Resolving MISS conceptions and misconceptions: A geological approach to sedimentary surface textures generated by microbial and abiotic processes

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ABSTRACT

The rock record contains a rich variety of sedimentary surface textures on siliciclastic sandstone, siltstone and mudstone bedding planes. In recent years, an increasing number of these textures have been attributed to surficial microbial mats at the time of deposition, resulting in their classification as microbially induced sedimentary structures, or MISS. Research into MISS has developed at a rapid rate, resulting in a number of misconceptions in the literature. Here, we attempt to rectify these MISS misunderstandings. The first part of this paper surveys the stratigraphic and environmental range of reported MISS, revealing that contrary to popular belief there are more reported MISS-bearing rock units of Phanerozoic than Precambrian age. Furthermore, MISS exhibit a pan-environmental and almost continuous record since the Archean. Claims for the stratigraphic restriction of MISS to intervals prior to the evolution of grazing organisms or after mass extinction events, as well as claims for the environmental restriction of MISS, appear to result from sampling bias. In the second part of the paper we suggest that raised awareness of MISS has come at the cost of a decreasing appreciation of abiotic processes that may create morphologically similar features. By introducing the umbrella term 'sedimentary surface textures', of which MISS are one subset, we suggest a practical methodology for classifying such structures in the geological record. We illustrate how elucidating the formative mechanisms of ancient sedimentary surface textures usually requires consideration of a suite of sedimentological evidence from surrounding strata. Resultant interpretations, microbial or non-microbial, should be couched within a reasonable degree of uncertainty. This approach recognizes that morphological similarity alone does not constitute scientific proof of a common origin, and reinstates a passive descriptive terminology for sedimentary surface textures that cannot be achieved with the current MISS lexicon. It is hoped that this new terminology will reduce the number of overly sensational and misleading claims of MISS occurrence, and permit the means to practically separate initial observation from interpretation. Furthermore, this methodology offers a scientific approach that appreciates the low likelihood of conclusively identifying microbial structures from visual appearance alone, informing the search for true MISS in Earth's geological record and potentially on other planetary bodies such as Mars.

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1. Introduction

Bedding surfaces in siliciclastic strata commonly preserve a wide variety of textures and small-scale sedimentary structures formed during, or shortly after, deposition by physical, chemical or biological processes (Fig. 1a-x). Such textures have an array of forms including, but not restricted to, small pits, wrinkles, millimetre-scale ripples, bubble-like textures, warts and a variety of intermediate forms. Modern analogy can clearly be used to explain certain textures, such as the pitted impressions left by raindrop impact, whereas some textures, such as wrinkle structures or runzelmarken (Häntzschel and Reineck, 1968; Reineck, 1969; Teichert, 1970; Hagadorn and Bottjer, 1997; Porada and Bouougri, 2007a, 2007b) have, until recent years, often been regarded as more enigmatic. When observed in the rock record, sedimentary surface textures may be divorced from their formative mechanisms by millions or billions of years. Furthermore, the interpretation of these mechanisms can be problematic where modern and experimental analogues show that different processes result in almost identical forms. Debates about which formation mechanisms may best explain given sedimentary forms have existed for almost as long as the science of modern geology: Buckland (1842) and Lyell (1851), for example, discussed the plausibility of rain drop impressions versus gas escape structures entering the geological record. Yet in early studies, and for the majority of the twentieth century, purely physical processes were most commonly invoked as formative mechanisms for sedimentary surface textures (e.g., Reineck and Singh, 1980; Allen, 1982).

In the last two decades, contributions from studies in the field of geomicrobiology have triggered an increasing recognition amongst geologists of the physical role that micro-organisms can play in siliciclastic sedimentary environments. Observations from modern sedimentary environments and laboratory experiments have clearly demonstrated that microbial mats, biofilms and aggregates can be directly and indirectly responsible for sculpting a wide variety of sedimentary textures on bedding planes. In light of this, a number of surface and near-surface textures in siliciclastic strata have increasingly been designated as microbially-induced sedimentary structures, or MISS (Noffke et al., 2001; see discussion of alternative terminologies later).

Improved understanding of the role of micro-organisms has unquestionably provided a major advance in our appreciation of the diversity and interaction of abiotic and biotic processes that shape the sedimentary record. However, as the relatively young field of study into MISS has grown, a number of questionable claims have been consistently repeated: (1) that MISS are more common in the Precambrian than the Phanerozoic; (2) that MISS are most often associated with non-actualistic environmental and taphonomic conditions in certain intervals of geological history; (3) that MISS are predominantly shallow-marine or tidal features; (4) that MISS were mostly, or exclusively, produced by photoautotrophic cyanobacteria; and (5) that MISS rarely occur in conjunction with higher metazoan life. A further unfortunate and unintended effect of the rapid rise of MISS studies has been that the abiotic role in forming certain sedimentary surface textures, including some wrinkle structures, has become increasingly overlooked. A wealth of largely 20th century research showing how sedimentary surface textures of almost identical form to proven MISS may be formed by purely physical processes including adhesion, loading, fluid escape, impact, flow and shrinkage is at risk of being lost in the literature as studies increasingly focus on searching for a microbial role. The potential impact of overlooking such abiotic forms may be detrimental, not only because some reported "MISS" in the literature may actually be abiotic features (Wellman and Strother, 2015), but also because physical structures themselves can reveal important palaeoenvironmental clues that assist the interpretation of sedimentary facies and their fossil assemblages.

The impetus for this paper arises from the prevalence of sedimentary surface textures, often resembling MISS, with which the authors are familiar from a wide stratigraphic and environmental range of Precambrian and Phanerozoic sedimentary successions and active sedimentary environments. These features have usually been encountered coincidentally, in field studies for which the prime aim was not to search for MISS in the rock record, and thus these occurrences (along, we suspect, with many other instances) remain largely under-reported. As a result, the abundance of Phanerozoic MISS is likely to be unknown to workers concentrating primarily on Precambrian successions, potentially resulting in misleading assumptions of non-actualistic conditions. This paper aims to document these cases and, in doing so, dispel a number of MISS 'myths'. The paper is organised as follows:

- The first part (Section 2) outlines and addresses the main misconceptions regarding the known stratigraphic and palaeoenvironmental range of MISS and MISS-like structures, partially with reference to a literature survey of papers that have explicitly recorded MISS occurrences in the geological record.
- The second part (Section 3) discusses how certain MISS in the rock record can be better understood if they are considered as a subset of a spectrum of similar *sedimentary surface textures*, some of which have
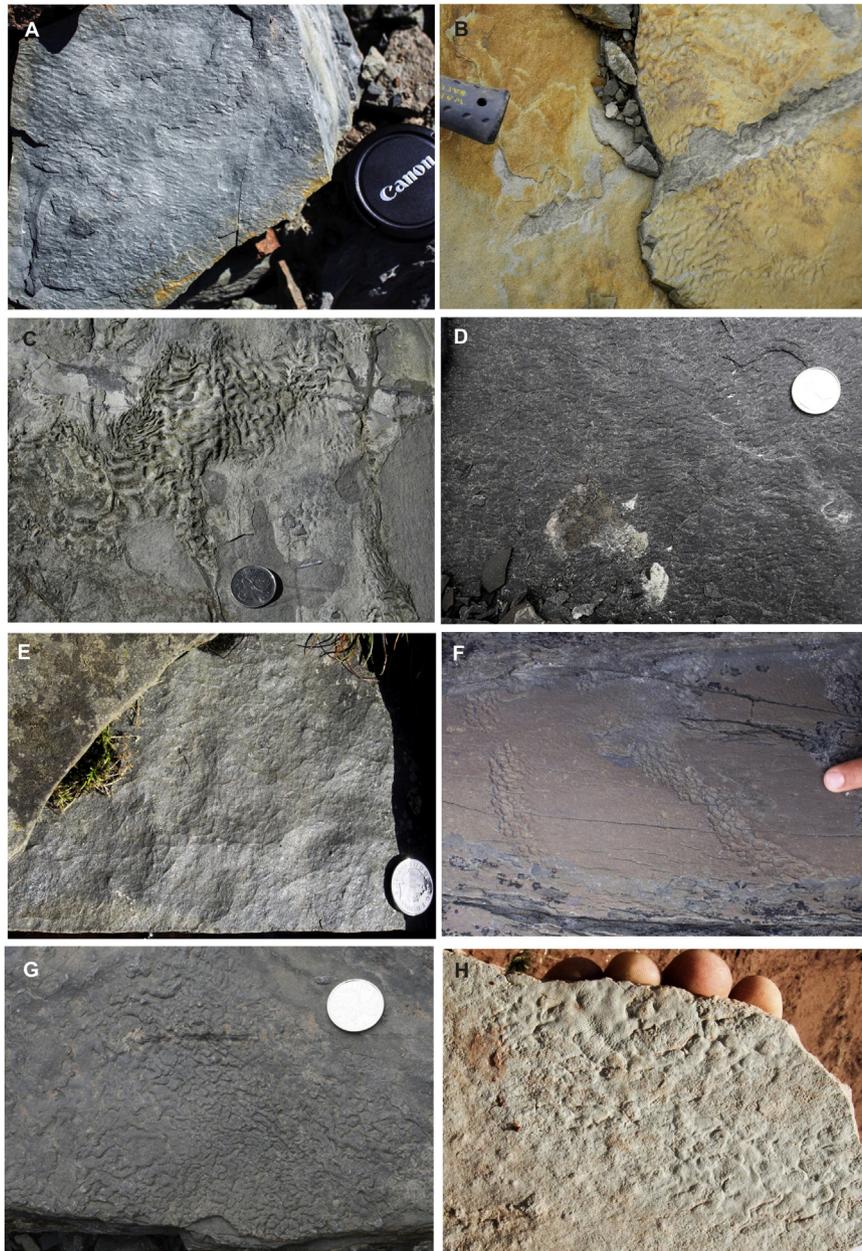
Fig. 1. Examples of sedimentary surface textures in the rock record. (a) Transverse wrinkles on the base of a mudstone bed. Siluro-Devonian coastal alluvial plain facies, Clam Bank Formation, Clam Bank Cove, Newfoundland, Canada. Diameter of camera lens cap is 58 mm. (b) Patch of curving transverse wrinkles on top of a siltstone bed. Late Devonian back-barrier and sabkha facies, Evieux Formation, Hoyoux, Belgium. Width of hammer shaft is 35 mm. (c) Recumbently oriented wrinkles on a mudstone bedding plane. Mississippian tidal facies, Horton Bluff Formation, Blue Beach, Nova Scotia, Canada. Diameter of coin is 24 mm. (d) Transverse wrinkles within fine-grained sandstones deposited on a storm-dominated shelf. Silurian (Llandovery) Ross Brook Formation, Arisaig, Nova Scotia, Canada. Diameter of coin is 24 mm. (e) Reticulate markings on top of siltstone. Neoproterozoic lacustrine facies of the Diabaig Formation, Badenscallie, Scotland. Diameter of coin is 25 mm. (f) Trains of reticulate ridges on top of siltstone. Ediacaran deep-marine facies of the Trepassey Formation, Mistaken Point Ecological Reserve, Newfoundland, Canada. (g) Overlapping transverse ridges and mounds on top of very fine sandstone bed. Pennsylvanian alluvial facies, Tynemouth Creek Formation, St. Martin's, New Brunswick, Canada. Diameter of coin is 24 mm. (h) Cuspate inverted mounds on base of siltstone, overprinted with very fine transverse wrinkles. Early Triassic playa lake facies, Aylesbeare Mudstone Formation, Chiselbury Bay, Devon, England. (i) Aristophycus branching structure in convex relief on top of coarse sandstone bed. Cambro-Ordovician braided fluvial channel facies, Frehel Formation, Erquy, Brittany, France. Length of pen is 136 mm. (j) Convex blister structures and reticulate mineralization on top of mudstone. Early Permian alluvial facies, Kildare Capes Formation, Prince Edward Island, Canada. (k) Bubble-like texture on upper surface of sandstone bed. Early Permian alluvial facies, Kildare Capes Formation, Prince Edward Island, Canada. Diameter of coin is 24 mm. (l) Craters of different dimensions, attributable to raindrop impact impressions, on upper surface with desiccation cracks. Middle Devonian alluvial facies of the Catskill Formation, New York, United States. Diameter of coin is 24 mm. (m) Spindle-shaped "synaeresis" cracks cross-cutting top of *Rosselia* trace fossil. Early Triassic shallow-marine facies, Newport Formation, Royal National Park, New South Wales, Australia. Diameter of coin is 29 mm. (n) "Synaeresis" cracks in association with a variety of small infaunal burrows, preserved on the base of a fine sandstone bed. Late Mississippian tidal facies, Alston Formation, Howick, Northumberland, England. (o) Sinuous branching sand crack within sandstone wave-ripple trough, possibly a poorly-developed instance of Manchuriophycus. Late Mississippian deltaic facies, Alston Formation, Taythes Gill, Cumbria, England. Diameter of coin is 27 mm. (p) Setulfs in convex relief on top of fine-grained sandstone. Silurian coastal alluvial facies, Tumblagooda Sandstone, Kalbarri, Western Australia. Diameter of coin is 24 mm. (q) Palimpsested millimetre-scale ripples oblique to main ripple crests, plus looping grazing trails. Early Mississippian tidal facies of the Horton Bluff Formation, Blue Beach, Nova Scotia, Canada. Length of pen is 136 mm. (r) Ornamented ripples on the base of a sandstone. Ediacaran emergent coastal facies of the Bonney Sandstone, Flinders Ranges, South Australia. (s) Cuspate forms on top of very fine grained sandstone. Early Pennsylvanian alluvial facies of the Tynemouth Creek Formation, New Brunswick, Canada. (t) Arumberia fabric. Cambro-Ordovician tidal facies of the Port Lazo Formation, Brehec, Brittany, France. Diameter of coin is 23 mm. (u) Pitted texture associated with Arumberia fabric. Cambro-Ordovician tidal facies of the Port Lazo Formation, Brehec, Brittany, France. Diameter of coin is 23 mm. (v) Patches of "Kinneyia"-like wrinkles and repichnial trails on bedding surface in shelfal Cambrian strata. Rozel Shale and Sandstone, Normandy, France. Diameter of coin is 22 mm. (w) "Kinneyia" texture on top of fine-grained sandstone bed. Middle Ordovician shallow-marine facies of the Stairway Sandstone Formation, Amadeus Basin, Northern Territory, Australia. (x) "Kinneyia" texture on top of fine-grained sandstone bed. Silurian coastal alluvial facies, Tumblagooda Sandstone, Kalbarri, Western Australia. Diameter of coin is 24 mm.
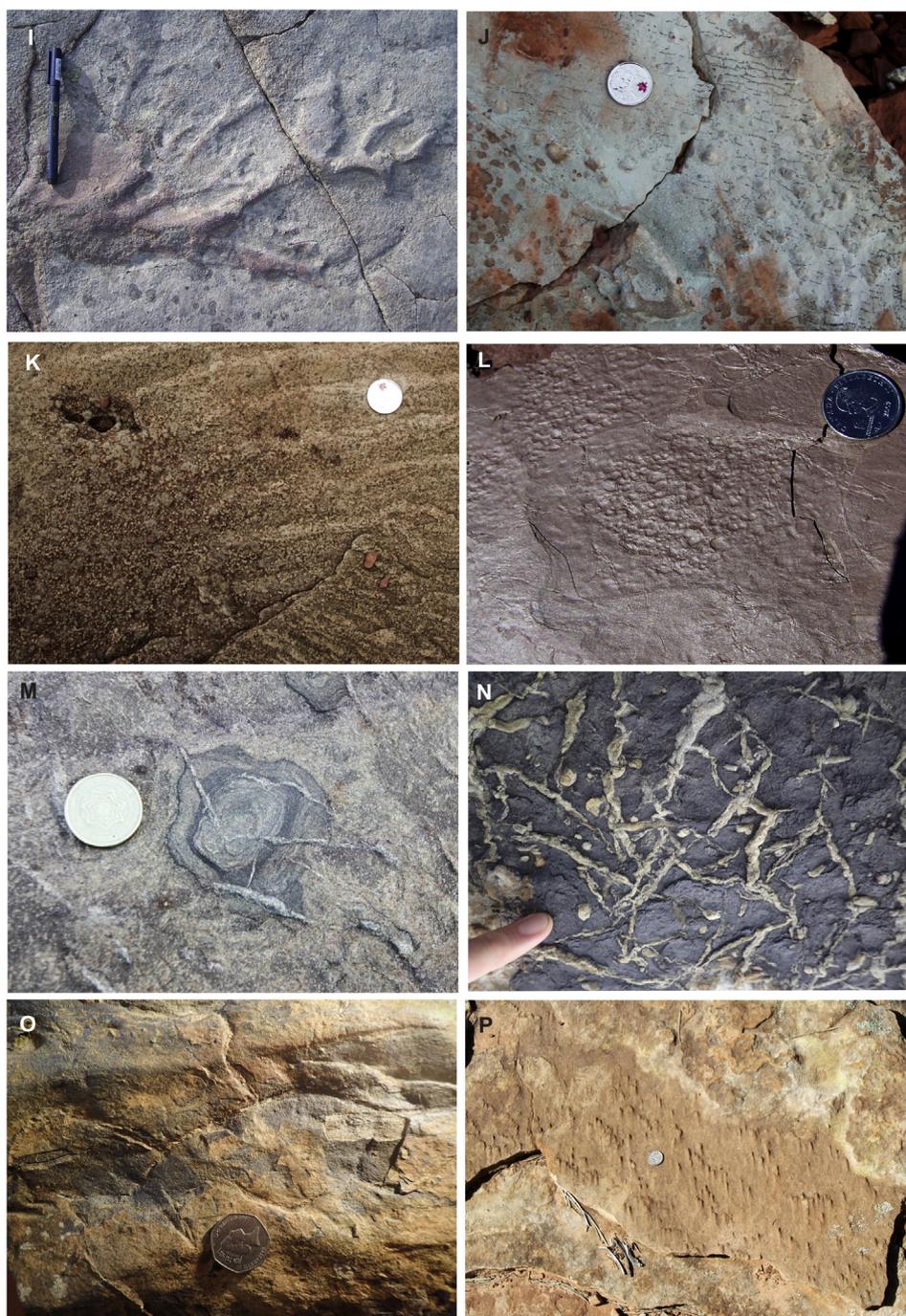
Fig. 1 (*continued*).

