and of the Erga beds of the Mezen Formation at the Zimnie Gory *Yorgia*–"*Epibaion*" excavation (Fig. 5C, D) show cross sections similar to modern and Quaternary cryoturbation. The Australian deformation is high amplitude like well–developed Quaternary involutions (Fig. 3D), but the Russian deformation extends less deeply like modern frost boils on Holocene lake beds (Fig. 3C). The Russian deformation of the *Yorgia*–"*Epibaion*" bed extends laterally 300 m and is described by Leonov *et al.* (2007, p. 23) thus, "The productive surface is cragged, fine and medium–hilly, with big, isometric in plan depressions. The surface changes in lateral direction to grained surface with plucking furrows, contained no soft–bodied remains." The Australian deformation level (1.8 m in Fig. 5A) can be traced laterally 100 m in Brachina Gorge, but is at the same stratigraphic horizon over 50 km from the Ediacara Hills south to Bunyeroo Gorge. Both Russian (Dzik, 2003; Leonov *et al.*, 2007) and Australian (Gehling, 2000; Retallack, 2012a) sections include soft sediment deformation on multiple horizons. These Ediacaran soft sediment deformations are comparable with frost boils seen in Quaternary cliffs (Fig. 2D; Patton & Hambrey, 2009) and excavations (Fig. 3C; Johnsson, 1963; Brown & Krieg, 1983; Hamilton & Ashley, 1993; Horváth *et al.*, 2005). Minor offsets and tension gashes in outcrop obscure the lithified Ediacaran examples (Fig. 5), just as shovel smoothing of pit walls and minor gullying obscure the Quaternary examples (Fig. 3). Other Ediacaran periglacial structures in South Australia include thufur mounds and tillites (Retallack *et al.*, 2014). Frost boils show rheid deformation, whereas thufur mounds are brecciated and have brittle uplifted slabs (Retallack, 2011, 2012a).

Ediacaran intrastratal deformation from Australia has previously been called "load casts" (Jenkins *et al.*, 1983) or "ball and pillow structure" (Gehling, 2000), and, in Russia, "plastic deformation of layered sand under load" (Dzik, 2003) and "convolute bedding structures" (Leonov *et al.*, 2007). Thus, they were interpreted as subsurface failure of a thixotropic layer due to water pressure variation or seismic shaking. Unlike seismically induced or gravity–driven load structures, mud volcanoes, sand blows, contorted lamination, dykes and breccia (Wheeler, 2002; Owen, 2003),

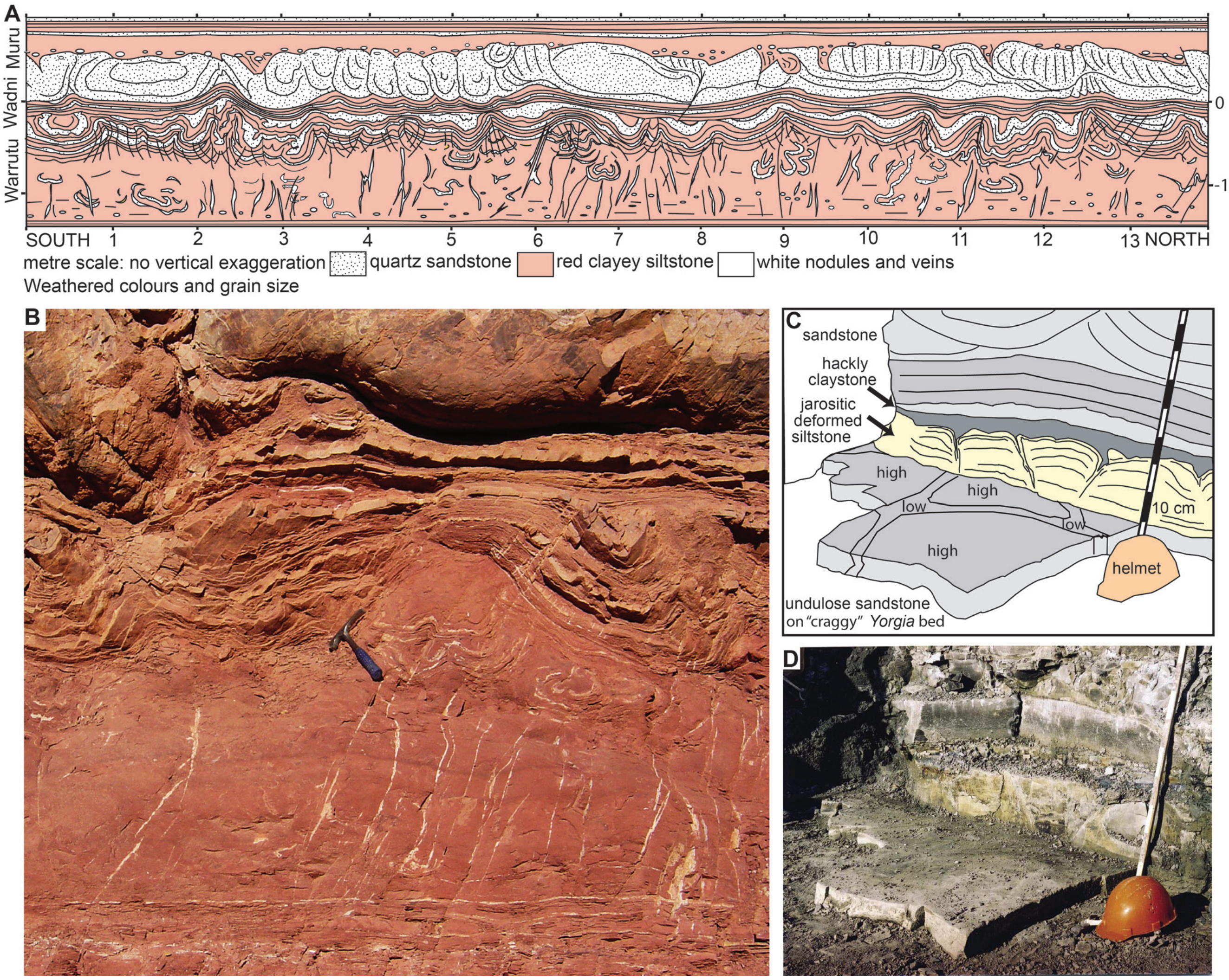


Fig. 5—Ediacaran high amplitude frost boils in section from the Ediacara Member of the Rawnsley Quartzite in Brachina Gorge, South Australia (A−B) and low amplitude frost boils from the "*Yorgias*"–"*Epibaion*" horizon of the Erga beds at Zimnie Gory, Russia (C−D). Only 5–8 m north in A is shown in the detailed photograph B. Data and images are from Leonov *et al.* (2007) and Retallack (2012a).

the distinctive deformation fades downward in multiple generations from the undulating surface to undeformed layers below. The Australian example shows at least four episodes of convolution more poorly preserved from the top down, and each onlapped by continuing sedimentation during deformation (Fig. 5A, B). These features are top–down alterations, not bottom–up convolution of an unstable layer. Furthermore, they lack injected dykes of breccia or sand from below as in seismic 'sand blows' (Wheeler, 2002). Other features ruling out load structures are the brittle failures ("stretch marks" of Dzik 2003 and "synaeresis cracks" of Gehling, 2000) associated with this deformation and tearing apart fossils such as *Dickinsonia*. Thin sections of Dzik (2003, his fig. 3A) and Retallack (2012a, his fig. 9A) show that these were not just shallow synaeresis or stretch dilations, but vertical, strongly–tapering, tension gashes and cracks, like those created by ice in ancient (Fig. 5A, B) and modern frost boils (Fig. 3A−C). This combination of brittle alternating with fluid deformation is evidence against purely fluid load casting (Gehling, 2000). It is also unlike mud cracks (Weinberger, 2001), or brittle mukkara structure of Vertisol soils from desiccation cracking and fragmentation (Retallack, 1986).