a microbial origin and some of which have an abiotic origin. Examples of the processes that may create sedimentary surface textures, with and without microbial mediation, are reviewed and illustrated.

• The third part (Section 4) discusses the problems in determining the formative mechanism of sedimentary surface textures in the geological record and introduces a new classification scheme that can be used to overcome these problems, with reference to original case studies from Palaeozoic and Mesozoic strata.

Unless otherwise stated in the text, the discussions presented in this paper deal only with features in siliciclastic settings, and do not encompass stromatolites, carbonate microbialites, or related structures (e.g., molar-tooth structures).

2. MISS conceptions and misconceptions

The potential role of micro-organisms and microbial mats in forming or mediating macroscopic sedimentary structures in siliciclastic strata is a relatively recent understanding in sedimentology, becoming better appreciated during the last decade of the 20th century (e.g., Krumbein, 1994; Noffke et al., 1996; Hagadorn and Bottjer, 1997; Schieber, 1998, 1999; Pflüger, 1999; Gerdes et al., 2000). Noffke et al. (2001) proposed that microbially-induced sedimentary structures should be considered a discrete class of sedimentary structures, and defined MISS as the products of interaction between physical sediment dynamics and microbial mats or biofilms. Although it is not explicit in the terminology, MISS are thus effectively understood to be

Fig. 1 (continued).

'microbial-mat-induced' and not simply the result of 'background' micro-organisms and their by-products. This is important because, even at the present day, microbial communities of bacteria and microphytobenthos are ubiquitous in natural sediments. Their secretion of cohesive extracellular polymeric substances (EPS) is increasingly understood to fundamentally affect sediment entrainment, transport rate, and bedform dimensions, even where thick surficial biofilms and microbial mats are not present (Garwood et al., 2013; Malarkey et al., 2015). As such, there is a natural background influence of micro-organisms on sedimentological processes even amongst 'abiotic' bedforms such as ripples. The particular significance of microbial mats and biofilms is that they provide a veneer to a sedimentary substrate, which behaves akin to a layer of "well-structured and stable water" (Krumbein, 1994). Gerdes (2010) defines microbial mats as "advanced biofilm

stages forming laminae on bedding surfaces where they reflect gaps in sedimentation or, in other terms, time for growth, biomass condensation and biological succession". They are initiated as different micro-organisms secrete EPS to sediment grains to modify physico-chemical conditions and permit either motility or adherence to a substrate, and they develop with time as the EPS expands around adjacent grains and coalesces with neighbouring pockets. Diverse communities of micro-organisms may be involved in this process, such that mature microbial mats contain populations of multiple trophic groups and a large diversity of species (summarised in Konhauser, 2007). From a sedimentological perspective, microbial mats act as an elastic surface membrane that fundamentally changes interactions between sediment substrates and overlying fluids: on a naked substrate, the key to bedform-sculpting is that a particular threshold in shear velocity will induce

grain movement; where a microbial mat is present, a particular shear threshold instead induces unstable oscillations in the membrane, which ultimately distorts and fails, catastrophically entraining clumps of microbially-bound sediment (Vignaga et al., 2013). Sedimentary structures and textures arising from effects of stabilization, mat growth, mat deformation and preservation due to the existence of such an elastic membrane are those most commonly included within the canon of MISS.

2.1. MISS in the rock record

Since their first description, MISS have received a large amount of attention, with multiple reference works, colloquia and reviews (some using alternative or contradictory nomenclature) appearing during the last decade (e.g., Schieber et al., 2007a; Noffke, 2010; Seckbach and Oren, 2010; Noffke and Chafetz, 2012). Two main avenues of research can be discerned in the study of micro-organism/sediment interactions: (1) the sedimentological role of micro-organisms in modern mats, environments or laboratory experiments (e.g., Gerdes et al., 2000; Shepard and Sumner, 2010; Hagadorn and McDowell, 2012; Garwood et al., 2013; Vignaga et al., 2013; Cuadrado et al., 2014; Malarkey et al., 2015); and (2) the ancient record of fossilized microbially-induced sedimentary structures (see references in Table 1). MISS terminology is more commonly applied in the latter of these fields, often utilizing comparison with visually similar modern counterparts (e.g., Grazhdankin and Gerdes, 2007), and commonly focussing on intervals of geological history where more complex life would traditionally be assumed to be absent or restricted (e.g., prior to the evolution of grazing metazoans (Buatois et al., 2013), or after major mass extinctions (Pruss et al., 2004; Mata and Bottjer, 2009a; Chu et al., 2015)). The importance of MISS in providing clues to the taphonomy of trace and body fossils is another common emphasis (Gehling, 1999; Mata and Bottjer, 2009a). MISS have also attracted attention in the field of astrobiology (Mata and Bottjer, 2009b; Noffke, 2015), as it is considered that the most likely evidence for any life on planets such as Mars would reflect the activity of micro-organisms (Oehler and Allen, 2012). With the rapidly expanding dataset of Martian Rover imagery, validation of visually diagnostic criteria for the identification of terrestrial MISS would be of great importance.

Although the stratigraphic record of MISS is known to continue throughout much of the Precambrian and Phanerozoic (e.g., Noffke, 2010; Fig. I.6.), the collective focus of many studies of ancient MISS has led to the frequently repeated claim that they were more common in the Precambrian (e.g., Gehling, 1999; Hagadorn and Bottjer, 1999; Porada and Bouougri, 2007a, 2007b; Sarkar et al., 2011; Bose et al., 2012). This was predicted by a hypothesis (pre-dating the definition of MISS) which argued that an 'agronomic revolution', sparked by the evolution of grazing and bioturbating metazoans, led to globally diminished microbial matgrounds at or near the Precambrian-Cambrian boundary (Seilacher and Pflüger, 1994; see also Bottjer et al., 2000). Contrary to this, recent palaeoecological work combining MISS and ichnological studies has suggested that early motile metazoans co-existed with matgrounds and exploited them for food and oxygen (cf. Gingras et al., 2011), and such a situation persisted through the latest Ediacaran and at least into the early/middle Cambrian (Buatois et al., 2014; Carbone and Narbonne, 2014). Therefore although MISS may have been more widespread prior to the evolution of burrowing, the agronomic revolution did not precipitate a catastrophic decline in matgrounds at the Ediacaran–Cambrian boundary; any transition was gradual and more nuanced.

The Phanerozoic record of specific types of MISS has also been discussed. Porada et al. (2008) suggested that "Kinneyia" wrinkles (see Section 3.3.7.) have a stratigraphic range extending from the Archean to the Jurassic, but could offer no conclusive explanation for their absence in younger strata. Wrinkle structures were claimed by Mata and Bottjer (2009a) to be more abundant during intervals of environmental stress, particularly after the end-Permian extinction, when bioturbating organisms decreased in size and number.

In terms of palaeoenvironmental range, it is commonly stated that the majority of ancient MISS occur in shallow-marine settings. Noffke et al. (2002) suggested that they were profuse in shallow sandy substrates due to the high translucence of quartz sand offering opportunities for phototrophic mats, whilst Mata and Bottjer (2009a, 2013) suggested that they would have dominated ecosystems below fair-weather wave base, ostensibly for the same reason but also because, at such depths, hydrodynamic conditions would have been less volatile. Occurrences of MISS in tidal depositional environments have also been commonly recorded, with analogy to abundant microbial mats known in similar modern settings. Because infaunal bioturbation was late to evolve in some Phanerozoic sedimentary environments, it has also been suggested that microbial matgrounds persisted to the late Palaeozoic in the innermost, freshwater regions of estuarine systems, as well as in fluvio-lacustrine deposits, glacial lakes and fjords (Buatois and Mángano, 2012). Where ancient MISS have been recorded from strata that were deposited outside of the tidal or shallow-marine realm, or are Phanerozoic in age, they are commonly considered as exceptions to the norm (e.g., Chu et al., 2015; Pazos et al., 2015).

2.2. Survey of MISS distribution

Despite the received statements regarding the stratigraphic and environmental range of MISS, there has been no complete recent survey of the recorded instances of MISS. In light of the apparent frequency of MISS-like structures in Phanerozoic deposits from the authors' own observations, coupled with increasing instances of 'anomalous' reports of MISS from outside of the Precambrian or the shallow-marine realm (e.g., Chu et al., 2015; Pazos et al., 2015), a literature survey was performed to identify the distribution of recorded MISS since the first definition of the term. The survey was undertaken using publications gathered from the Web of Science database (wok.mimas.ac.uk) which fulfilled at least one of two criteria: (1) the term "microbial induced sedimentary structure" or "microbially induced sedimentary structure" in the 'topic' field; or (2) the paper by Noffke et al. (2001), which originally defined MISS, in the 'cited reference' field. For each instance, the age and interpreted depositional environment for the MISS-bearing unit was recorded, in addition to the purpose of the study recording the MISS. Purposes were categorized as: (1) A study explicitly concerned with reporting an occurrence of MISS within a palaeoenvironmental or stratigraphic framework; (2) A study discussing the taphonomic effects of microbial mats, inferred through the presence of MISS; or (3) A study where the report of MISS was incidental to the main concern of the original paper.

As of July 2015, this search yielded 131 publications concerning 100 discrete stratigraphic units and 15 modern localities upon which our data analysis was performed (Table 1). Inevitably this search will have missed certain key publications, however, for the purpose of identifying a potential bias in the literature we argue that the records used provide a representative sample of the existing literature on MISS. Three of the references used (Gerdes et al., 2000; Porada et al., 2008; Mata and Bottjer, 2009a), summarized work from earlier authors. The MISS-bearing units in these instances are included here referenced to the secondary review article rather than the primary source as it was usually the review paper that explicitly recorded MISS, reinterpreting features described in older papers (e.g., the "foam marks" of Wunderlich (1970) reinterpreted as likely microbial "Kinneyia" by Porada et al. (2008)). As this is a survey of existing publications, the list excludes suspected MISS illustrated for the first time in this paper (from successions that we studied without the explicit intention of looking for MISS, and which are stratigraphically and environmentally biased towards our personal research interests).

Where MISS were explicitly recorded they were included in this survey: we have not excluded any features that we would deem more likely to have an abiotic origin, nor have we ourselves reinterpreted any published accounts of abiotic features as MISS. It is not known how the trends depicted would vary if the MISS (and other structures)

Table 1
List of incidences of MISS used in construction of Figs. 2–4. Taphonomy column indicates instances where the relevance of MISS for taphonomic studies of Ediacaran macrobiota (E) or trace fossils and trackways (T) was the main focus of at least one of the studies. Incidental column records where the record of MISS was incidental within a study concerned with other aspects of the rock unit in question (Y).