Another curious observation explained by the frost boil hypothesis is why cohorts and imprints of large *Yorgia* and *Dickinsonia* are displaced into arcs, but small *Dickinsonia*, *Praecambridium* and *Parvancorina* are scattered randomly on the same slabs (Ivantsov & Malakhovskyaya, 2002). Frost boil activity is most pronounced during years of unusual freeze–thaw, and most affects perennial long–lived sessile creatures such as lichens and mosses (Walker *et al.*, 2011). Some *Dickinsonia* individuals lived for many thousands of years, judging from relative soil development under

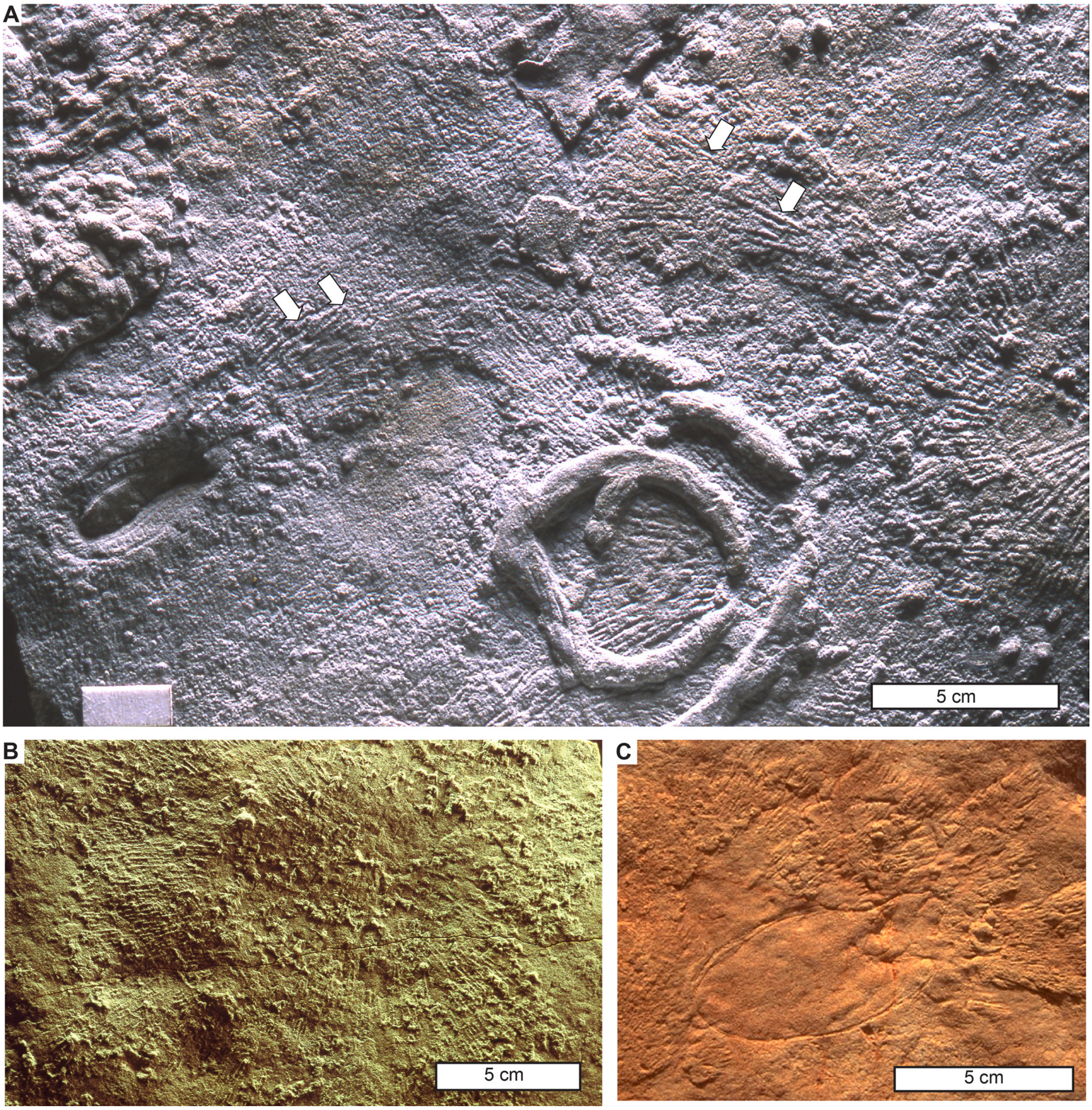


Fig. 6—Putative Ediacaran radular scratch marks, "*Kimberichnus teruzzi*", of the supposed mollusk *Kimberella quadrata*, all on undersides of beds and interpreted here as needle ice casts. Arrows in panel A show needles with both hollow and covered ends, as evidence that they were oblique to surface: one end under the mud and the other end protruding. (A), 3493/5137 Paleontological Institute, Moscow from Zimnie Gory Locality, Zimnie Gory Formation. (B), 3993/5619 Paleontological Institute, Moscow from Solza River Locality, Zimnie Gory Formation. (C), P35657 South Australian Museum from Brachina Gorge, Ediacara Member of Rawnsley Quartzite. Photos A−B courtesy of Dima Grazhdankin.

fossiliferous surfaces (Retallack, 2013b). Small *Dickinsonia*, *Praecambridium* and *Parvancorina* may represent youthful cohorts not yet culled by a lethal freeze–thaw season. Gutters between the frost boils accumulated imprints and dead polsters of the oldest cohorts of vendobionts by this hypothesis, blown along these depressions.

The view of vendobionts as sessile organisms on cold desert soils favoured here (Retallack 2013b, 2019) has been considered falsified by evidence of high energy subaqueous deposition (by Zakrevskaya, 2014; Evans *et al.*, 2015; Tarhan *et al.*, 2015; McMahon *et al.*, 2020). These high energy events are known to have been unidirectional from knocked–down fronds and partial erosion of *Dickinsonia* oriented in the same

Fig. 7—Modern limpet radular scraping of cyanobacteria from siltstone of Kimmeridge Bay, Dorset, UK. Photo courtesy of Jessica Winder.

direction (Evans *et al.*, 2015, 2019a, b; Tarhan *et al.*, 2015; Droser *et al.*, 2019). Thus they are more like unidirectional floods (Retallack, 2017a, 2019) than multidirectional storm currents which produce hummocky bedding in shallow seas and lakes (Dott & Bourgeois, 1982; Eyles & Clark, 1986). Re-examination of sedimentary facies of the Ediacara Member reveals flooding alternating with thin wind–drift layers (interflag sandstone laminae), and occasional upper flow regime flooding (massive facies: Retallack, 2019). Other eolian features documented in the Ediacara Member include climbing translatent stratification, setulfs, and wind dissected ripples (McMahon *et al.*, 2020). Low boron content of both Russian and Australian *Dickinsonia* are evidence of non–marine environments (Retallack, 2020). Nor is the idea of vendobionts as sessile and long–lived contradicted by sterols taken as evidence that *Dickinsonia* was a mobile animal (Bobrovskiy *et al.*, 2018), because cholesterol is also found in glomeromycotan fungi and red algae (Retallack, 2020), which are known in Ediacaran rocks from spores, vesicles (Retallack, 2015) and permineralized fragments (Yuan *et al.*, 2005). New examples of "intravital damage" of *Dickinsonia* from Russia (Ivantsov *et al.*, 2020) are additional evidence of lichen–like growth of terminal meristems and of frost damage. The disrupted zones have shrunken and wrinkled, and separate one or two regrown axes. The shrunken and wrinkled damage zone is most like frost damage of lichens (Benedict, 1990, 2009) and plants (Silberbauer–Gottsberger *et al.*, 1977), and unlike scars (Niessen *et al.*, 1999) or limb regrowth of animals (Birnbaum & Alvarado, 2008). The double axes of regrowth are like a system of apical and lateral meristems as in lichens (Hammer, 2000) and plants (Sugimoto *et al.*, 2011), rather than subterminal growth zones of segmented animals (Shen *et al.*, 2014; Dunn *et al.*, 2017).

RE–EXAMINATION OF "*KIMBERICHNUS*"

Original description as backhoe proboscis scraping

The Ediacaran fossil *Kimberella* (Fig. 6A, C) has been regarded as an early mollusc (Fedonkin & Waggoner, 1997), and associated scratches on the slab were considered feeding traces by Seilacher *et al.* (2005) and Seilacher (2007). These long (up to 3 cm) and narrow hyporelief ridges were formally named ichnogenus "*Kimberichnus*" by Ivantsov (2013), but bear no resemblance to the serried ranks of short scrapes created by modern molluscs (Fig. 7: see also Gehling *et al.*, 2014), which are better referred to the ichnogenus *Radulichnus* (Dornbos *et al.*, 2004). These differences in the traces led to the proposal of a feeding mechanism unique to *Kimberella*, by means of a bifid radula at the end of an extensible proboscis used to scrape microbial mats backwards in the manner of a mechanical backhoe (Gehling *et al.*, 2014).

Problems with backhoe proboscis interpretation

Re–examination of "*Kimberichnus*" from the Flinders Ranges of Australia and White Sea of Russia (Fig. 6) confirmed four problems with the radular scraping hypothesis of Gehling *et al.* (2014).

First, "*Kimberichnus*" are not grooves scraped into the surface with ploughed and overturned margins (Figs 2, 7), but needles skewering the surface obliquely (Fig. 6). The needles commonly show a hollow part (thus immersed in the surface), a tubular part (a groove in the surface but ridge on the cover slab) and a covered part (thus emergent from the surface: arrows in Fig. 6A). Some needles are wide (wedge morph) and considered paired by Gehling *et al.* (2014), although pairing is difficult to see in closely spaced examples (Fig. 6C). Others are narrow with sharp ends and screw dislocations in which the edges twist along their length (arrows of Fig. 6A). Furthermore, many "*Kimberichnus*" grooves are criss–crossing rather than strictly aligned (Fig. 6A). Rather than the expected short ploughing of a reflexed proboscis, the needle morph of "*Kimberichnus*" has continuity over lengths of as much as 31 mm, and each appears inserted outwards over and under others for about twice the length of *Kimberella* or its imagined proboscis.