Age	Unit	Location	Facies	Taphonomy?	Incidental?	Authors
Archean	Buck Reef Chert	South Africa	Shallow marine			Tice (2009)
Archean	Dresser Formation	Australia	Tidal			Noffke et al. (2013)
Archean	Fortescue Group	Australia	Tidal			Flannery et al. (2014)
Archean	Moodies Group	South Africa	Tidal			Noffke et al. (2006b), Noffke (2007), Heubeck (2009)
Archean	Mozaan Group	South Africa	Shallow marine			Noffke et al. (2003)
Archean	Pongola Supergroup	South Africa	Tidal			Noffke et al. (2008)
Archean	Witwatersrand Supergroup	South Africa	Shallow marine			Noffke et al. (2006a) Noffke (2007)
Paleoproterozoic	Chorhat Sandstone	India	Tidal			Sarkar et al. (2006)
Paleoproterozoic	Gulcheru Formation	India	Tidal			Chakrabarti and Shome (2010)
Paleoproterozoic	Koldaha Shale	India	Deep marine			Banerjee and Jeevankumar (2005)
Paleoproterozoic	Makbageng Formation	South Africa	Desert			Simpson et al. (2013)
Paleoproterozoic	Pretoria Group	South Africa	Tidal to Shallow marine			Parizot et al. (2005), Bosch and Eriksson (2008), Eriksson et al. (2012)
Mesoproterozoic	Bangemell Supergroup	Australia	Deep marine			Martin (2004)
Mesoproterozoic	Belt Supergroup	United States	Shallow marine			Schieber (1998)
Mesoproterozoic	Chattisgarh Supergroup	India	Shallow marine			Chakraborty et al. (2012), Sarkar et al. (2014)
Mesoproterozoic	Chuanlinggou Formation	China	Deep marine			Shi et al. (2008)
Mesoproterozoic	Copper Harbor Conglomerate	United States	Fluvial			Wilmeth et al. (2014)
Mesoproterozoic	Dripping Spring Quartzite	United States	Fluvial			Beraldi-Campesi et al. (2014)
Mesoproterozoic	Huangqikou Formation	China	Tidal			Lan et al. (2013)
Mesoproterozoic	Keweenan Supergroup	United States	Fluvial			Sheldon (2012)
Mesoproterozoic	Mukun Group	Russia	Desert and Fluvial			Petrov (2014)
Mesoproterozoic	Ruyang Group	China	Tidal			Tang et al. (2012)
Mesoproterozoic	Stoer Group	Scotland	Fluvial			Prave (2002)
Mesoproterozoic	Vindhyan Supergroup	India	Shallow marine			Sarkar et al. (2014)
Mesoproterozoic	Yunmengshan Formation	China	Shallow marine			Xing et al. (2010)
Neoproterozoic	Bhander Group	India	Tidal			Kumar and Pandey (2007)
Neoproterozoic	Carbonate and Quartzite Group	Morocco	Tidal			Bouougri and Porada (2002)
Neoproterozoic	Diabaig Formation	Scotland	Lacustrine			Callow et al. (2011)
Neoproterozoic	Jodhpur Group	India	Tidal to Shallow marine			Samanta et al. (2011), Sarkar et al. (2008, 2014), Kumar and Ahmad (2014)
Neoproterozoic	Luoyo Group	China	Tidal			Tang et al. (2012)
Neoproterozoic	Roan Group	Zambia	Tidal			Porada and Druschel (2010)
Neoproterozoic	Sierras Bayas Group	Argentina	Tidal			Porada and Bouougri (2008)
Ediacaran	Conception and St. John's Groups	Canada	Deep marine	E		Laflamme et al. (2012)
Ediacaran	Kimberley region	Australia	Shallow marine			Lan and Chen (2012), Lan et al. (2013)
Ediacaran	Longmyndian Supergroup	England	Shallow marine	E		Callow and Brasier (2009)
Ediacaran	Nama Group	Namibia	Tidal to Shallow marine			Noffke et al. (2002), Bouougri and Porada (2007), Elliott et al. (2011) Álvaro (2012)
Ediacaran	Nouatil Group	Mauritania	Lacustrine			
Ediacaran	Rawnsley Quartzite	Australia	Shallow marine	E		Gehling and Droser (2009)
Ediacaran	Taseeva Group	Russia	Shallow marine			Liu et al. (2013)
Ediacaran	White Sea Region	Russia	Shallow marine	E		Callow and Brasier (2009), Zakrevskaya (2014)
Cambrian	Caerfai Group	Wales	Shallow marine		Y	Loughlin and Hillier (2010)
Cambrian	Campito Formation	United States	Shallow marine			Mata and Bottjer (2013)
Cambrian	Chapel Island Formation	Canada	Shallow marine			Buatois et al. (2014)
Cambrian	Gros Ventre Formation	United States	Shallow marine	T		Csonka and Brandt (2012)
Cambrian	Harkless Formation	United States	Shallow marine	T		Bailey et al. (2006), Ahn and Babcock (2012)
Cambrian	Mobergella Sandstone	Germany	Shallow marine		Y	Grimmberger (2010)
Cambrian	Poleta Formation	United States	Shallow marine			Mata and Bottjer (2013)
Cambrian	Puncoviscana Formation	Argentina	Deep marine			Buatois and Mángano (2003), Mata and Bottjer (2009a)
Cambrian	Swedish Middle Cambrian	Sweden	Shallow marine			Calner and Eriksson (2012)
Cambrian	Tunnel City Group	United States	Shallow marine			Eoff (2014)
Cambrian	Volcancito Formation	Argentina	Shallow marine			Tortello and Esteban (2007)
Cambrian	White-Inyo formations	United States	Shallow marine			Marenco and Bottjer (2008)
Cambrian	Wisniówka Sandstone Formation	Poland	Shallow marine	T		Sadlok (2013)
Cambrian	Wood Canyon Formation	United States	Tidal			Mata and Bottjer (2009a)
Ordovician	Beach Formation	Canada	Shallow marine			Harazim et al. (2013)
Ordovician	Montagne Noire formations	France	Tidal to Shallow marine			Noffke (2000), Mata and Bottjer (2009a)
Ordovician	New Richmond Sandstone	United States	Shallow marine			Gerdes et al. (2000)
Ordovician	Turisalu Formation	Estonia	Deep marine		Y	Hints et al. (2014)
Silurian	Burgsvik Formation	Sweden	Shallow marine			Calner and Eriksson (2012)
Silurian	Gray Sandstone Formation	Wales	Shallow marine		Y	Hillier and Morrissey (2010)
Silurian	Sundvollen Formation	Norway	Fluvial		Y	Davies et al. (2006)
Silurian	Tanezzuft Shale	Libya	Shallow to Deep marine			Porada et al. (2008), Mata and Bottjer (2009a)

Table 1 (*continued*)

Age	Unit	Location	Facies	Taphonomy?	Incidental?	Authors
Silurian–Devonian	Lower Old Red Sandstone	Wales	Fluvial			Marriott et al. (2013)
Silurian–Devonian	Río Seco de los Casaños Formation	Argentina	Deep marine			Pazos et al. (2015)
Devonian	Muth Formation	India	Tidal			Draganits and Noffke (2004)
Devonian	Nellenköpfchen beds	Germany	Tidal			Porada et al. (2008), Mata and Bottjer (2009a)
Devonian	Presto-El Peral section	Bolivia	Shallow marine		Y	Gaillard and Racheboeuf (2006)
Devonian	Zachełmie section	Poland	Tidal	T		Narkiewicz et al. (2015)
Carboniferous	Joggins Formation	Canada	Fluvial	T		Prescott et al. (2014)
Carboniferous	Stull Shale	United States	Tidal			Mata and Bottjer (2009a)
Carboniferous–Permian	Itararé Group	Argentina	Lacustrine		Y	Netto et al. (2009)
Carboniferous–Permian	Santa Elena Formation	Argentina	Shallow marine			Buatois et al. (2013)
Permian	Bacchus Marsh Formation	Australia	Shallow marine		Y	Webb and Spence (2008)
Permian	Clear Fork Formation	United States	Lacustrine		Y	Lucas et al. (2011)
Permian	Robledo Mountains Formation	United States	Fluvial		Y	Voigt et al. (2013)
Triassic	Beduh Shale Formation	Iraq	Shallow Marine			Mata and Bottjer (2009a)
Triassic	Bódvaszilas Sandstone	Hungary	Tidal			Mata and Bottjer (2009a)
Triassic	Kockatea Shale Formation	Australia	Shallow marine			Luo et al. (2011)
Triassic	Liujiagou Formation	China	Lacustrine			Chu et al. (2015)
Triassic	Middle Bundsandstein	Germany	Lacustrine			Wehrmann et al. (2012)
Triassic	Moenkopi Formation	United States	Shallow marine			Pruss et al. (2004), Mata and Bottjer (2009b)
Triassic	Oued Oum Er Rbiaa Formation	Morocco	Lacustrine	T		Hminna et al. (2013)
Triassic	Thaynes Formation	United States	Shallow marine			Mata and Bottjer (2009a)
Triassic	Werfen Formation	Italy	Shallow marine			Pruss et al. (2004), Mata and Bottjer (2009a)
Triassic–Jurassic	Santo Domingo Formation	Argentina	Lacustrine		Y	Genise et al. (2009)
Jurassic	Hettangian of Helmstadt	Germany	Shallow marine			Porada et al. (2008)
Jurassic	Höganäs Formation	Sweden	Fluvial			Calner and Eriksson (2012)
Jurassic	Kirkpatrick Basalt	Antarctica	Lacustrine		Y	Stigall et al. (2008)
Jurassic	Schwarzen Jura	Germany	Shallow marine			Porada et al. (2008)
Jurassic	Stormberg Group	Lesotho	Fluvial	T		Smith et al. (2009)
Cretaceous	Agrio Formation	Argentina	Tidal	T		Fernandez and Pazos (2014)
Cretaceous	Allen Formation	Argentina	Tidal		Y	Armas and Sanchez (2011)
Cretaceous	Dakota Formation	United States	Tidal			Gerdes et al. (2000)
Cretaceous	Haman Formation	South Korea	Fluvial			Paik and Hyun-Joo (2014)
Cretaceous	Jiaguan Formation	China	Fluvial	T		Dai et al. (2015)
Cretaceous	Sousa Basin	Brazil	Lacustrine and fluvial	T		Carvalho et al. (2013)
Paleogene	Green River Formation	United States	Lacustrine			Schieber (2007)
Neogene	Rio Negro Formation	Argentina	Tidal			Carmona et al. (2012)
Quaternary	Cape Vani sedimentary rocks	Greece	Tidal			Kilias (2012)
Quaternary	Gotland Deep cores	Baltic Sea	Deep marine			Virtasolo et al. (2011)
Recent	Aarhus Bay	Denmark	Shallow marine			Flood et al. (2014)
Recent	Al Zeeb sabkha	Saudi Arabia	Tidal			Aref et al. (2014)
Recent	Bahia Blanca estuary	Argentina	Tidal	T		Cuadrado et al. (2011, 2012, 2013, 2014)
Recent	Costa Rica margins	Costa Rica	Deep marine			Flood et al. (2014)
Recent	Gulf of Mexico	United States	Deep marine			Flood et al. (2014)
Recent	Lake Aghormi	Egypt	Lacustrine			Taher and Abdel-Motelib (2014)
Recent	Lake J, Devon Island	Canada	Lacustrine			Chutko and Lamoureux (2009)
Recent	Mellum Island	Germany	Tidal			Gerdes and Klenke (2007)
Recent	Mojave Desert	United States	Desert			Williams et al. (2012)
Recent	Pitanguinha Lagoon	Brazil	Lacustrine			Damazio and Silva e Silva (2006)
Recent	Ras Gemsa sabkha	Egypt	Tidal			Taher and Abdel-Motelib (2014)
Recent	Red Sea coast	Saudi Arabia	Tidal			Taj et al. (2014)
Recent	Sonoran Desert	United States	Lacustrine			Beraldi-Campesi and Garcia-Pichel (2011)
Recent	Texas coast	United States	Tidal			Bose and Chafetz (2009, 2012)
Recent	Tunisian sabkhas	Tunisia	Tidal			Bouougri and Porada (2012)

described within the original papers were to be redefined using the gradations of certainty implied in the terminology proposed in Section 4.3 (and a confident reassessment is beyond the scope of this paper). As such, the literature survey cannot be claimed to show an accurate distribution of true MISS through geological time, but does reveal potential biases and misconceptions amongst those structures presently interpreted as microbially induced.

2.2.1. Stratigraphic range of reported MISS

The stratigraphic distribution of reported MISS in the literature survey is illustrated in Fig. 2. Fig. 2a shows that, contrary to received claims (e.g., Gehling, 1999; Hagadorn and Bottjer, 1999; Porada and Bouougri, 2007a, 2007b; Sarkar et al., 2011; Bose et al., 2012), 60% of the presently reported MISS-bearing rock units are actually Phanerozoic in age. The false perception of an existing Precambrian dominance may result from a visibility bias arising from the aims of the original papers, shown in Fig. 3. For studies recording MISS in Precambrian strata, 92.2% were concerned directly with highlighting the occurrence of MISS as the main focus of the study (the remainder discussed the importance of MISS as taphonomic factors in the preservation of Ediacaran fossils). The survey yielded no studies of Precambrian strata where MISS were only recorded as one aspect amongst many of facies character. This contrasts with Phanerozoic strata, where 20.9% of the MISS occurrences were recorded incidentally as simply one aspect of facies character. These incidental reports of MISS came from studies that were primarily concerned with other facets of a given rock unit, and have not been as

A   **B**
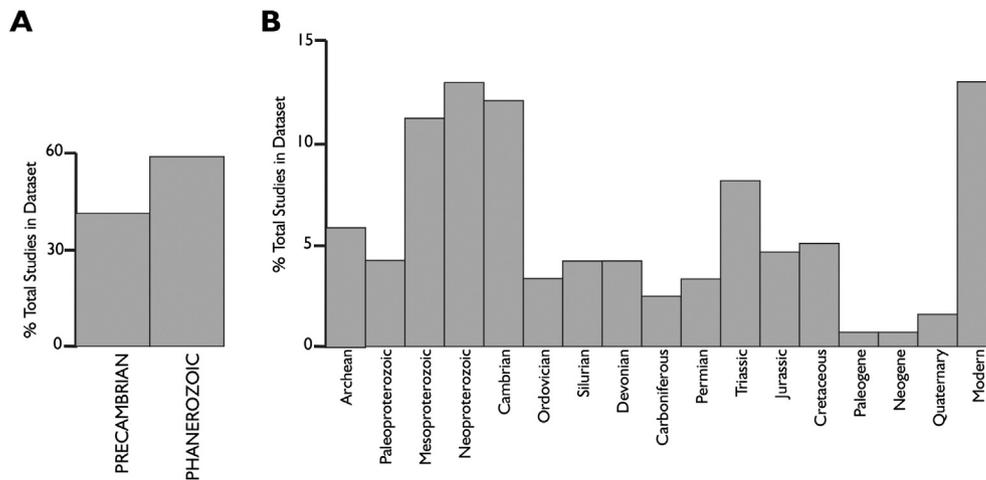
Fig. 2. Distribution of reported MISS in the global stratigraphic record, from studies listed in Table 1. (a) Proportion of MISS recorded in the Precambrian and Phanerozoic. (b) Proportional distribution by Eon (for Archean), Era (for later Precambrian) and Period (for Phanerozoic). Note that, where given age crossed two periods (e.g., Silurian–Devonian), a 0.5 value was given to each period.

widely cited as MISS-bearing units compared to those where the reporting of MISS was the primary topic of a paper. We suggest that the greater sedimentological, palaeontological and ichnological diversity of Phanerozoic units means that MISS, where they are recorded, are more likely to be considered as just one aspect amongst many of the character of a rock unit. In contrast, in Precambrian units that often lack body and trace fossils and tend to be less sedimentologically diverse, MISS are both more likely to be noticed and also perceived as a key characteristic of a unit that warrants reporting in a MISS-specific publication.

Whilst Fig. 2a clearly demonstrates that it is now possible to say that *known instances* of MISS-bearing *rock units* are more common in the Phanerozoic than the Precambrian, we caution against a literal reading of this trend as a true reflection of MISS abundance through geological time, due to the completeness of the rock record and a lack of resolution beyond rock unit-scale in the database. Even assuming that the rock record at outcrop has been sampled efficiently (Dunhill et al., 2012), two opposing factors remain that indicate that further testing of MISS abundance through time is required. On the one hand, it may be argued that MISS are only perceived to be more abundant in the Phanerozoic because far more undeformed and unmetamorphosed strata of that age are exposed. However, counterbalancing this bias, Precambrian examples in the dataset represent perhaps as much as 2.0 to 2.5 billion years, in contrast to some 0.5 billion years for the Phanerozoic examples; thus the Precambrian numbers could be argued to be less prominent.

Furthermore, we emphasise that the survey cannot account for the abundance of MISS *within* individual rock units, as this information is rarely recorded in the original papers. It may be that Precambrian MISS-bearing units contain such features on a majority of bedding surfaces and that the frequency of their occurrence diminishes drastically in the Phanerozoic: or, conversely, it may not. At present it is problematic to state either case with certainty without relying on anecdotal evidence, as papers documenting MISS rarely shed light on the proportion of bedding planes in a unit that are actually devoid of MISS. The absence of hard data documenting the relative proportions of MISS-bearing bedding planes to MISS-devoid bedding planes in both Precambrian and Phanerozoic sections, as well as the proportion of individual bed surfaces covered with MISS, requires rectifying in future studies in order to permit the development of a more refined understanding of the stratigraphic and environmental distribution of these features.

Fig. 2b shows reported MISS occurrences for subdivisions of the Precambrian and Phanerozoic and reveals a moderate spike in reported MISS occurrences during the Triassic, previously postulated to reflect

subdued burrowing in the wake of the end-Permian mass extinction (e.g., Pruss et al., 2004; Chu et al., 2015). However, the trend may again reflect a visibility bias: almost every instance of Triassic MISS was reported within papers focussed on demonstrating the existence of MISS in Triassic strata (Table 1, Fig. 3; the only exception being an incidental report from the Triassic–Jurassic Santo Domingo Formation of Argentina (Genise et al., 2009)). We suggest that, after the first description of MISS, Early Triassic rocks were quickly identified as likely MISS-bearing and were actively searched for such features by researchers, whilst 'unexceptional' intervals of the Phanerozoic were relatively overlooked. This artefact is made more visible by a bias arising from the editorial policy of 'high impact' journals, which tend only to publish reports of MISS in the geological record when they are found in conjunction with episodes of significance for evolution or extinction. In future years, the intensity of this apparent spike may diminish as more instances of MISS are reported from 'unexceptional' intervals of geological history: potentially mirroring the record of carbonate microbialites, where a previously supposed Early Triassic boom has recently been brought into question (Gingras et al., 2011; Vennin et al., 2015). The reduction in bioturbation across the Permian–Triassic boundary (e.g., Twitchett and Barras, 2004; Hofmann et al., 2015) appears to be a genuine trend when compared with a significant pre-existing archive of ichnological records from neighbouring geological periods. We suggest that the supposedly concurrent 'explosion' of MISS requires further investigation of, and comparison with, the MISS record of 'unexceptional' intervals to ensure that it is not a sampling artefact.

A third major trend seen in Fig. 2 is a significant dip in the number of reported MISS instances during the Cenozoic. Such a trend has previously been noticed for specific MISS such as "Kinneyia" wrinkles (Porada et al., 2008). Given the persistence of MISS in older strata and at the present day, it is highly unlikely that this dip reflects a lull in microbial mat activity. Rather, it may reflect the larger proportion of unconsolidated sediment of this age and the correspondingly lesser number of bedding plane exposures where MISS may be found: in almost all the Paleogene to Quaternary instances listed in Table 1, MISS are inferred from bed profiles rather than bedding planes.

Figs. 2 and 3 confirm Noffke's (2010) assertion that MISS or MISS-like structures are present in the sedimentary record from the Archean to the present day, but also illustrate that certain stratigraphic intervals have received more research focus than others. The Early Triassic and the Precambrian are unquestionably interesting episodes in which to search for evidence of microbial life. Following the tenet that the 'present is the key to the past', direct comparison of their sedimentary signatures with those of equivalent modern environments will
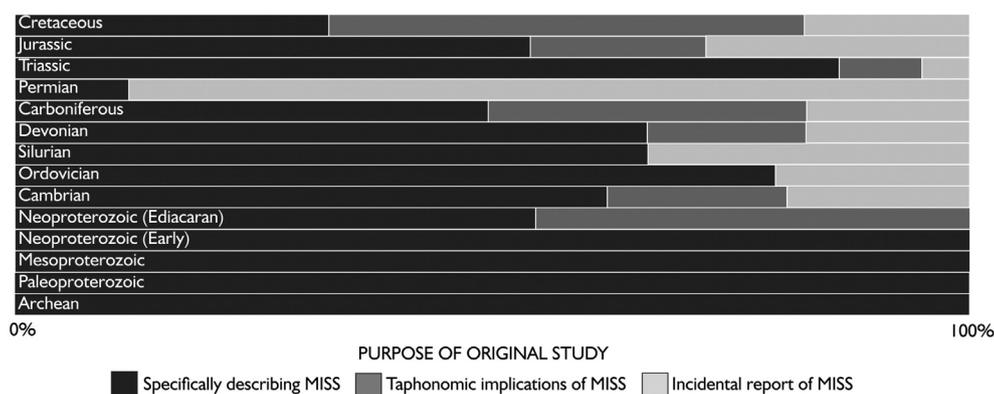
Fig. 3. Purpose of studies describing MISS for each interval, shown as a proportion of total studies (each individual reference in Table 1 considered as a discrete datapoint). Purpose divided into (a) studies where the description and interpretation of the presence of MISS was the main focus of the paper, (b) studies where the taphonomic importance of MISS was the main focus, and (c) where the presence of MISS was noted incidentally, as one sedimentary feature amongst many others.

doubtless reveal profound differences that may require a non-actualistic explanation. However, this does not preclude the fact that, when looking at a Neoproterozoic succession, there are 541 million years-worth of intervening strata in which there could be intervals where the differences are not quite so stark. A renewed focus on suspected microbial signatures in hitherto overlooked Phanerozoic strata may yield important insights into the contributions of microbial activity to the geological record.

2.2.2. Environmental range of reported MISS

Fig. 4 highlights the interpreted palaeoenvironmental settings of the MISS-bearing units in Table 1. The environments have been split into four categories, based on the descriptions in the original papers. Of these, "paralic" refers to any facies interpreted as supratidal, intertidal or shallow subtidal, and "nonmarine" encompasses lacustrine, alluvial and desert environments (listed separately in Table 1). The chart shows a continuous pan-environmental record of MISS from the Archaean to the present day. The greater proportion of paralic or tidal MISS in the Precambrian may reflect the relative rarity of other diagnostic facies signatures (sedimentary and palaeontological) for distinguishing marine versus nonmarine deposition during that interval, and a tendency to rely on analogy with the modern tidal environments where MISS are most commonly studied today (e.g., Gerdes et al., 2000; Cuadrado et al., 2014). For these reasons, the distribution seen for the Phanerozoic is arguably most reflective of the true distribution at any point in Earth history (as the Phanerozoic has a balance of easier sedimentological or palaeontological differentiation of marine vs. nonmarine facies than for the Precambrian, and more equal accessibility to continental through deep-marine strata than for the modern). Shallow-marine MISS are proportionally more commonly recorded in the Phanerozoic than the Precambrian or recent (Fig. 4, Table 1). This seemingly refutes the suggestion that the evolution of bioturbation resulted in the *total* disappearance of subtidal mats after the Cambrian (e.g., Seilacher, 2007)

2.2.3. Implications for non-actualistic and anachronistic facies

This literature survey suggests that previous statements that MISS are dominantly Precambrian and shallow-marine or tidal features are questionable. Fluctuations in MISS abundance in response to factors such as metazoan grazing may be more subtle than has previously been envisaged. The assumption that MISS are anachronistic features because they are most commonly present when metazoan grazing is subdued may lead to over-interpretation from an individual occurrence of MISS, and requires robust integration of other sedimentological, ichnological and palaeontological data (e.g., Buatois et al., 2014).

Schieber et al. (2007b) highlighted the fact that microbes with the potential to form mats have been ever-present in a multitude of

environments since the Archean (Tice and Lowe, 2004), and that matgrounds occur only when populous microbial communities have been able to adopt mat formation as a strategy for optimising their survival. As they note, the Cambrian advent of certain metazoans did not eliminate these constituent microbes, and it is equally true that it has never just been competition from metazoans that hinders mat formation: highly localised microbial population levels and constituents, sedimentation rate, chemical conditions, interference from non-metazoan eukaryotes, and hydrodynamic energy may hinder or promote mat formation (e.g., Seilacher and Pflüger, 1994; Hagadorn and McDowell, 2012; Mata and Bottjer, 2013). The evolution of bioturbation and grazing clearly added an additional constraint on mat formation (Buatois and Mángano, 2012), but it was never, and is not, the only such constraint. In reality, highly variable physico-chemical factors and the excess spatial availability of sedimentary substrate versus the abundance of bioturbators or mat-forming microbes result in a distribution of both mats and bioturbation that is spatially patchy even today.

The previously perceived distributions of MISS have been used to speculate upon non-actualistic conditions, and correspondingly unique sedimentary records, during certain intervals of Earth history. Bose et al. (2012) claimed that almost all wet sediment surfaces within the photic zone were colonized by microbial mats during the Precambrian, although there is actually no physical evidence for this: certainly not *every* waterlain bedding surface of Precambrian sedimentary rock shows evidence for microbial mat colonization, even in the form of putative MISS. The relative abundance of microbial mats on Precambrian shallow-marine shelves has been suggested to have played a role in determining deposition, erosion and sedimentary architecture in the Precambrian marine realm (Eriksson et al., 2013).

The oldest reported non-marine MISS occur in the Paleoproterozoic (Simpson et al., 2013) and it has been suggested that microbial communities would have been important for stabilising Precambrian rivers and modulating sediment delivery (Bose et al., 2012; Petrov, 2014, 2015). However, this has been disputed by Long (2011) who highlighted the apparent scarcity of convincing MISS-like structures within fluvial sandstones of that age. MISS are also rare in pre-vegetation fluvial successions in the early Palaeozoic (Davies and Gibling, 2010; Davies et al., 2011), suggesting that: (1) even where non-marine microbial mats did form, in the majority of instances they could not resist reworking during fluvial flood events, and so could be argued to have had a negligible net effect on global river functioning, and (2) as, in most instances, there was a high propensity for physical reworking, the record of MISS in ancient alluvium will be significantly incomplete and unlikely to provide clues regarding the actual abundance of microbial mats in the Precambrian nonmarine realm. We contend that, when compared with the sedimentological impact of even the most primitive embryophytes (Davies and Gibling, 2010; Davies et al., 2011), microbial mats had a
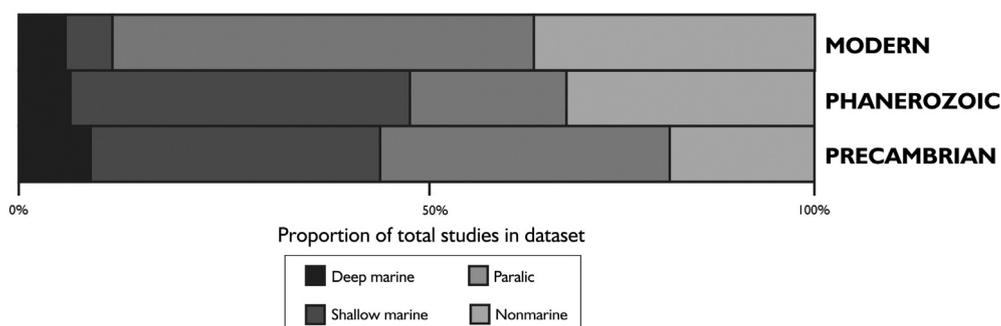
Fig. 4. Environmental distribution of recorded MISS (as a proportion of total studies) for the Precambrian, Phanerozoic and Recent.

minimal impact on rivers. The distinct sedimentary characteristics of Precambrian alluvium are more readily explained by the absence of vegetation (Long, 2011) than the abundance of microbial mats (even if the hypothesised fecundity of matgrounds is later proven to be a genuine characteristic of "pre-vegetation" rivers).

2.2.4. Implications for taphonomic studies

MISS have commonly been cited as one line of evidence for extensive microbial matgrounds during the latest Neoproterozoic. It has been suggested that matgrounds or biofilms created unique taphonomic conditions that permitted the preservation of soft-bodied Ediacaran macro-organisms as "death-mask assemblages" (e.g., Gehling, 1999; Gehling et al., 2005). However, our survey indicates that, even including a self-selecting bias (as matgrounds have been searched for in the Neoproterozoic), the recorded abundance of MISS in this interval is not markedly exceptional and only marginally greater than that of the Mesoproterozoic or Cambrian. Thus, evidence from the known stratigraphic distribution of MISS may lend support to the contention that the disappearance of the Ediacaran macrobiota was evolutionary, and not simply the result of the removal of a microbial mat-related taphonomic window (Buatois et al., 2013; Laflamme et al., 2013; Carbone and Narbonne, 2014; Darroch et al., 2015). This does not contradict observations that certain biofilms (rather than full MISS-forming microbial mats) may have played a key role in the ecology and taphonomy of Ediacaran organisms (Gingras et al., 2011; Meyer et al., 2013), but does underline the importance of making robust holistic comparisons with younger or unexceptional strata before asserting claims for non-actualistic taphonomic conditions.