Second, grooves of "*Kimberichnus*" not only radiate from *Kimberella* fossils that protruded from the original sedimentary surface (Fig. 6A, C). They are just as likely to radiate from fissures, including radial cracks around uplifted clods (concentric ridges in bed cast of Fig. 6A), and divots in the sedimentary surface (small pelletoidal casts of Fig. 6B). Of 13 specimens of "*Kimberichnus*" illustrated by Gehling *et al.* (2014) only six are associated with *Kimberella*, and seven radiate from sedimentary irregularities.

Third, *Kimberella* with a supposed molluscan muscular foot left no trace of relocation in any of the known specimens

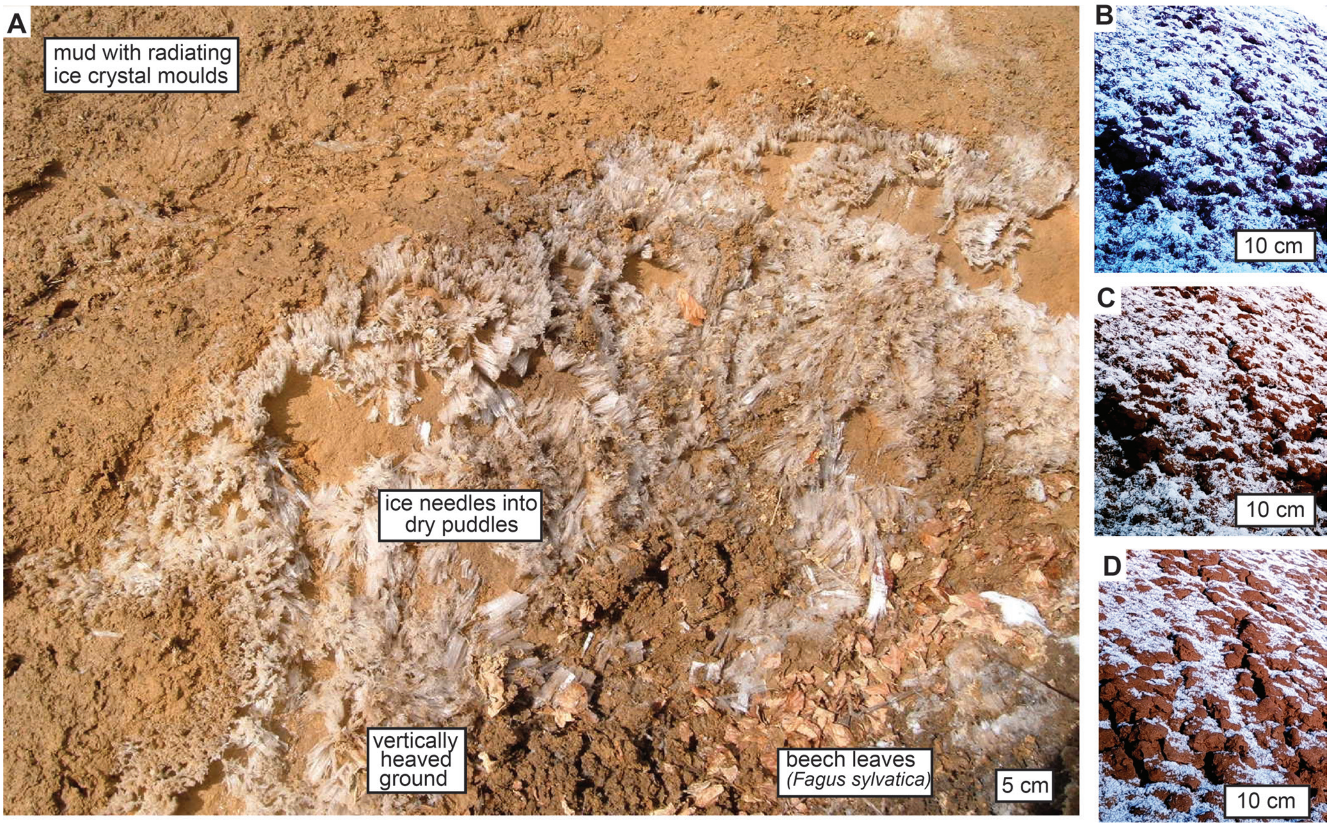


Fig. 8—Horizontal needle ice: (A), ice moulds (upper left) within mud and needles (lower right) within small dry puddles on a mountain trail at the ski resort of Postavaru, Romania (25 February 2007) courtesy of Stefan Puscasu; (B–D), formation and dissolution of needle ice in badlands of Ruby Basin, 6 km southeast of Painted Hills Oregon, respectively at 7.12 a.m. 24 February 2018, 7.42 a.m.24 February 2018 and 8.32 a.m. 26 February 2018, courtesy of Noah P. Kannegeisser.

of "*Kimberichnus*", nor on less microbially encrusted surfaces lacking "old elephant skin". Supposed escape traces of *Kimberella* (Fedonkin *et al.*, 2007b) are merely elongate individual fossils, not an inverted trail, nor cemented tunnel roof. Although it has been argued that the microbial mat was too firm or constantly renovated to preserve a trace (Ivantsov, 2013; Gehling *et al.*, 2014), this did not prevent preservation of other trails with levees, sometimes feeding on *Dickinsonia* (Gehling & Droser, 2018).

Fourth, there is never any indication of smudging or bulging in impressions of "*Kimberichnus*" comparable with scrapes of the trilobite trace fossil *Rusophycus* (Fig. 2). The low relief "*Kimberichnus*" needle casts were not only filled downward, but penetrate upward into overlying sandstone, and are thus similar to poorly preserved body fossils bridging irregularities in the substrate (Fig. 6A, B).

Alternative hypothesis as needle ice

"*Kimberichnus*" can also be interpreted as casts of needle ice crystals in horizontal sprays within clayey or microbial surfaces (as in the upper left part of Fig. 8A). A variety of ice forms also protrude horizontally from the margins of small puddles (Fig. 8A center), and also from organic debris, biological soil crust pinnacles, and soil pieces proud of the soil surface (Fig. 8C–D). Nucleating Ediacaran objects included *Kimberella*, which rose above the surface, and may have a prominent spray of needles emanating from one end (Fig. 6A). Such sprays may have been extruded from *Kimberella* cavities, but that does not mean they were created by living *Kimberella*, because modern needle ice extrudes from particular hollows of dead plant debris (Fig. 9A–E). Ediacaran horizontal sprays from nucleating fossils have attracted most attention (Seilacher, 2007; Gehling *et al.*, 2014), but vertical dislocation of large rounded clods are also found preserved as ring cracks (Fig. 6A), as well as many small displaced clods (Fig. 6B). Elevation of small soil clods on vertical palisades of ground ice, and uplift of larger clods by ice palisades are common in modern needle ice (Fig. 9C). Furthermore, ice palisades nucleate from shallow depths of supercooling to leave rounded holes, now the round–bottomed casts of ring cracks (Fig. 6A), and not sharply tapering desiccation cracks (Weinberger, 2001). Ivantsov's (2011) observation that Ediacaran grooves of "*Kimberichnus*" are not found within arcs of "*Epibaon*" is explained by their different mechanisms of formation. Frost boils form in frigid climates (Walker *et*


A
1 cm
B
1 cm
C
1 cm
D
1 cm
E
1 cm
F
1 cm

al., 2011), whereas needle ice is an ephemeral product of local weather events in frigid to cool temperate and alpine climates (Lawler, 1988). Thus frost boils and needle ice are most commonly found separately, but can occur together in modern soils (Walker *et al.*, 2011).

Measurements of the length and width of Ediacaran scratches revealed two distinct size populations representing needle and wedge morphs, both an order of magnitude larger than modern molluscan radular scratches (Fig. 10). A wide array of crystal forms and sizes can be recognized in ground ice: frost flowers (Fig. 9A; Mason *et al.*, 1963), frost needles (Fig. 9B; Mason *et al.* 1963), frost palisades (Fig. 9C; Lawler 1989, 1993), frost hair (Fig. 9D; Hillefors, 1976; Wagner & Mätzler, 2008), frost shawls (Fig. 9E; Herschel, 1833; Matthews, 1999), and frost feathers (Fig. 9F; Arakawa 1955). Frost flowers may be represented by the wedge morph of "*Kimberichnus*" (Fig. 6C), frost needles by the needle morph of "*Kimberichnus*" (Fig. 6A, B), and frost palisades displacing divots and small clods are also recognizable (Fig. 6A, B). By this model, the mound of *Kimberella* (Fig. 5C) and the central nubbin of "*Coronacollina*" (Clites *et al.*, 2012) were hydrated internally, but their observed marginal folds focused horizontal needle growth into cold air and surrounding slimy clay or soil (as in Fig. 9A–B). Other patterns of modern ice needles shown in Fig. 9 also are known from other Ediacaran fossils. Palisade needles (Fig. 9C) were misidentified as *Pteridinium* by Dyson (1985), according to Jenkins (1986). The frost feather pattern (Fig. 9F) may have been misinterpreted as spicules in "*Palaeophragmodictya*" (Gehling & Rigby, 1996, Serezhnikova, 2007). Different kinds of Ediacaran fossils had different propensities for nucleation of particular ice crystal forms, and many Ediacaran fossils did not nucleate needle ice.