In the literature survey, the Ediacaran Period is an interval from which MISS were particularly likely to be described as indicators of a microbial mat contribution to fossil taphonomy — in 45.5% of the Ediacaran-focussed MISS studies listed in Table 1. A further spike in studies using MISS to imply taphonomic conditions was seen in the Cretaceous – in 50% of the studies – and the values for both of these intervals are markedly higher than those for the other studied intervals (the next highest being the Cambrian at 18.8%; Fig. 3). In the Cretaceous instances, rather than referring to soft-bodied organisms, mats were often deemed to have increased the quality of dinosaur footprint preservation (see Section 4.3). We note that no claims have been made that this apparent abundance of MISS accounts for the post-Cretaceous disappearance of dinosaur footprints from the rock record. However, the marked spikes in these two intervals might suggest that the potential taphonomic importance of MISS is more likely to be invoked when fossils of heightened academic interest happen to be found on bedding surfaces (i.e., found preserved in the same bedding-parallel orientation as MISS).

2.2.5. Implications for the composition of microbial communities

Fig. 4 shows that a high proportion of reported MISS-bearing strata were deposited outside of the photic zone, illustrating just how common non-photoautotrophic mats are in the rock record. For example, between 6–9% of recorded MISS come from deep-marine environments in modern, Phanerozoic and Precambrian instances. This has implications for the micro-organisms responsible for the formation of MISS, which have often been assumed to be cyanobacteria based on the misconception that MISS only occur where photoautotrophic organisms were able to survive (Noffke, 2009; Mata and Bottjer, 2009a). This misconception is a recent development. Early work on suspected microbial structures stressed that, particularly in deep-marine environments, microbial mat structures were unlikely to have been photoautotrophic (Simonson and Carney, 1999), but since then most MISS are routinely interpreted as dominantly cyanobacterial. In a textbook on MISS, Noffke (2009) explicitly stated that it was not proven to be the case that all MISS must have been produced by cyanobacteria. However, that textbook still stated, as one of the criteria for establishing the biogenicity of MISS, that "MISS [must] occur in the 'microbial mat depositional facies' that enhances development and preservation of photoautotrophic microbiota" (Noffke, 2009, p. 176). Mata and Bottjer (2009a) listed a number of potential MISS (specifically, wrinkle structure) producers, including cyanobacteria, colourless sulfur-oxidizing bacteria (such as the family *Beggiatoceae*) and green sulfur bacteria, but concluded that cyanobacteria were the primary candidates responsible for the formation of wrinkle structures, because "wrinkles structures are observed to occur almost exclusively in palaeoenvironments no deeper than shallow shelf, suggestive of organisms with a dependence on photosynthesis" (Mata and Bottjer, 2009a, p. 189). As a caveat, they did also note that this was not an easy attribution for all wrinkle structures, citing the wrinkle structures in deep-marine turbidites described by Buatois and Mángano (2003). However, as the actual abundance of known deep-marine MISS is clearly far greater than one case study, it can be noted with certainty that non-cyanobacterial microbial communities have created MISS and that these have been preserved in the geological record.

Micro-organisms that form mats, and potentially MISS, come from all three domains of the tree of life and include bacteria, archea and diatoms. However, it is presently impossible to determine the particular community responsible for the formation of MISS from the morphology of sedimentary surface texture alone. Even where actual fossils of micro-organisms exist it can be impossible to visually determine their phylogenetic affinity (e.g. distinguishing between microbial filaments of sulfur-oxidizing bacteria and cyanobacteria; Williams and Reimers, 1983). Modern observations of MISS actively being produced by filamentous *Beggiatoceae* in intertidal to deep-marine settings (Flood et al., 2014) have demonstrated that the microbial communities need not necessarily have been photoautotrophic in any instance in geological time, and the pan-environmental facies distribution of these features since the Archean (Fig. 4) demonstrates that many probably were not. The mat-forming capabilities and constraints of Precambrian bacteria are assumed to be consistent with modern analogues, but this need not necessarily be so: we don't currently know, for example, when EPS formation would have evolved. Furthermore, other organisms, such as algae, may blanket a substrate without forming a true mat, but are equally capable of imparting MISS-like textures onto sedimentary

substrates (see Section 3). Without preserved fossil context it may be impossible to discern whether or not algae were present during the formation of the textures being studied, but as they have been present across both marine and nonmarine environments since at least the Neoproterozoic (Wellman and Strother, 2015), their potential contribution to the formation of sedimentary structures should not be overlooked.

2.3. Summary of the distribution of reported instances of MISS

The above sections highlight the fact that the record of features described as MISS extends from the Archean to the present day and across a wide variety of environments. MISS are not dominantly Precambrian features (as presently recorded), they are unlikely to demonstrate (in themselves) particular non-actualistic conditions, and they cannot all have been formed by photoautotrophic cyanobacteria. The breadth of potential strata in which MISS may occur limits their merits as tools for palaeoenvironmental reconstruction where only their presence or absence is considered. However, when they are considered as one aspect of a suite of sedimentological and ichnological data their recognition can shed valuable light on the specific depositional conditions of a given environment. Greater understanding of the significance of MISS will develop if they are considered as just one aspect of a studied rock unit: the future collection of data regarding the proportion of MISS-devoid bedding planes within MISS-bearing rock units promises to shed new light on the true stratigraphic and environmental distribution of MISS in the geological record.

The increased recognition of MISS in recent years shows how prevalent these features are in the rock record: arguably so much so that they should no longer be considered extraordinary when they are encountered in strata of any age or facies. However, although microbial mat communities feasibly and commonly induce sedimentary surface textures on bedding planes, they are not the only potential mechanism for the development of "MISS-like" features. Multiple abiotic process also induce similar features, but the current terminology and research trends in MISS studies have led to the understanding and recognition of these becoming increasingly marginalized. MISS misconceptions have additionally arisen due to the often imprecise classification and terminology that is currently in use. The following section addresses these issues, and demonstrates how considering MISS as one common and expected subset of a spectrum of microbial and abiotic sedimentary surface textures can provide a practical means of recognizing, describing and interpreting these features in the geological record.

3. Revaluating MISS terminology

Existing classification schemes for MISS in the rock record are profuse and often conflicting. Noffke et al. (2001) proposed two overarching classifications dependent on whether MISS were observed on bedding planes or internally within sedimentary beds, and Noffke (2009, 2010) subsequently identified 17 types of MISS based on their mode of genesis (within four groups associated with biostabilization, baffling/trapping, growth and binding). Schieber (2004) offered an alternative classification of MISS on the basis of processes involved in their formation. Sarkar et al. (2008) classified MISS depending on whether their form was due to sedimentary structures being induced by microbial mats, representing fossilized mat growth, or having been protected by microbial mats. Eriksson et al. (2010) suggested reclassifying some MISS as MRS (microbially-related sedimentary structures), while Gehling and Droser (2009) classified some Ediacaran MISS within a broader class of textured organic surfaces (TOS). These terms all carry explicit connotation that microbial or organic activity has played a role in the formation of a given feature. This can be clearly demonstrated in modern environments, where the use of microbial-specific terminology is wholly appropriate (Bouougri et al., 2007; Cuadrado et al., 2014). However, for studies concerning the rock record, except

in rare instances where fossilized proof of microbial activity is later found to be exceptionally preserved, the application of the term 'MISS' may unsatisfactorily conflate description and interpretation. In effect, the rapid rise of studies into MISS has led to a surfeit of definitions and redefinitions that have resulted in a paucity of terminology appropriate to describe sedimentary surface textures without adding a layer of interpretation. None of the existing schemes are capable of satisfactorily accounting for (1) the fact that abiotic processes can also result in morphologically-similar pseudo-MISS (e.g., Kocurek and Fielder, 1982; Allen, 1985; Long, 1993, 2007; McLoughlin et al., 2008), or (2) that the geological record contains an overwhelming abundance of sedimentary surface textures, the majority of which may never have their origin conclusively resolved, and for which it is unsatisfactory to have to presuppose either the presence or absence of microbial mats.

In practice, it can be impossible to assign a specific texture in the rock record into these classification schemes, which do not allow passive description of a texture. This is particularly true when textured surfaces are first encountered during field-based studies — in the absence of non-interpretive terminology, and without immediate proof of microbial involvement, it is often challenging to find primary descriptions for the multitude of irregular surface textures that may be found in an outcrop. As a result, many MISS studies have opted for informal descriptions of textures on a case-by-case basis, resulting in a slew of terminology. A comprehensive catalogue of such terms is beyond the scope of this paper, but commonly used terms include descriptors such as "multiple-directed ripple marks" (e.g., Noffke, 1998), visual comparisons such as "elephant-skin texture" (e.g., Runnegar and Fedonkin, 1992), descriptions with implicit interpretation such as "gas domes" (e.g., Noffke, 2010), relics of retired (non-italicized) taxonomic nomenclature such as "Kinneyia" or "Manchuriophycus" (e.g., Porada and Bouougri, 2008) or "wrinkle structures" (e.g., Mata and Bottjer, 2009a). Other less common examples include "cauliflower structures" (e.g., Gerdes et al., 1993), "lizard-skin textures" (e.g., Eriksson et al., 2007b), "microbial buns" (e.g., Kumar and Ahmad, 2014), "molehill-like structures", "pepperpots" and "fairy rings" (e.g., Gerdes et al., 1994; Marriott et al., 2013). Here we would argue that such flexible terminology is pragmatic when faced with the extreme diversity of MISS-like forms. It is clearly not a taxonomic approach, but it fulfills the current purpose of exploring the diversity of these textures. However, when using such informal terms, care should also be taken to ensure that these terms are consistently applied. "Elephant-skin texture" has by now become a bucket term used to describe so many morphologically-different textures that it is has become effectively meaningless (e.g., compare, amongst numerous other examples, the morphologically distinct 'elephant skin' in Bottjer and Hagadorn, 2007, Fig. 4; Porada and Bouougri, 2007b, Fig. 2C; Kumar and Ahmad, 2014, Fig. 6D; Beraldi-Campesi et al., 2014, Fig. 2G). For this reason, regulation and organisation of these terms will be desirable in the future.

Many MISS share identical or similar morphologies with features created by non-microbial processes (Gingras, 2002; Porada and Bouougri, 2007a, 2007b; Shepard and Sumner, 2010), and so are not diagnostic of biological activity through visual comparison alone. Unfortunately, an apparently common implicit attitude to sedimentary surface textures at present may arguably be paraphrased as "if it can't be proven to be MISS, it isn't relevant". This attitude risks blinding the geological community to many features (abiotic or otherwise) that may be significant for the characterization or interpretation of specific sedimentary units. The need to provide terminology that both encompasses and distinguishes between biotic and abiotic formation mechanisms for sedimentary surface textures is emphasised by the history of research into wrinkle structures.

3.1. The wrinkle problem

Sedimentary structures resembling small wrinkles have long caused consternation amongst geologists (e.g., Häntzschel and Reineck, 1968;

Reineck, 1969; Hunter, 1969, 1973; Teichert, 1970; Klein, 1977; Singh and Wunderlich, 1978; Kopaska-Merkel and Grannis, 1990; Hagadorn and Bottjer, 1997, 1999; Porada and Bouougri, 2007a, 2007b). Prior to the appreciation that some of these may be of microbial origin (Hagadorn and Bottjer, 1997, 1999; Porada and Bouougri, 2007a, 2007b), runzelmarken or runzelmarks (literally "wrinkle marks" from German) were first described by Reineck (1969) to refer to a series of irregular markings observable in both modern tidal flats and the geological record. Klein (1977), in a survey of sedimentary structures forming in active tidal environments, used 'runzelmarks' as a catch-all to refer to a variety of features having visual similarity of form, but different (abiotic) formative mechanisms. His application of the terminology meant that 'runzelmark' referred solely to the physical texture left on a sedimentary substrate, clearly stating that almost identical runzelmarks could form from mechanisms ranging from the suction of sediment by beach foam to the reworking of raindrop impressions by wave swash. This approach was criticised shortly afterwards by Singh and Wunderlich (1978) who argued that it was inappropriate to group multiple structures together if they clearly had different formation mechanisms. In this instance, Singh and Wunderlich (1978) arguably made a valid case: if the formation mechanism can be actively observed, then the description of a given sedimentary feature should reflect that. However, Klein's (1977) approach is by far the most appropriate for geological studies of relict textures. By reserving terminology for the passive description of a physical texture on a sedimentary surface, observation and interpretation can be clearly separated; this is essential when it is clearly realised that visual similarity of form does not constitute scientific proof of a common origin.

Hagadorn and Bottjer (1997) were amongst the first to successfully demonstrate that wrinkles on bedding surfaces could also be produced by microbial action, but their survey of previous descriptions of wrinkle formation underrepresented those studies that had found wrinkles forming in the absence of microbial mats. As an example, they wrote (p. 1047) that "Allen (1985) invoked purely physical mechanisms of sediment loading to account for surface structures" in tidal sediments of the Severn Estuary in southwest England — yet the abiotic formation of those wrinkles was not just invoked: it was clearly observed, described and figured in the original paper. Subsequently, in a review of modern and ancient wrinkle structures, Porada and Bouougri (2007b) accepted that both abiotic and microbial processes could produce wrinkled sediment surfaces but, in an attempt to resolve confusion arising from contrary historical definitions of 'wrinkle *marks*', 'wrinkle *structures*' and 'runzelmarken', made the recommendation that the term "wrinkle structure" should be reserved solely for those structures where a microbial origin was deemed "likely but a clear classification not possible". Subsequently, Mata and Bottjer (2009a) claimed that, although many hypotheses had been put forward for the formation of wrinkles, "nearly all… [were] requiring the presence of a cohesive microbial mat at the sediment's surface". This statement ignored the abundance of pre-MISS sedimentological literature that documented their formation in the absence of microbial mats by purely physical loading, deformation or shearing (e.g., Dzulynski and Walton, 1965; Dzulynski and Simpson, 1966; Reineck, 1969; Teichert, 1970; Corbett, 1973; Singh and Wunderlich, 1978; Reineck and Singh, 1980; Allen, 1985; Gibling and Stuart, 1988; Kopaska-Merkel and Grannis, 1990; Long, 1993) and the recommendation of McLoughlin et al. (2008) that the term should only be defined in a non-genetic way (similar to Klein, 1977), given that similar features can be produced synthetically.

In light of the clear existence of abiotic wrinkles, the hijacking of the purely textural descriptor "wrinkle structures" as an exclusively MISS term leaves a nomenclatural void for a vast array of sedimentary structures formed by non-microbial processes. If this protocol continues to be accepted, many putatively abiotic sedimentary structures now lack a passive descriptive terminology, unless a formative mechanism can be inferred (e.g., micro-loading, adhesion marks, swash marks). Thus,

the recommendation of Porada and Bouougri (2007b) is untenable outside of studies whose objective is to actively search for MISS.

Herein, we use the term "wrinkle" simply to record a certain morphological character of sedimentary bedding planes, without inference of formative mechanism, consistent with the description of other sedimentary structures. The same approach has precedence with other sedimentological terms such as "ripple". A ripple (mark) is simply a microform on top of a substrate, and the terminology thus refers to morphology alone: further interpretation and explanatory context is required to determine process of formation (for example, superficially similar microforms may be formed as a ballistic ripple by saltation in air, or by steady tractional grain migration in flowing water). In this way, "wrinkles" are defined as irregular, parallel or networked assemblages of (sub)millimetre-scale surficial ridges and/or pits on a bedding surface. The term is applied non-genetically as wrinkles can have multiple microbial or abiotic origins (Klein, 1977; McLoughlin et al., 2008), and different types, amongst other sedimentary surface textures, are discussed in Section 3.3.

3.2. Sedimentary surface textures: an umbrella term for MISS, problematic and abiotic features

In light of the issues discussed above, we here propose a new classification scheme, introducing "Sedimentary Surface Textures" as an umbrella-term that incorporates MISS, abiotic textures, and problematic textures, to enable better distinction and description of them all. Fig. 5 illustrates this concept: a sedimentary surface texture is a purely material characteristic of the fabric of a bedding plane; determining the pathways of its origin requires inductive reasoning. Sedimentary surface textures include a wide range of early-formed features observed on bed surfaces that may be microbially-induced (MISS), generated by one or more abiotic processes, or include an array of features of biotic and abiotic origin. They are commonly cryptic due to the subtle and varied imprint imparted by these processes; the likely tendency of microbial and abiotic features to be superimposed on each other; and the vagaries of diagenesis, deformation and weathering. The term is intended for practical use in the field and laboratory, explicitly acknowledging the difficulty of working with subtle biotic and abiotic features, many of which are problematic to describe and to attribute to particular processes. Associated with the use of the term is a qualification of the level of certainty in recognising the features as biotic or abiotic: this is discussed separately in Section 4.3., following the review of potential formative mechanisms in Section 3.3. Once the degree of certainty is established, other more specific and genetic classifications may be applicable. We believe that this approach will be of value for analysing purely physical as well as biological features, and may also have utility in evaluating other problematic features, including some structures previously described as trace fossils.

With an already overwhelming glossary of terms it may be seen as undesirable to promote new nomenclature, but the proposed approach addresses a number of problems arising from the current terminology for MISS-like structures: (1) resolving the problem that a conclusive demonstration of a microbial role in the formation of these textures may be initially impossible or impractical, yet the textures themselves can still be significant sedimentary characteristics of particular rock units; (2) permitting a terminology that clearly encompasses abiotic and problematic textures and so prevents the need for sensationalist claims for MISS occurrence; and (3) an increased recording of potentially microbial structures from those geological investigations for which it may be impractical to thoroughly test every single sedimentary surface texture for conclusive proof of a microbial role.

Illustrating the compelling need for such a classification scheme, Noffke (2015) suggested that, through perceived visual similarity of form, certain textures that were imaged by the NASA Curiosity Rover on Mars may be microbially-induced sedimentary structures. However, the most parsimonious interpretation of these particular features is that

they are abiotic erosion and weathering textures that postdate the deposition of the Martian sedimentary rocks – their similarity to terrestrial MISS is superficial at best. If evidence for ancient microbial life is found on Mars, it may well be most evident from indirect clues such as MISS, but the magnitude of such a discovery would necessitate strong evidence. The new terminology proposed here clearly separates textures that are testable possibilities from definitive MISS, allowing observations to be described without inadvertently making sensational claims.

It should be noted that certain forms of MISS do not fall within the classification of sedimentary surface textures as they form larger discrete sedimentary structures, rather than patterned bedding planes. Examples include roll-up structures and rip-up clasts arising from shear-forced structural failure of a mat. Fossilized roll-ups, sand chips and erosional remnants of mats are clear 'body fossil' evidence of former microbial mats (see, for example, Fig. 11g-h; Beraldi-Campesi and Garcia-Pichel, 2011; Bouougri and Porada, 2012) and occur due to tearing of the mat under flow regimes that would induce ripple, dune or plane-bed conditions on a naked substrate (Hagadorn and McDowell, 2012).

3.3. The formation of sedimentary surface textures

Sedimentary surface textures arise because of the disturbance, reorganisation, removal or addition of sediment grains on a substrate, before or shortly after burial. The sole difference between abiotic structures and MISS is that during the formation of MISS, the substrate was coated with an organic, elastic veneer comparable to "static and well-ordered water" (Krumbein, 1994; Vignaga et al., 2013) that affected substrate rheology, stability, and resilience to physico-chemical stresses. In the following sections we group sedimentary surface textures by the type of physical process that has acted upon them, and consider how the presence or absence of a microbial mat could mediate the signatures of these processes. We illustrate the variety of sedimentary surface textures found in the rock record (and actively forming in modern environments) with reference to the main process involved: (1) Sticking (adhesion, accretion and baffling); (2) Loading; (3) Fluid or gas escape; (4) Impression; (5) Shear; (6) Shrinkage; (7) Palimpsested and problematic origins (Fig. 5).

In each of the following instances it is important to distinguish between how these structures may be formed within a mat itself, and how they may be formed within the underlying sedimentary substrate (e.g., by mats dredging up underlying grains (Noffke et al., 2001)). The surficial forms that may develop on or within the mat membrane require preservation of original mat material if they are to enter the rock record. Where sedimentary surface textures occur in granular sediment, on bedding planes that lack evidence for fossilized mats, any observable similarity between them and the observable textures formed within modern microbial mats is likely to be superficial. For example, Thomas et al. (2013) were able to experimentally reproduce "Kinneyia" forms in a synthetic mat, but their explanation of how such forms could be transferred into the underlying substrate in the absence of the original organic material was speculative. In other instances, observations of structures forming in actual mat material, such as those arising from the tangling of microbial filaments (Shepard and Sumner, 2010), are clearly more likely to be translated into the rock record as they actively induce new processes (such as baffling). It is crucial to recognise that surficial pattern formation on any medium above a substrate (be it fluid water or a microbial mat) does not necessarily result in an identical pattern forming in the granular sediment that underlies it. For example, during vigorous oscillation of a water body, the crests of the ripples on the moving water will be sharp, whilst the resultant ripple marks on the sediment surface will be smoothed, with the obverse true of gently oscillating wave ripples. How the surficial form of a microbial mat is translated into underlying sediment is poorly understood, and (depending on mat thickness, species, grain-size) may not necessarily observe a universal rule of (dis)similarity. The problem with identifying this in field examples of modern mats is that (1) the mats may be opaque, exhibiting no clue as to the underlying sediment form; and (2) if the
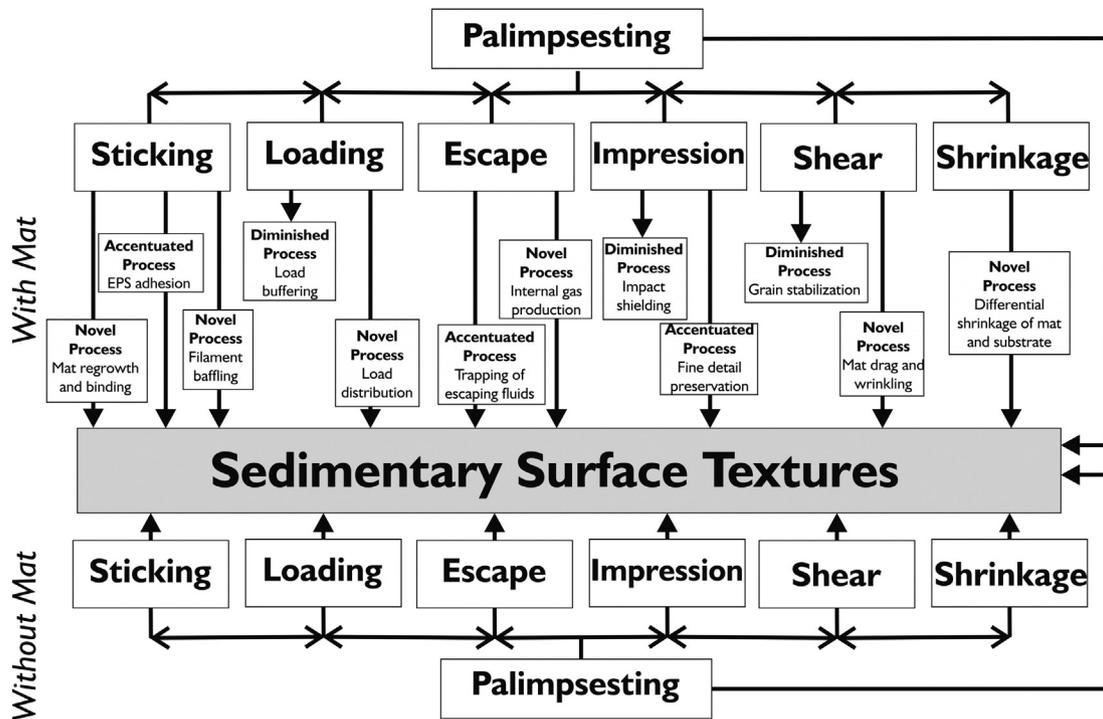
Fig. 5. Pathways involved in the creation of sedimentary surface textures, both in the presence and absence of MISS. The presence of a microbial mat may promote accentuated formation of a texture that would form on a naked substrate, diminish the formation of a texture, or result in a novel texture that could not form in the absence of a mat. Each of the illustrated pathways may be expected to result in a discrete texture for a given set of constants (e.g., grain-size, rate and intensity of process). Spatial and temporal variability in nature means that the diversity of potential textures is far greater than implied in this figure. In occurrences that are not actively forming, only the sedimentary surface texture itself is immediately presented, so determining the pathways involved in its formation requires inductive reasoning.

sediment itself is unconsolidated, it cannot be separated from the sticky viscous mat for observation purposes without disturbing any surface texture present.

3.3.1. Textures formed by sticking (adhesion, accretion and baffling) (Figs. 6-8)

Sedimentary substrates may accrete additional grains by packages of individual grains sticking to them and, in doing so, develop discrete sedimentary surface textures. The stickiness of the substrate may be abiotic (e.g., due to pore water tension, or cohesive sediment), or biotic (e.g., from EPS, or baffling by microbial or algal filaments).

Adhesion ripples (recorded in older literature as aeolian microridges or antiripplets), adhesion warts and asymmetric adhesion warts are the most common abiotic sedimentary surface textures induced by an adhesive substrate (Fig. 6). Adhesion ripples develop where dry sand is blown by wind over a moist substrate. Water capillary action between the grains on the receptive substrate permit sand grains to stick to the surface, and the adhesion ripples build out into the direction of the oncoming wind, with their steeper sides facing the wind direction (Fig. 6a-d,g) (Van Straaten, 1953; Kocurek and Fielder, 1982). Where wind direction changes rapidly and grains fall vertically onto the wet substrate, adhesion warts form, without the linear arrangement seen in adhesion ripples (Fig. 6e-f,h; Reineck and Singh, 1980; Kocurek and Fielder, 1982; Olsen et al., 1989). Morphological variability of adhesion ripples and marks can be extreme, as properties of the sediment-water interface (in terms of the balance of capillary moisture and dry sediment supply) may exhibit rapid temporal variation as local sand-transporting winds vary in strength and direction, and sand dries. Adhesion features may also be palimpsested onto rain-sculpted surfaces (Section 3.3.4; Olsen et al., 1989). Successive generations of adhesion ripples may have a high angle of climb, and a relatively high preservation potential (Hunter, 1969, 1973). Even if the intricate detail seen in the textures of modern adhesion ripples is absent in examples in the rock record, irregular sedimentary surface textures (Fig. 1g) or cross-lamination (Fig. 7) may record their partial preservation.

In microbial mat settings, the adhesive qualities of EPS are well-documented (Lundkvist et al., 2007; Garwood et al., 2013; Malarkey et al., 2015), and it may 'glue' individual sand grains to a substrate — a process that may be seen in oriented sand grains in thin sections of microbial mats (Noffke, 2010). The accretion of sediment may also be promoted by the baffling of microbial mats. Reticulate wrinkles may develop on the surface of a microbial mat when randomly oriented filamentous bacteria glide, collide and clump together (Shepard and Sumner, 2010). There is potential that such a reticulate pattern may be translated into the sedimentary substrate by the baffling effects of the filaments (Noffke et al., 2001). Although these structures in bacterial mats require microbial cells to be motile, an analogue can be seen in the reticulate tangling of filamentous algae (Fig. 8), which appears to occur passively when algal strands tangle in standing or draining water, leaving them with the capacity to trap sedimentary particles and imparting a patchy reticulate texture to underlying sediments.

3.3.2. Textures formed by loading (Fig. 9)

When a layer of denser sediment-water slurry is superimposed over a lighter sediment-water substrate, the upper unit will load down into the underlying unit (Allen, 1982). Loading commonly results in the development of positive hyporelief bulbous textures on the base of a sedimentary bed, the diameters of which range from millimetres to tens of centimetres (Fig. 9). In conjunction with this, features in negative epirelief may be preserved on the top of the underlying bed (Fig. 9a): if these are particularly dense, then the underlying surface will be dominated by ridges (superficially appearing in positive epirelief) reflecting flame structures where the lower unit was squeezed between sinking lobes from the upper bed. Loading occurs across many scales, and exhibits intense variability dependent on whether there is also an element of current shear during loading, and the relative viscosities of the

loading and loaded sediments. Where the overlying sediment is more viscous than that on which it rests, as is most commonly the case, positive hyporelief pendulous lobes will form in the downsinking sediment (Dzulynski and Simpson, 1966). However, where the inverse is the case similar "lobes" will appear as positive epirelief in the underlying bed (Dzulynski and Simpson, 1966). Loading structures may be highly variable even along the same bedding surface (Dzulynski and Walton, 1965; Dzulynski and Simpson, 1966), due to natural variability in the viscosity of the overloading sediment (for example, downstream decreases in a turbidite due to dilution by ambient water). Wrinkles of apparently identical morphology to wrinkles in microbial mats may also form by abiotic loading in tidal environments (Allen, 1985; Hagadorn and Bottjer, 1997). In such instances, the relationship of the structures to syndepositional features (such as crossing trails, Allen, 1985) may show that they are the result of loading rather than microbial activity. As an example of this, Brasier et al. (2013) demonstrated that the 'bubble trains' of the Ediacaran Trepassey Formation of Newfoundland (Fig. 1f), originally suggested to be microbial roll-up features (Laflamme et al., 2012), were more likely load casts. The cross-cutting of ripples and sole-marks by the 'bubble trains', absence of evidence for their deformation by current action, and similarity to known loading features in turbidites (Dzulynski, 2001), together suggested that loading is the most parsimonious explanation for their formation.