Ice crystal casts are known from a geological record back to Neoproterozoic, and include simple isolated needles without preferred orientation within shales (Talbot, 1981; Bandel & Shinaq, 2003). Similar ice needles have been observed to form under water in Arctic Oceans (Riemnitz *et al.*, 1986). More like "*Kimberichnus*" are ice needle sprays, ice feathers, and ice shawls illustrated from Ordovician periglacial shales of West Africa (Denis *et al.*, 2007; Nutz *et al.*, 2013; Girard *et al.*, 2015). Similar modern ice crystal sprays have been found in modern tidal flats (Dionne, 1985), and muddy lake margins (Mark, 1932), and may require microbial mats or microbial earths for nucleation. Experimental studies have

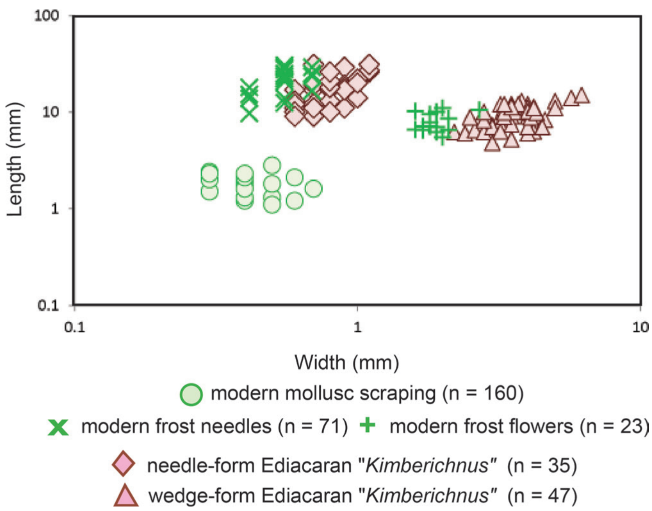


Fig. 10—Measurements of length and width of scratch marks from the radulae of modern marine molluscs (mainly limpets and chitons) on siltstone at Point Loma near San Diego, California (see Dornbos *et al.*, 2004), are very distinct from length and width of frost needles (Fig. 9B) and flowers (Fig. 9A), and comparable fossils from the Ediacara Member of the Rawnsley Quartzite in South Australia, including the needle–morph of "*Kimberichnus*" (South Australian Museum P35663 from Mt Scott) and the wedge–morph of "*Kimberichnus*" (South Australian Museum P35651a from Bathtub Gorge, see Gehling *et al.*, 2014).\

shown that ice needle molds are only preserved in matrix of grain sizes finer than 0.4 mm (Allan, 1926). The Ediacaran examples described here are oriented in sprays controlled by extrusion from other objects, like modern needle ice (Fig. 8), frost flowers (Fig. 9A), frost hair (Fig. 9D), and frost shawls (Fig. 9E). The needle ice impressions described here were all associated with "old elephant skin" surfaces with healed and sutured cracks diagnostic of biological soil crusts (Retallack, 2012a). Thus they penetrated tough biomats enriched in clay (Retallack, 2013b), which preferentially preserved them as casts when the ice melted and the matrix hardened as it dried out, as observed in clayey soils today (Fig. 8).

Needle ice is also known as pipkrake, frost ribbons, and frost whiskers, and is formed when cold–front air encounters soil or plant debris saturated previously by rain, so that needles protrude many millimetres into cold air, water or mud from the saturated zone (Lawler, 1989, 1993). Much needle ice is vertical from saturated ground, but subhorizontal splays protrude from mounds of earth, or erect parts of

←

Fig. 9—Varied forms of ground ice proud of the substrate. Each of these delicate structures may have been found in Ediacaran paleosols as the basis for what are considered here invalid genera: *Kimberichnus* (Gehling *et al.*, 2014), *Coronacollina* (Clites *et al.*, 2012), and *Palaeophragmodictya* (Gehling & Rigby, 1996). (A), Frost flower from roadside pond near Frisco, Colorado (2 May, 2011). (B), Frost needles at edge of pond in Chugach State Park, near Eagle River, Alaska (29 October 2011). (C), Frost palisades uplifting soil clods southwest of Granges–sur–Vologne, France (28 December, 2008). (D), Frost hair extruded from stick at Mt Maxwell, British Columbia (28 December, 2003). (E), Frost shawl on grass near Shepherdsville, Kentucky (2 December, 2006). (F), Frost feather on water surface, Dillon Reservoir, Colorado (4 December, 2011). By and with permission of Robert Berwyn of Summit County Citizen's Voice (A, F), Ray Bulson of Wilderness Visions (B), and Thomas Bresson of Belfort, France. Others from Wikimedia Commons.

plants (Herschel, 1833; Hillefors, 1976; Matthews, 1999). Subhorizontal frost needles and feathers also form at the surface of ephemeral ponds (Arakawa, 1955; Mason *et al.*, 1963). During the Ediacaran, there were no vascular land plants, but a variety of quilted fossils (Seilacher, 1992, 2007) existed to nucleate ice crystals larger than modern molluscan radular scrapes (Fig. 10). Such shallow ephemeral ponds and soil flooding are compatible with interpretation of the sedimentary beds as paleosols (Retallack, 2013b).

IMPLICATIONS FOR EDIACARAN PALEOCLIMATE

Frost boils, and other unsorted polygons form in climates with mean annual air temperature of 0 to –4 ºC, mean air temperature of coldest month –8 ºC, mean air temperature of warmest month 5 to 9 ºC, freezing index of 1000 to > 7000 ºC days per year, thawing index 1000–2000 ºC days per year, with rapid temperature drops in moderately continental settings (Williams, 1986). Their formation is aided by fine grain size and soil organic matter, documented to have increased during Ediacaran soil formation (Retallack, 2012b, 2013b).

Needle ice is common today in a variety of temperate climates from 48–64º north latitude and 34–78º south latitude at sea level, but also is found in tropical regions at elevations of 3400–5300 m (Lawler, 1988). This interpretation of "*Kimberichnus*" as crystal pseudomorphs of needle ice requires molding by clay–organic matrix, which has been inferred for "old elephant skin" substrates in both Russia and South Australia (Retallack, 2012a), and demonstrated by geochemical study of paleosols beneath fossiliferous surfaces in South Australia (Retallack, 2012b, 2013b). Horizontal needle ice is most common in water–saturated lowlands, including surficial ephemeral ponds (Fig. 8).

Needle ice and frost boils can now be added to a variety of other periglacial features common in Ediacaran paleosols of South Australia (Fig. 5), including loess, thufur mounds, and weak chemical differentiation of paleosols (Retallack, 2007; Retallack *et al.*, 2014). There are also three stratigraphic levels in the Ediacaran stratotype section of South Australia with dropped pebbles, which can be correlated with successive international Gaskiers (580 Ma), Fauquier (571 Ma), Bou–Azzer (566 Ma) and Hankalchough (551 Ma) glacial advances (Chumakov, 2009; Vernhet *et al.*, 2012; Retallack *et al.*, 2014). Such indications of cold paleoclimate including icebergs are notable because of their low paleolatitude: 11.8 ± 2.5º for the Brachina Formation of South Australia (Schmidt & Williams, 2010). The Ediacaran White Sea Group of Russia, with its evidence of frost boils and needle ice (Fig. 1A-C, 6A, B), was also at low paleolatitudes of 23.3 ± 4.8º (Popov *et al.*, 2002). Furthermore, these Ediacaran frosty paleoclimates were at sea level, but needle ice and frost boils are unknown at such low latitudes today (Lawler, 1988, Walker *et al.*, 2011). Paleosols and paleokarst at paleoelevation of 1 to 500 m are known in the Wonoka Formation of South Australia (Retallack *et al.*, 2014), but the Ediacara Member with indications of frost includes other intervals of intertidal facies (Retallack, 2012b, 2013c), so accumulated near sea level. The fossils from the Mezen Formation of Russia are in upper shoreface facies of a delta (Grazhdankin, 2004).