Such examples illustrate that many pseudo-MISS sedimentary surface textures can be explained as a result of loading by overlying sediment, and do not require the presence of a microbial mat for their development. However, this does not preclude the fact that surfaces colonized by mats may be rapidly buried by sediment and experience loading themselves. In such instances, the presence of a microbial mat may resist loading by overlying sediment such that only minor loading is developed in instances where miniature ball and pillow structures would otherwise be expected in unprotected substrates (Schieber, 1986, 2004). Noffke (2010) suggested that many wrinkle textures could be produced by loading due to squeezing of water out of microbial mats after burial, although such a post-depositional process cannot been observed in modern microbial mats. Seilacher (2007) suggested that "elephant-skin textures" were miniature load casts formed underneath microbial mats.

Soft-sediment deformation may also be induced by increased pressure from the overlying water column (Dalrymple, 1979), and this has been suggested to permit the formation of wrinkles that may be indistinguishable from microbial mat related wrinkles. Long (1993, 2007) described wrinkled surfaces within sets of hummocky cross-strata. Given that the formation of hummocky cross-sets requires rapid accumulation of sediment under combined flow conditions (Dumas and Arnott, 2006; Immenhauser, 2009), Long (1993, 2007) argued that it was sedimentologically implausible that microbial mats could have sufficient time to form on the hummock surfaces. Instead, Long (1993, 2007) proposed that they developed due to grain collapse in the uppermost part of the sediment pile — pore fluid pressure was envisaged to increase through the cyclic application of stress at the storm wave base; ultimately the rapid dissipation of pore pressure would lead to a loss of shear strength and the development of wrinkles. In instances where there is no other evidence for hummock surfaces surviving for a prolonged interval at the interface of the substrate and water column (e.g., the appearance of grazing trails implying the opening of the colonization window), this purely physical process may be the simplest explanation for wrinkled hummocks.

3.3.3. Textures formed by fluid or gas escape (Fig. 10)

The escape of gas, air or water towards the surface of a substrate may lead to a number of primary sedimentary surface textures. In these instances, the main difference between a surface with a microbial mat and a bare substrate is that the former is more likely to trap the escaping fluid, and will also permit the primary production of additional gases as microbial communities respire and decay (Gerdes et al., 1993; Noffke
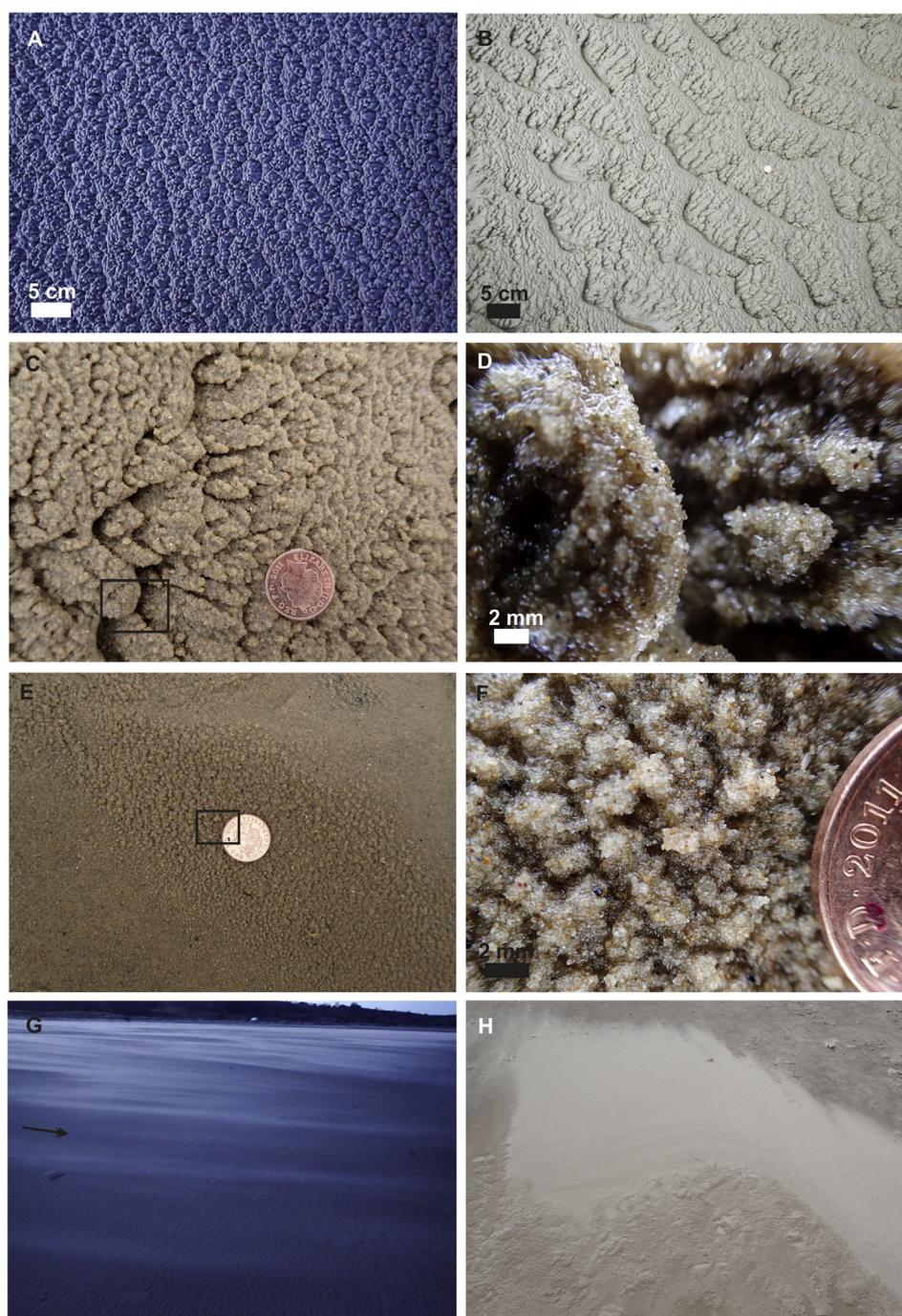
Fig. 6. Sedimentary surface textures formed by adhesion, accretion and baffling in modern sediments where microbial mats are absent. (a) Adhesion ripples with steep stoss sides (wind moving from left of image). Actively forming on wet beach sands below the high tide line during ebb tide, Alnmouth, Northumberland, England. (b) Flat topped adhesion ripples with adhesion ladder ripples forming in troughs. Actively forming in strong wind conditions as soon as water of tidal prism retreated during ebb tide, Het Zwin, Belgium. (c–d) Close-up images of stoss side of actively accreting adhesion ripples, showing extent of water tension in pores of sand and the initial adherence of wind-blown sand grains prior to their being subsumed by water tension. Actively forming on wet beach sands below the high tide at turn of ebb to flood tide, Holkham, Norfolk, England. Diameter of coin is 20 mm. (e–f) Close-up images of actively accreting adhesion warts at same locality, warts forming preferentially over ripples as they accrete on an inclined side of a drainage channel, sheltered from the wind. Diameter of coin is 20 mm. (g) Active formation of adhesion ripples as sheets of aeolian sand blow over wet beach (in direction of arrow). Movement by saltation is hindered as a proportion of grains become accumulated into stoss sides of adhesion ripples. Alnmouth, Northumberland, England. (h) Instantaneous preservation of adhesion warts. Adhesion warts formed during start of ebb tide when sand was wet. Continued drying of sand, coupled with drop in wind intensity, means that small low amplitude dune patches of dry sand now migrate slowly over previously formed adhesion warts (and footprints), offering an initial pathway towards preservation. Bamburgh, Northumberland, England. Field of view is c. 1 metre.

et al., 1996; Gerdes et al., 2000). Trapped gases arising from beneath a microbial mat may cause doming of the mat surface (Gerdes et al., 1993; Dornbos et al., 2007). In cyanobacterial mats, domes may give rise to blister textures that develop as the gas bubbles in the highly elastic EPS film become stabilized and overgrown by microbes (Fig. 10c; Stolz, 2000; Bouougri et al., 2007). Where multiple gas bubbles develop underneath a mat and burst, these may result in characteristic sedimentary surface textures of multiple adjacent blisters, termed 'lizard-skin textures' by Eriksson et al. (2007b). Oxygen-rich bubbles, such as those seen in Fig. 10a–d, may remain stable for weeks or months if they are not disturbed, permitting them to become enmeshed by filamentous cyanobacteria, and potentially preserved (Bosak et al., 2010). Bubbles may accrete inorganic sediment grains as well as microbial material (Fig. 10a; Menard, 1950).
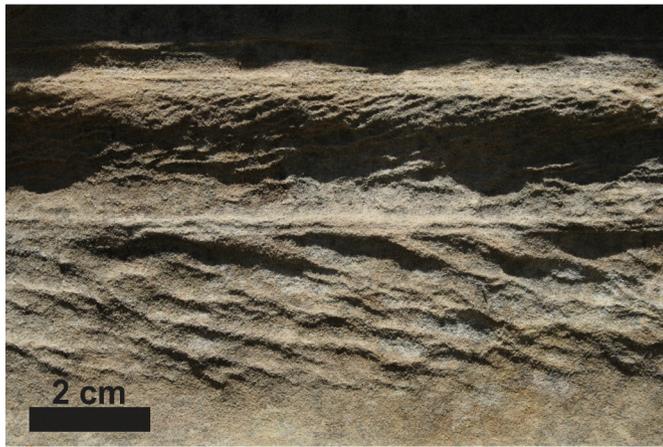
Fig. 7. Preservation potential of adhesion ripples illustrated by accretionary adhesion ripple cross-lamination in the Cambrian Wonewoc Formation. Wisconsin Dells, Wisconsin, United States. For surface expression, see Dott et al. (1986); their Fig. 2).

Generation of gas bubbles due to microbial decomposition (methanogenesis) can also occur in sediments that do not have surficial microbial mat communities (Boudreau, 2012). In such naked substrates, the escape of trapped gas, or air, is more likely to result in pit and mound structures, which record gas emergence at the surface as small (<1 cm diameter) shallow pits or blisters (Häntzschel, 1941; Shrock, 1948; Reineck and Singh, 1980). Some such gas escape structures closely resemble raindrop imprints (Buckland, 1842; Rindsberg, 2005).

The textures shown in Fig. 10g were observed to have formed abiotically as a thin veneer of clay (and particulate coal) settled in a drying puddle in a tyre rut on the access track to an open cast coal mine. Small (2–3 mm diameter) bubbles developed in the clay veneer, and then either burst or collapsed in on themselves. Such features are an abiotic analogue to microbial mats, which also have different material properties to the substrates on which they rest. They strongly resemble simple Ediacaran pseudofossils such as *Beltanelliformis minutae* (McIlroy et al., 2005). However, these Ediacaran structures, recently reinterpreted as fluid escape structures constrained by microbial biofilms (Menon et al., 2016), can show evidence for the presence of
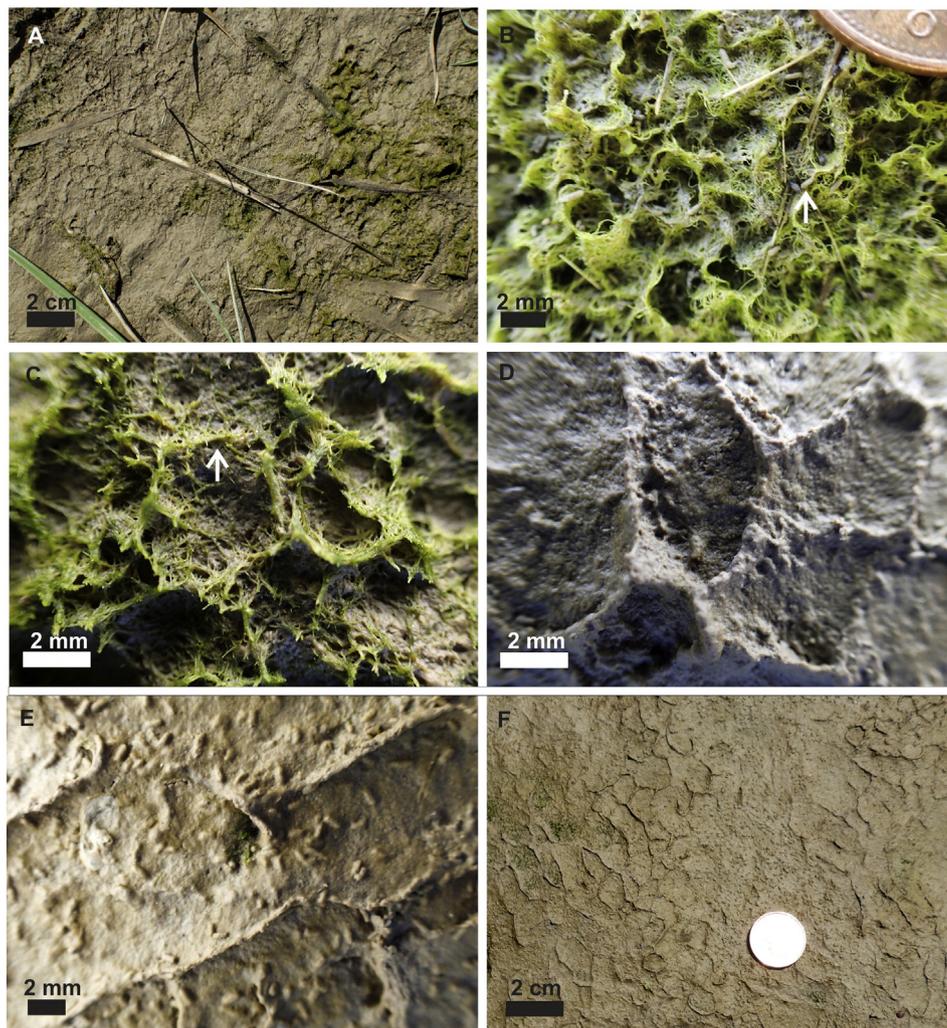
Fig. 8. Sedimentary surface textures formed by adhesion, accretion and baffling in modern sediments where microbial and algal mats are present. Examples from the tidal reaches of the River Rother, Sussex, England, at low tide. (a) Patches of filamentous algae on muddy tidal deposit. Filaments have become tangled into a reticulate pattern that is present both on the algal mats and the bare sediment. (b) Close-up image of tangling of algal filaments. Resultant 'nests' have the capacity to trap other objects, such as suspected egg case (arrowed). (c) Trapping of mud leads to collapse flattening of certain septate ridges of the reticulate structure, leading to an effective enlargement of each of the individual nests within the structure. (d) Eventual encasement of entire structure by mud, preserving only the most pronounced reticulate septae with a correspondingly larger dimension than the reticulate patterns in the algal mat itself. (e) Close-up of preserved ridges, plus mud-coated detritus (suspected egg cases as in b) trapped between them. (f) Resultant texture on now bare sediment, acting as a locus for immediate colonization by other microbial elements (to the left of the image).
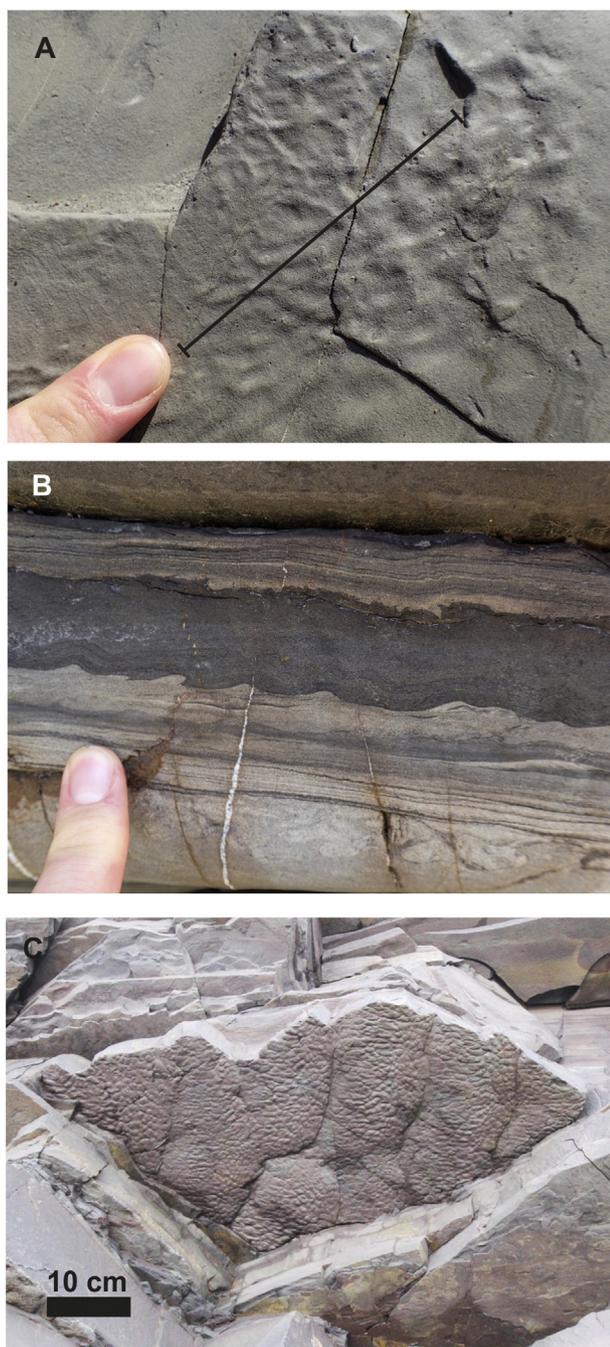
Fig. 9. Examples of wrinkles arising from loading in the Early Pennsylvanian Bude Formation, Cornwall, England. (a) Epirelief wrinkles with no discernible orientation on top of fine sandstone turbidite bed. (b) Cross-sectional view of loading in the same facies. Dimensions of load structures initially appear in excess of the wrinkle marks, but if the section were cut along the line shown in a, this would not be the case. (c) Hyporelief counterpart to load induced wrinkles on the base of an overlying bed, showing capacity for formation of inverted wrinkles on underlying beds.