Ediacaran halite inclusions are evidence of tropical seawater temperatures of only 23.1 ± 5ºC (Meng *et al.*, 2011), and cool tropical waters also are indicated by relatively high $\delta^{18}O$ values of Ediacaran marine carbonates (Tahata *et al.*, 2013). Ikaite pseudomorphs (glendonites) indicative of cold (–1.9 ºC to +3 ºC) marine waters have been reported from low paleolatitude Ediacaran rocks of China (Wang *et al.*, 2017). Cold temperatures at sea level in tropical paleolatitudes are evidence of Ediacaran paleoclimates very different to modern. Although not as cold as the Cryogenian Period, with its unusually extensive glaciers and Gelisol paleosols (Williams, 1986; Retallack *et al.*, 2015), the Ediacaran Period was also a globally cold interval of Earth history.

IMPLICATIONS FOR TAXONOMY

"*Epibaon*" and "*Kimberichnus*" have been proposed as trace fossils of Ediacaran large animals, but this study advances alternative hypotheses of them as artefacts of vagrant lichens and of needle ice (Fig. 11). By this view, "*Epibaon*" represents poorly preserved or ventral impressions (taphomorphs) of organisms with prior names of *Dickinsonia* and *Yorgia,* and "*Kimberichnus*" constitutes inorganic casts (pseudomorphs) of needle ice occasionally radiating from hollow *Kimberella*. Thus neither *"Epibaon*" nor "*Kimberichnus*" are regarded as valid ichnogenera. As outlined above, other invalid genera may have been ice needles ("*Coronacollina*" of Clites *et al.*, 2012), and frost feathers ("*Palaeophragmodictya*" of Gehling & Rigby, 1996).

Reinterpretation of "*Epibaion*" and "*Kimberichnus*" as non–motile forms supports a range of evidence that many iconic Ediacaran unskeletonized fossils were not marine animals. This now includes a variety of new observations beyond the periglacial structures outlined here. Seilacher (1992, 2007) first outlined features of these fossils precluding animal affinities, such as segmentation offset on midlines (thus not annelid segments), and lack of marginal musculature in discoids (thus not jellyfish). Segmentation offsets remain indisputable for *Yorgia* (Ivantsov, 2011, 2013), but a few *Dickinsonia* have since been found with segments apparently crossing the midline (Evans *et al.*, 2017). Discoids are no longer regarded as jellyfish, but as microbial colonies (Grazhdankin & Gerdes, 2007) or holdfasts (Tarhan *et al.*, 2015). Putative Ediacaran sea pens did not have separate polyps added from the base, but were complex fractal sheets growing from the apex (Antcliffe & Brasier, 2007). Putative Ediacaran sponges lack any diagnostic features of Porifera (Antcliffe *et al.*, 2014). Putative Ediacaran foraminifera added

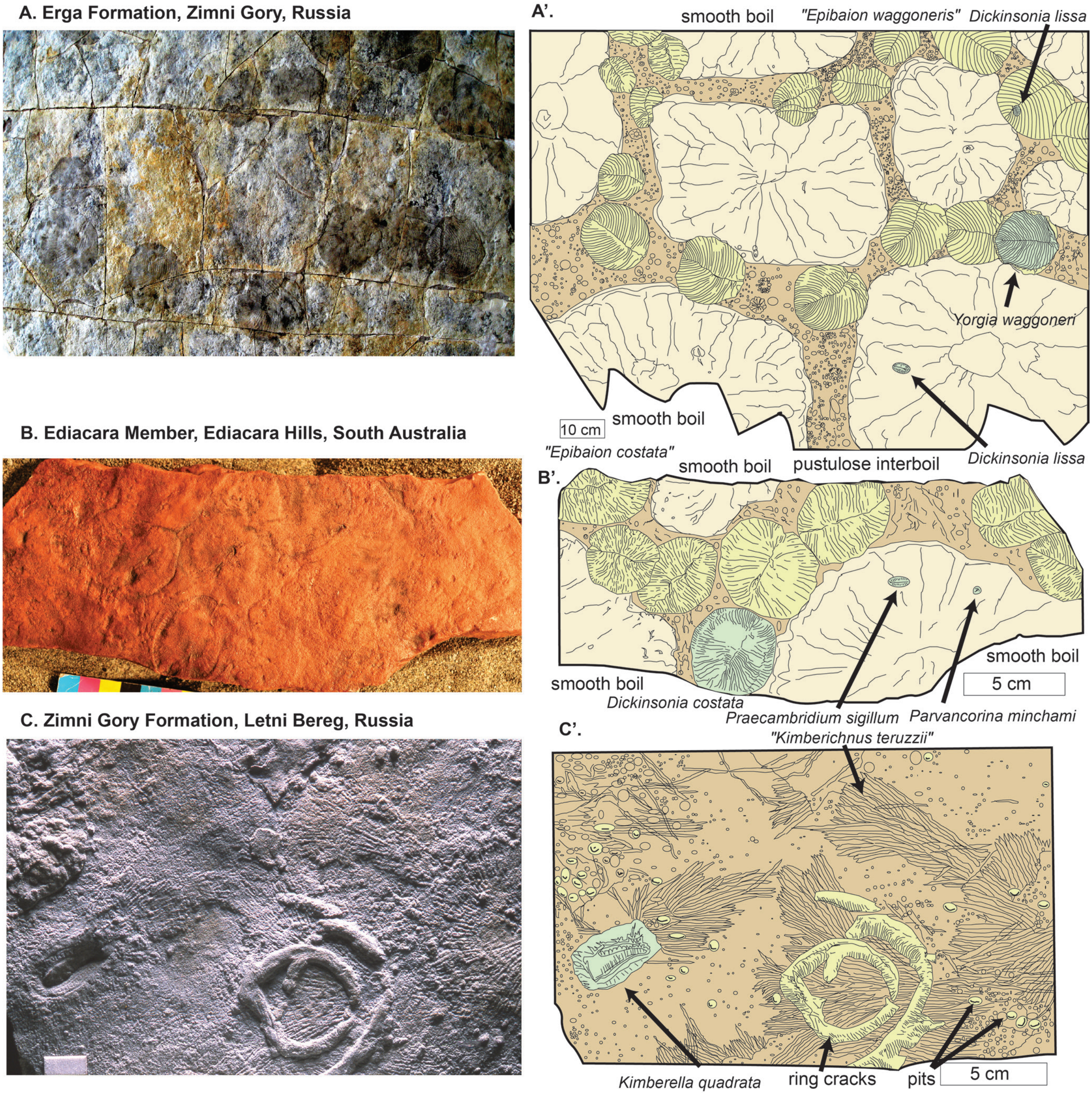


Fig. 11—Photographs (A–C) and interpretive sketches (A'–C') of supposed trace fossils as Ediacaran frost boils (A−B) and needle ice (C). (A), *Yorgia waggoneri* (taphomorph = "*Epibaon waggoneris*") crowded into gutters between frost boils with scattered individuals of small *Dickinsonia lissa*. (B), *Dickinsonia costata* (taphomorph = "*Epibaion costata*") crowded into gutters between frost boils with scattered *Praecambridium sigillum* and *Parvancorina minchami*. (C), "*Kimberichnus terruzzi*" (pseudomorph) needle–ice radiating from soil crust pinnacles and *Kimberella quadrata*, with soil pits (yellow) created by ice lifting of pellets (brown). Additional area shown in A' is from Ivantsov and Malakhovskaya (2002). Specimens are 44–686 KP in Arkhangelsk Regional Museum from Yorgia bed, Erga beds, Mezen Formation, Zimnie Gory locality (A), P14359 in South Australian Museum from Ediacara Member of Rawnsley Quartzite in Ediacara Hills (B), 3493/5137 in Paleontological Institute, Moscow from Letni Bereg, Solza River locality, Zimnie Gory Formation (C).

chambers in branching patterns unlike any known Protozoa (Antcliffe *et al.*, 2011). Architecture of some Ediacaran fossils has high fractal dimensionality (1.6−2.4) more like plants and fungi than animals (Cuthill & Conway Morris 2014). Feeding trails on *Dickinsonia* have been attributed to scavengers eating buried animals (Gehling & Droser, 2018), but the worm traces have laterally mounded levees as evidence that they fed on immobile *Dickinsonia* at the surface. Basal feeding threads like mycorrhizae (Antcliffe *et al.,* 2015; Liu & Dunn, 2020) and satellite vegetative propagules (Mitchell *et al.*, 2015) are also more like lichens than animals. Ediacaran fossils are common on "old elephant skin" textured surfaces, a trace fossil (*Rivularites*) of biological soil crusts, and not with the usual trace fossils of aquatic mats (*Rugalichnus*). Rollups and redeposited mat fragments are hallmarks of aquatic microbial mats, yet not a single case of mat redeposition has been reported with *Rivularites* and Ediacaran fossils in South Australia or Russia (Seilacher, 2007; Retallack, 2012b; Zakrevskaya, 2014). Mat redeposition has been noted in Ediacaran lacustrine to intertidal facies of England and Newfoundland with the woven–filamentous microtexture and flexuous morphology of *Rugalichnus* mats (Callow & Brasier, 2009; Retallack, 2016; Stimson *et al.*, 2017), and these are distinct from the presumed microbially stabilized sandstone intraclasts figured from the Ediacara Member by Tarhan *et al.* (2017). Supposed "hummocky cross-beds" found with Ediacaran fossils (Tarhan *et al.*, 2015) are low (4 cm) isolated megaripples, unlike genuine large (25–20 cm) hummocky stratification in cosets (Dott & Bourgeois, 1982). Ripple marked and other fossiliferous beds have silica cements with Ge: Si ratios of 1–10 μmol/mol (Tarhan *et al.*, 2016), diagnostic of soil rather than marine cements (Retallack, 2017b). Finally, other Ediacaran fossils were found in life position within what have been interpreted as well–drained gypsic and calcic paleosols, so may have been sessile lichens or microbial colonies (Retallack, 2013b).

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Table 1—Diameters and grain size of fossil and modern frost boils.

Specimen	Location	Formation	m grain size	m diameter	
P14359	Ediacara Hills	Ediacara Member	0.00006	0.16	Retallack 2007
P14359	Ediacara Hills	Ediacara Member	0.00006	0.18	Retallack 2007
44–686 KP	Zimni Gory	Yorgia Bed, Erga Formation	0.00001	0.44	Ivantsov 2011
44–686 KP	Zimni Gory	Yorgia Bed, Erga Formation	0.00001	0.38	Ivantsov 2011
44–686 KP	Zimni Gory	Yorgia Bed, Erga Formation	0.00001	0.48	Ivantsov 2011
44–686 KP	Zimni Gory	Yorgia Bed, Erga Formation	0.00001	0.37	Ivantsov 2011
44–686 KP	Zimni Gory	Yorgia Bed, Erga Formation	0.00001	0.43	Ivantsov 2011
	Kvadehuksletta, Spitsbergen	surface soil	0.04	1.1	Kessler & Werner, 2003
	Kvadehuksletta, Spitsbergen	surface soil	0.04	1.7	Kessler & Werner, 2003
	Kvadehuksletta, Spitsbergen	surface soil	0.04	1.05	Kessler & Werner, 2003
	Kvadehuksletta, Spitsbergen	surface soil	0.04	0.95	Kessler & Werner, 2003
	Kvadehuksletta, Spitsbergen	surface soil	0.04	0.8	Kessler & Werner, 2003
	Kvadehuksletta, Spitsbergen	surface soil	0.04	1.3	Kessler & Werner, 2003
	Kvadehuksletta, Spitsbergen	surface soil	0.04	0.85	Kessler & Werner, 2003
	Denali highway Alaska	surface soil	0.09	1.6	Kessler & Werner, 2003
	Denali highway Alaska	surface soil	0.09	1.67	Kessler & Werner, 2003
	Denali highway Alaska	surface soil	0.09	1.1	Kessler & Werner, 2003
	Denali highway Alaska	surface soil	0.09	1.7	Kessler & Werner, 2003
	Denali highway Alaska	surface soil	0.09	1.43	Kessler & Werner, 2003
	Denali highway Alaska	surface soil	0.09	1.15	Kessler & Werner, 2003
	Howe Island, Alaska	surface soil	0.00008	0.62	Walker *et al.*, 2011
	Howe Island, Alaska	surface soil	0.00008	0.32	Walker *et al.*, 2011
	Howe Island, Alaska	surface soil	0.00008	0.43	Walker *et al.*, 2011
	Howe Island, Alaska	surface soil	0.00008	0.46	Walker *et al.*, 2011
	Howe Island, Alaska	surface soil	0.00008	0.37	Walker *et al.*, 2011
	Howe Island, Alaska	surface soil	0.00008	0.27	Walker *et al.*, 2011
	Trinchera Peak, Colorado	surface soil	0.55	3.1	Vopata *et al.*, 2006
	Trinchera Peak, Colorado	surface soil	0.55	2.9	Vopata *et al.*, 2006
	Trinchera Peak, Colorado	surface soil	0.55	2.3	Vopata *et al.*, 2006
	Trinchera Peak, Colorado	surface soil	0.55	3.8	Vopata *et al.*, 2006
	Trinchera Peak, Colorado	surface soil	0.55	4.7	Vopata *et al.*, 2006
	Trinchera Peak, Colorado	surface soil	0.55	5.8	Vopata *et al.*, 2006
	Trinchera Peak, Colorado	surface soil	0.55	2	Vopata *et al.*, 2006
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.55	Walker *et al.*, 2011
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.44	Walker *et al.*, 2011
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.36	Walker *et al.*, 2011
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.17	Walker *et al.*, 2011
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.57	Walker *et al.*, 2011
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.52	Walker *et al.*, 2011
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.56	Walker *et al.*, 2011
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.33	Walker *et al.*, 2011
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.35	Walker *et al.*, 2011
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.48	Walker *et al.*, 2011
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.43	Walker *et al.*, 2011
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.49	Walker *et al.*, 2011
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.82	Walker *et al.*, 2011
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.41	Walker *et al.*, 2011
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.45	Walker *et al.*, 2011
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.22	Walker *et al.*, 2011
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.45	Walker *et al.*, 2011
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.32	Walker *et al.*, 2011
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.29	Walker *et al.*, 2011
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.26	Walker *et al.*, 2011
	Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.34	Walker *et al.*, 2011

Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.46	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.42	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.31	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.28	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.24	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.41	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.34	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.46	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.43	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.33	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.24	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.68	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.11	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.32	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.31	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.29	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.29	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.27	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.22	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.22	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.24	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.12	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.31	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.18	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.51	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.16	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.31	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.43	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.09	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.52	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.31	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.3	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.28	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.13	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.44	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.18	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.28	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.19	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.32	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.28	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.37	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.27	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.35	Walker *et al*., 2011
Isachsen, Ellef Ringnes Island	surface soil	0.000003	0.55	Walker *et al*., 2011
Green Cabin, Banks Island	surface soil	0.00008	0.12	Walker *et al*., 2011
Green Cabin, Banks Island	surface soil	0.00008	0.15	Walker *et al*., 2011
Green Cabin, Banks Island	surface soil	0.00008	0.13	Walker *et al*., 2011
Green Cabin, Banks Island	surface soil	0.00008	0.24	Walker *et al*., 2011
Green Cabin, Banks Island	surface soil	0.00008	0.44	Walker *et al*., 2011
Green Cabin, Banks Island	surface soil	0.00008	0.13	Walker *et al*., 2011
Green Cabin, Banks Island	surface soil	0.00008	0.44	Walker *et al*., 2011
Green Cabin, Banks Island	surface soil	0.00008	0.28	Walker *et al*., 2011
Green Cabin, Banks Island	surface soil	0.00008	0.32	Walker *et al*., 2011
Green Cabin, Banks Island	surface soil	0.00008	0.22	Walker *et al*., 2011
Green Cabin, Banks Island	surface soil	0.00008	0.31	Walker *et al*., 2011
Green Cabin, Banks Island	surface soil	0.00008	0.39	Walker *et al*., 2011
Green Cabin, Banks Island	surface soil	0.00008	0.38	Walker *et al*., 2011

Green Cabin, Banks Island	surface soil	0.00008	0.42	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.15	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.12	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.38	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.29	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.33	Walker *et al.*, 2011
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Green Cabin, Banks Island	surface soil	0.00008	0.13	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.24	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.46	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.37	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.33	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.31	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.26	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.32	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.37	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.45	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.22	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.34	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.54	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.61	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.43	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.61	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.47	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.43	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.71	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.51	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.52	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.17	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.22	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.19	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.23	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.51	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.23	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.31	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.39	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.28	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.42	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.44	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.43	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.37	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.41	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.33	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.19	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.35	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.37	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.38	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.19	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.22	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.44	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.48	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.44	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.47	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.54	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.12	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.48	Walker *et al.*, 2011

Green Cabin, Banks Island	surface soil	0.00008	0.1	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.32	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.38	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.46	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.57	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.32	Walker *et al.*, 2011
Green Cabin, Banks Island	surface soil	0.00008	0.36	Walker *et al.*, 2011
Monte Alvear, Argentina	surface soil	0.25	5.4	Valcarcel–Diaz *et al.*, 2006
Monte Alvear, Argentina	surface soil	0.25	1.2	Valcarcel–Diaz *et al.*, 2006
Monte Alvear, Argentina	surface soil	0.25	2.2	Valcarcel–Diaz *et al.*, 2006
Monte Alvear, Argentina	surface soil	0.25	1.1	Valcarcel–Diaz *et al.*, 2006
Monte Alvear, Argentina	surface soil	0.25	1.4	Valcarcel–Diaz *et al.*, 2006
Monte Alvear, Argentina	surface soil	0.25	4.8	Valcarcel–Diaz *et al.*, 2006
Galbraith Lake, Alaska	surface soil	0.000004	0.84	Overduin & Kane, 2006
Galbraith Lake, Alaska	surface soil	0.000004	0.4	Overduin & Kane, 2006
Galbraith Lake, Alaska	surface soil	0.000004	0.3	Overduin & Kane, 2006
Galbraith Lake, Alaska	surface soil	0.000004	0.9	Overduin & Kane, 2006
Galbraith Lake, Alaska	surface soil	0.000004	0.8	Overduin & Kane, 2006
Galbraith Lake, Alaska	surface soil	0.000004	0.5	Overduin & Kane, 2006
Galbraith Lake, Alaska	surface soil	0.000004	0.2	Overduin & Kane, 2006
Galbraith Lake, Alaska	surface soil	0.000004	0.35	Overduin & Kane, 2006
Galbraith Lake, Alaska	surface soil	0.000004	0.4	Overduin & Kane, 2006
Galbraith Lake, Alaska	surface soil	0.000004	0.6	Overduin & Kane, 2006
Leihagen Hill, Spitsbergen	surface soil	0.01	0.82	Boike *et al.*, 2007
Leihagen Hill, Spitsbergen	surface soil	0.01	0.57	Boike *et al.*, 2007
Leihagen Hill, Spitsbergen	surface soil	0.01	0.62	Boike *et al.*, 2007
Leihagen Hill, Spitsbergen	surface soil	0.01	0.72	Boike *et al.*, 2007

Table 2—Length and width of "*Kimberichnus*" and ice needles and molluscan scrapings.

Location	**Age**	**length mm**	**width mm**	**Reference**
Point Loma, California	modern	1.2	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	1.3	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	1.6	0.7	Dornbos *et al.*, 2004
Point Loma, California	modern	1.1	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	2.1	0.6	Dornbos *et al.*, 2004
Point Loma, California	modern	1.9	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	1.3	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	1.2	0.6	Dornbos *et al.*, 2004
Point Loma, California	modern	1.7	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	1.6	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	1.5	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	2.8	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	2.1	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	2	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	2.3	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	2.4	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	2.3	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	1.5	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	1.7	0.6	Dornbos *et al.*, 2004
Point Loma, California	modern	2.1	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	1.2	0.35	Dornbos *et al.*, 2004
Point Loma, California	modern	1.4	0.25	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.45	Dornbos *et al.*, 2004
Point Loma, California	modern	1.6	0.5	Dornbos *et al.*, 2004

Point Loma, California	modern	1.4	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	1.5	0.6	Dornbos *et al.*, 2004
Point Loma, California	modern	1.3	0.35	Dornbos *et al.*, 2004
Point Loma, California	modern	1.6	0.55	Dornbos *et al.*, 2004
Point Loma, California	modern	1.9	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	2	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.45	Dornbos *et al.*, 2004
Point Loma, California	modern	1.2	0.25	Dornbos *et al.*, 2004
Point Loma, California	modern	1.6	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	2.4	0.65	Dornbos *et al.*, 2004
Point Loma, California	modern	2.1	0.45	Dornbos *et al.*, 2004
Point Loma, California	modern	2.2	0.6	Dornbos *et al.*, 2004
Point Loma, California	modern	1.6	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	1.9	0.35	Dornbos *et al.*, 2004
Point Loma, California	modern	1.9	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	1.2	0.6	Dornbos *et al.*, 2004
Point Loma, California	modern	0.8	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	1.3	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.6	Dornbos *et al.*, 2004
Point Loma, California	modern	1.9	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	1.55	0.35	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	1.9	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	2.1	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.35	Dornbos *et al.*, 2004
Point Loma, California	modern	1.4	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	2.6	0.6	Dornbos *et al.*, 2004
Point Loma, California	modern	2.4	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	1.5	0.45	Dornbos *et al.*, 2004
Point Loma, California	modern	1.9	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	2.3	0.55	Dornbos *et al.*, 2004
Point Loma, California	modern	3.9	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	2.7	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	1.6	0.35	Dornbos *et al.*, 2004
Point Loma, California	modern	2.2	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	3.4	0.35	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	1.7	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	1.7	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	1.9	0.35	Dornbos *et al.*, 2004
Point Loma, California	modern	2	0.6	Dornbos *et al.*, 2004
Point Loma, California	modern	1.9	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	2.3	0.6	Dornbos *et al.*, 2004
Point Loma, California	modern	2.7	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	1.9	0.6	Dornbos *et al.*, 2004
Point Loma, California	modern	3.3	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	3.2	0.35	Dornbos *et al.*, 2004
Point Loma, California	modern	2	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	1.6	0.7	Dornbos *et al.*, 2004
Point Loma, California	modern	1.4	0.25	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	2	0.35	Dornbos *et al.*, 2004
Point Loma, California	modern	2.2	0.6	Dornbos *et al.*, 2004
Point Loma, California	modern	2.1	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	1.7	0.4	Dornbos *et al.*, 2004

Point Loma, California	modern	1.8	0.35	Dornbos *et al.*, 2004
Point Loma, California	modern	2	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	1.7	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	2.1	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	2.2	0.6	Dornbos *et al.*, 2004
Point Loma, California	modern	1.9	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	1.3	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	2.2	0.45	Dornbos *et al.*, 2004
Point Loma, California	modern	2.4	0.35	Dornbos *et al.*, 2004
Point Loma, California	modern	1.6	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	0.9	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.35	Dornbos *et al.*, 2004
Point Loma, California	modern	1.7	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	2.2	0.65	Dornbos *et al.*, 2004
Point Loma, California	modern	1.9	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	1.7	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.35	Dornbos *et al.*, 2004
Point Loma, California	modern	1.2	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	1.5	0.6	Dornbos *et al.*, 2004
Point Loma, California	modern	1.2	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	1.1	0.35	Dornbos *et al.*, 2004
Point Loma, California	modern	2.1	0.7	Dornbos *et al.*, 2004
Point Loma, California	modern	1.9	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	2	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	2.1	0.6	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.7	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	1.9	0.25	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.35	Dornbos *et al.*, 2004
Point Loma, California	modern	1.9	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	2	0.45	Dornbos *et al.*, 2004
Point Loma, California	modern	1.7	0.45	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	1.2	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	2.4	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	3.2	0.45	Dornbos *et al.*, 2004
Point Loma, California	modern	2.7	0.6	Dornbos *et al.*, 2004
Point Loma, California	modern	1.1	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	2.4	0.55	Dornbos *et al.*, 2004
Point Loma, California	modern	2.2	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	1.2	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	1.5	0.45	Dornbos *et al.*, 2004
Point Loma, California	modern	2	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	2.1	0.3	Dornbos *et al.*, 2004
Point Loma, California	modern	2.2	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	2.3	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	2.2	0.6	Dornbos *et al.*, 2004
Point Loma, California	modern	1.3	0.65	Dornbos *et al.*, 2004
Point Loma, California	modern	1.1	0.6	Dornbos *et al.*, 2004
Point Loma, California	modern	1.2	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	1.3	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	1.3	0.45	Dornbos *et al.*, 2004

Point Loma, California	modern	1.2	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.4	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.7	Dornbos *et al.*, 2004
Point Loma, California	modern	1.8	0.6	Dornbos *et al.*, 2004
Point Loma, California	modern	1.9	0.6	Dornbos *et al.*, 2004
Point Loma, California	modern	2.2	0.5	Dornbos *et al.*, 2004
Point Loma, California	modern	1.6	0.5	Dornbos *et al.*, 2004
Sanjia, China	Cambrian	6.2	3.5	Dornbos *et al.*, 2004
Sanjia, China	Cambrian	6.3	2.7	Dornbos *et al.*, 2004
Sanjia, China	Cambrian	9.2	2.2	Dornbos *et al.*, 2004
Sanjia, China	Cambrian	11.2	2.6	Dornbos *et al.*, 2004
Sanjia, China	Cambrian	6.1	1.8	Dornbos *et al.*, 2004
Sanjia, China	Cambrian	12.4	1.8	Dornbos *et al.*, 2004
Sanjia, China	Cambrian	11.5	3.1	Dornbos *et al.*, 2004
Sanjia, China	Cambrian	12.6	1.8	Dornbos *et al.*, 2004
Sanjia, China	Cambrian	11.5	1.6	Dornbos *et al.*, 2004
Sanjia, China	Cambrian	12.1	2.1	Dornbos *et al.*, 2004
Sanjia, China	Cambrian	8.7	2.3	Dornbos *et al.*, 2004
Sanjia, China	Cambrian	12.1	1.9	Dornbos *et al.*, 2004
Sanjia, China	Cambrian	8.5	1.5	Dornbos *et al.*, 2004
Sanjia, China	Cambrian	11.3	2.2	Dornbos *et al.*, 2004
Chugach State Park, Alaska	modern	24.9	0.6	herein
Chugach State Park, Alaska	modern	29.0	0.6	herein
Chugach State Park, Alaska	modern	27.6	0.6	herein
Chugach State Park, Alaska	modern	23.5	0.7	herein
Chugach State Park, Alaska	modern	22.1	0.6	herein
Chugach State Park, Alaska	modern	20.7	0.6	herein
Chugach State Park, Alaska	modern	9.7	0.4	herein
Chugach State Park, Alaska	modern	15.2	0.4	herein
Chugach State Park, Alaska	modern	13.8	0.4	herein
Chugach State Park, Alaska	modern	16.6	0.7	herein
Chugach State Park, Alaska	modern	13.8	0.6	herein
Chugach State Park, Alaska	modern	18.0	0.4	herein
Chugach State Park, Alaska	modern	12.4	0.6	herein
Chugach State Park, Alaska	modern	24.9	0.7	herein
Chugach State Park, Alaska	modern	23.5	0.6	herein
Chugach State Park, Alaska	modern	29.0	0.6	herein
Chugach State Park, Alaska	modern	30.4	0.6	herein
Chugach State Park, Alaska	modern	29.0	0.6	herein
Chugach State Park, Alaska	modern	29.0	0.7	herein
Chugach State Park, Alaska	modern	29.0	0.6	herein
Chugach State Park, Alaska	modern	27.6	0.6	herein
Chugach State Park, Alaska	modern	29.0	0.6	herein
Chugach State Park, Alaska	modern	16.6	0.7	herein
Chugach State Park, Alaska	modern	33.1	0.8	herein
Chugach State Park, Alaska	modern	34.5	0.7	herein
Chugach State Park, Alaska	modern	35.9	0.7	herein
Chugach State Park, Alaska	modern	37.3	0.8	herein
Chugach State Park, Alaska	modern	31.8	0.4	herein
Chugach State Park, Alaska	modern	31.8	0.4	herein
Chugach State Park, Alaska	modern	30.4	0.7	herein
Chugach State Park, Alaska	modern	29.0	0.6	herein
Chugach State Park, Alaska	modern	22.1	0.7	herein
Chugach State Park, Alaska	modern	15.2	0.3	herein
Chugach State Park, Alaska	modern	13.8	0.4	herein
Chugach State Park, Alaska	modern	12.4	0.4	herein
Chugach State Park, Alaska	modern	12.4	0.6	herein

Chugach State Park, Alaska	modern	11.0	0.7	herein
Chugach State Park, Alaska	modern	16.6	0.7	herein
Chugach State Park, Alaska	modern	22.1	0.8	herein
Chugach State Park, Alaska	modern	20.7	0.7	herein
Chugach State Park, Alaska	modern	20.7	0.6	herein
Chugach State Park, Alaska	modern	19.3	0.4	herein
Chugach State Park, Alaska	modern	18.0	0.4	herein
Chugach State Park, Alaska	modern	18.0	0.4	herein
Chugach State Park, Alaska	modern	18.0	0.4	herein
Chugach State Park, Alaska	modern	15.2	0.4	herein
Chugach State Park, Alaska	modern	19.3	0.4	herein
Chugach State Park, Alaska	modern	20.7	0.6	herein
Chugach State Park, Alaska	modern	22.1	0.4	herein
Chugach State Park, Alaska	modern	19.3	0.3	herein
Chugach State Park, Alaska	modern	12.4	0.8	herein
Chugach State Park, Alaska	modern	18.0	0.4	herein
Chugach State Park, Alaska	modern	16.6	0.4	herein
Chugach State Park, Alaska	modern	15.2	0.4	herein
Chugach State Park, Alaska	modern	19.3	0.6	herein
Chugach State Park, Alaska	modern	20.7	0.4	herein
Chugach State Park, Alaska	modern	20.7	0.4	herein
Chugach State Park, Alaska	modern	22.1	0.6	herein
Chugach State Park, Alaska	modern	18.0	0.7	herein
Chugach State Park, Alaska	modern	20.7	0.6	herein
Chugach State Park, Alaska	modern	18.0	0.6	herein
Chugach State Park, Alaska	modern	19.3	0.6	herein
Chugach State Park, Alaska	modern	20.7	0.7	herein
Chugach State Park, Alaska	modern	19.3	0.6	herein
Chugach State Park, Alaska	modern	19.3	0.4	herein
Chugach State Park, Alaska	modern	20.7	0.4	herein
Chugach State Park, Alaska	modern	20.7	0.4	herein
Chugach State Park, Alaska	modern	18.0	0.6	herein
Chugach State Park, Alaska	modern	19.3	0.6	herein
Chugach State Park, Alaska	modern	22.1	0.6	herein
Chugach State Park, Alaska	modern	20.7	0.7	herein
Chugach State Park, Alaska	modern	23.5	0.6	herein
Chugach State Park, Alaska	modern	22.1	0.4	herein
Chugach State Park, Alaska	modern	20.7	0.6	herein
Chugach State Park, Alaska	modern	15.2	0.7	herein
Chugach State Park, Alaska	modern	9.7	0.6	herein
Chugach State Park, Alaska	modern	11.0	0.7	herein
Chugach State Park, Alaska	modern	12.4	0.6	herein
Chugach State Park, Alaska	modern	11.0	0.6	herein
Chugach State Park, Alaska	modern	9.7	0.4	herein
Mt Scott, South Australia	Ediacaran	19	0.9	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	17	0.7	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	11	0.6	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	14	1	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	11	0.9	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	19	0.8	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	31	0.7	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	17	0.8	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	29	0.9	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	19	0.7	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	18	0.9	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	18	0.8	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	19	0.9	Gehling *et al.*, 2014

Mt Scott, South Australia	Ediacaran	17	0.6	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	13	0.8	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	21	1	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	19	0.9	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	12	0.7	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	13	0.6	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	18	0.9	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	12	0.6	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	10	0.6	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	13	0.8	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	9	0.7	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	10	0.8	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	26	1.1	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	22	1	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	27	1.1	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	17	0.9	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	18	0.8	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	11	0.7	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	21	0.8	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	31	1.1	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	20	1	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	26	0.8	Gehling *et al.*, 2014
Mt Scott, South Australia	Ediacaran	9	0.6	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	6.2	2.2	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	9	4.2	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	8.3	4.6	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	9	3.2	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	7.3	3	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	6.3	4.2	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	9	4	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	9.8	4.1	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	12	3.2	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	11	3.7	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	10	3.8	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	6	4	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	12	4	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	7	4	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	12	3.5	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	8.8	4.1	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	13	5	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	6	2.4	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	6.5	2.6	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	9	3.5	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	6.2	2.8	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	10	2.8	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	4.8	3	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	7.5	3.2	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	7	3	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	7.4	3.5	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	8.2	2.8	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	8.8	2.5	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	10	2.8	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	11	3.3	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	13	3.8	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	5.2	3.5	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	6.3	3.2	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	8.9	3.3	Gehling *et al.*, 2014

Bathtub Gorge, South Australia	Ediacaran	14	5.7	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	15	6.2	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	10	3.6	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	11	4	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	12	3.7	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	9.9	3.3	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	10.1	4	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	9.8	4.3	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	11.3	4.2	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	11	5	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	11.3	3.5	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	12	3.3	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	7	4.5	Gehling *et al.*, 2014
Bathtub Gorge, South Australia	Ediacaran	11	4.2	Gehling *et al.*, 2014
Beckenridge, Colorado	modern	10.5	2.7	herein
Beckenridge, Colorado	modern	11	2	herein
Beckenridge, Colorado	modern	10	1.9	herein
Beckenridge, Colorado	modern	7	1.9	herein
Beckenridge, Colorado	modern	6.5	1.7	herein
Beckenridge, Colorado	modern	6.2	1.9	herein
Beckenridge, Colorado	modern	6.5	2.1	herein
Beckenridge, Colorado	modern	9.5	1.8	herein
Beckenridge, Colorado	modern	10.2	1.6	herein
Beckenridge, Colorado	modern	8.6	2.1	herein
Beckenridge, Colorado	modern	7.1	1.8	herein
Beckenridge, Colorado	modern	5.5	2	herein
Beckenridge, Colorado	modern	7.8	1.8	herein
Beckenridge, Colorado	modern	7.1	1.7	herein
Beckenridge, Colorado	modern	6.6	1.6	herein
Beckenridge, Colorado	modern	7.3	2.2	herein
Beckenridge, Colorado	modern	9.6	1.5	herein
Beckenridge, Colorado	modern	10.2	2	herein
Beckenridge, Colorado	modern	10.7	1.4	herein
Beckenridge, Colorado	modern	11	1.7	herein
Beckenridge, Colorado	modern	12.7	1.9	herein
Beckenridge, Colorado	modern	12.4	2.3	herein
Beckenridge, Colorado	modern	10.8	1.5	herein
Beckenridge, Colorado	modern	6.1	1.6	herein