microbial surface communities that appear to have passively trapped escaping fluids and confined surface impressions to particular laminae. This example reiterates the long-understood realisation that the often symmetric form of escape structures (in clay veneers or biofilms) may mimic biogenic form (Cloud, 1960), and demonstrates that similar structures can be formed in both the presence and absence of microbial involvement.

Air and gas in the sediment subsurface may lead to secondary sedimentary surface textures if the top of the substrate is planed off by erosion (Figs. 10e-f). Spongy or bubbly textures and fenestrae can develop

below the surface of a substrate due to air or gas escape. Such textures may arise due to gas diffusion from microbial mats (Noffke et al., 1996; Gerdes et al., 2000), or they may occur abiotically when air becomes trapped in sand (Emery, 1945). For example, air is readily trapped in intertidal sediment due to the phase lag between the rise and fall of the tidal prism and beach groundwater, leading to the formation of cavities as trapped air expands into bubbles (De Boer, 1979) (Fig. 10e-f). The truncation of bubble sand through surficial erosion may result in exposed surfaces that preserve a wrinkled texture (Emery, 1945). Abiotic bubble sand (Emery, 1945; De Boer, 1979) and microbial sponge pore sand (Noffke et al., 1996) may be morphologically identical. Sediment-free air bubbles in otherwise sediment-laden fluids may result in prominent holes within the veneer of sediment left behind by the flow (Fig. 10h).

The enigmatic and relatively rare 'pseudofossil' Aristophycus (Fig. 1i) is a branching structure in positive epirelief that has traditionally been regarded as problematic (Osgood, 1970). Seilacher (1982) considered the structure to represent expulsion of pore water through burrow cavities during compaction. Knaust and Hauschke (2004) considered it to represent dewatering of unconsolidated sands, trapped under a cap of sealed clay. Seilacher (2007) and Kumar and Ahmad (2014) suggested that it may record the laterally dissipating movement of escaping fluidized sediment trapped under a microbial mat. Where it has been previously reported, Aristophycus is often recorded in close association with other potential microbial structures including "Kinneyia" (Häntzschel and Reineck, 1968; Osgood, 1970; Jensen, 1997; Knaust and Hauschke, 2004; Kumar and Ahmad, 2014), Manchuriophycus (Bridge and Droser, 1985; Knaust and Hauschke, 2004) and Arumberia (Kumar and Ahmad, 2014). However, in each of these instances the dimensions and preservational facies of Aristophycus vary significantly, suggesting that the term may actually have been loosely applied to a number of superficially-similar problematic phenomena. In the instance shown in Fig. 1i (coarse-grained alluvial sandstone of the Cambrian Frehél Formation, France), no additional evidence for microbial mats, a seal of clay, or burrow cavities were seen in direct association with the structures (although Arumberia is known from stratigraphically-equivalent mudstones). Thus, in many instances, Aristophycus remains an enigmatic feature, and the involvement or otherwise of microbial mats in its formation remains to be proven.

3.3.4. Textures formed by impression (Fig. 11)

The recognition of raindrop impressions (Fig. 11a-c) in the sedimentary record dates back to Cunningham (1839) (with detailed description by Lyell (1851)), though their similarity to gas escape structures, plus doubts about their preservation potential, meant that their existence in the rock record was sporadically questioned for over a century (Buckland, 1842; Moussa, 1974). It is now accepted that discrete raindrop impressions are relatively common in the rock record (Metz, 1981) (compare Figs. 1l and 11b), but the form of such impressions may vary significantly depending on the substrate and the type of precipitation (Ghadiri, 2004). Individual impressions may be elliptical if the impact trajectory is oblique (Shrock, 1948), they may be larger and more discoidal with a raised central area where the impression is made from dripping (Fig. 11d; Twenhofel, 1921; Lanier et al., 1993), or they may be large and deep, with sharper rims where the precipitation falls as hail (Lyell, 1851; Reineck and Singh, 1980). Raindrop imprints have been suggested to be an example of an abiotic sedimentary surface texture for which the sedimentary stratigraphic record can reveal an evolutionary history independent of biological evolution. It has been suggested that the linear evolution of the atmosphere towards a less dense state is recorded by different (smaller) morphologies in raindrop imprints of Archean age (Som et al., 2012). However, the size distribution of raindrop imprints within a given surface may more likely record rainfall rate at that location (Kavanagh and Goldblatt, 2015). If rain is so heavy that multiple raindrop imprints interfere with one another, distinct raindrop impressions may be hard to discern,
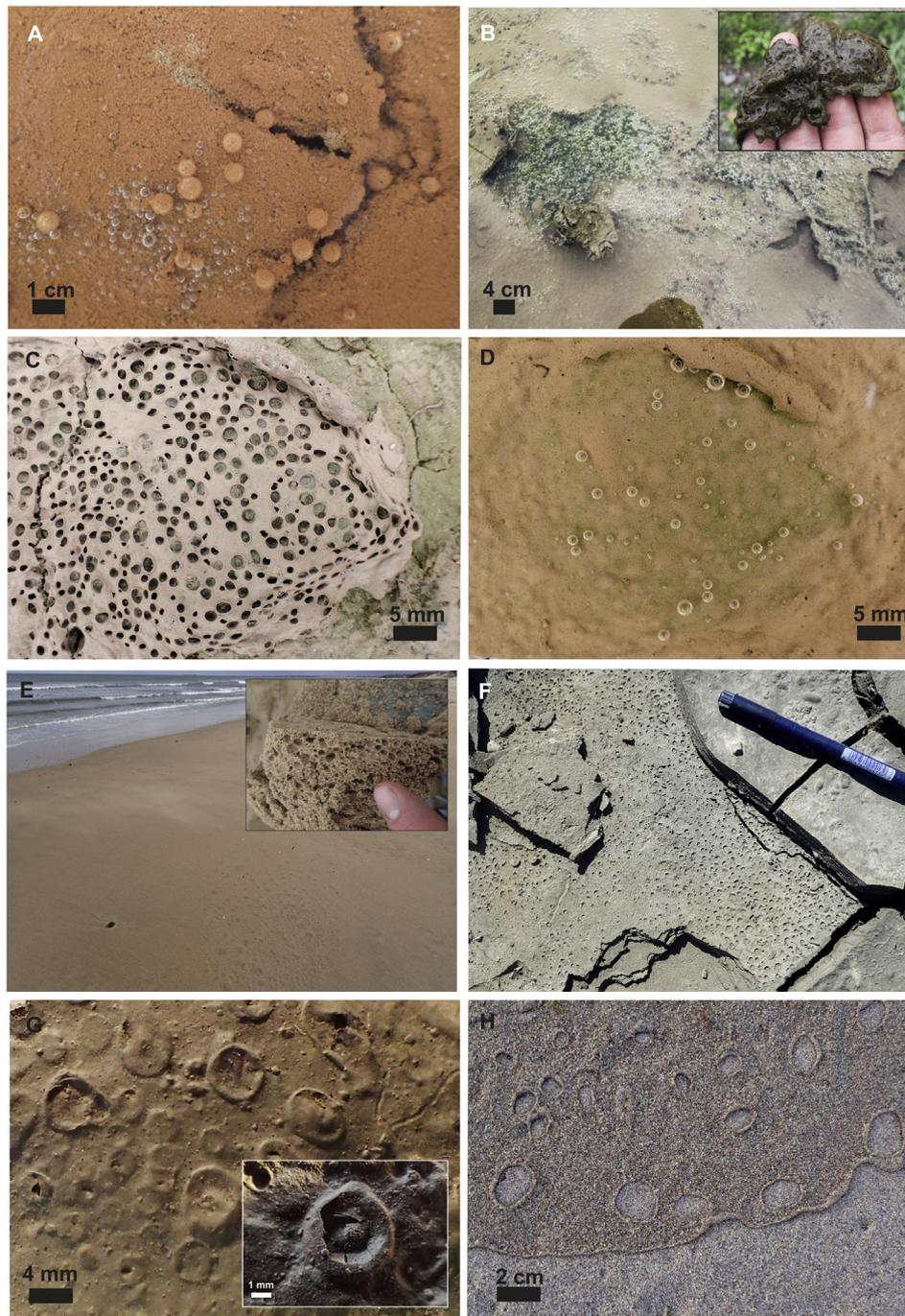
Fig. 10. Modern examples of the contribution of air and gas to the formation of sedimentary surface textures in both the presence and absence of microbial mats. (a) Respiring microbial community in a stagnant puddle on top of a coastal landslip. Larger bubbles are coated with both microbial matter and sediment grains and are arranged around a bird footprint. Hastings, Sussex, England. (b) Microbial mats developed in roadside puddle, actively respiring bubbles of oxygen that may burst inside the EPS-rich sediment, leading to prominent bubbled texture (inset). Bisk, Siberia, Russia. (c–d) Dormant microbial mat in dried freshwater puddle, showing temporary preservation of bubble texture. Second image shows same mat healed and re-spiring 3 days later, after heavy rain has refilled puddle but with no addition of sediment. Cape John, Nova Scotia, Canada. (e) Air escape bubbles developing near strandline on beach during falling tide, Bamburgh, Northumberland, England. Inset: subsurface structure of bubble sand developed during falling tide, Scolt Head Island, Norfolk, England. (f) Air escape bubbles formed beneath clay cap of a desiccation crack, Mont Saint-Michel Bay, Normandy, France. Length of pen is 136 mm. (g) Clay and particulate coal film on the surface of a dried puddle in a tyre rut on an access track of an opencast coal mine. As finest sediment settles out of suspension, trapped air forms bubbles in surface veneer as the puddle dries and desiccates. Although clearly abiotic, certain burst bubbles (e.g., inset) bear a resemblance to impressions previously interpreted as fossils (e.g., *Intrites punctatus* (*sensu* McIlroy et al., 2005) from Edi-acaran strata). Bachat, Siberia, Russia. (h) Patterns formed by swash on a beach where swashing water was laden with sediment. Sediment was transported by the film of water but not within the air bubbles that were trapped in the swash by the breaking wave, resulting in an adhesive sediment veneer with characteristic holes reflecting bubble locations. Texture was formed at high tide and persisted on the beach for a full tidal cycle. Sandwood Bay, Sutherland, Scotland.

and instead a rain impact microtopography may develop that has a strong morphological similarity to adhesion marks (although with the steeper sides downwind) (Fig. 11c; Clifton, 1977; Olsen et al., 1989; Robb, 1992). By extension, such rain impact microtopography also has the potential to be mistaken for MISS (e.g., compare Figs. 11c and 1r).

Other media that may impart an impression into a substrate include crystals, foam and bubbles (Allen, 1967; Reineck and Singh, 1980; Cooper and Jackson, 2001). Crystals of ice or salt may leave sharply de-fined impressions of their former presence in substrates (Reineck and Singh, 1980), and the *in situ* melting of frozen water or foam can also

produce a strongly wrinkled sedimentary surface texture (Fig. 11e). Reineck & Singh (1980; their Figs. 80–82) provide illustrations of how bubbles of foam can leave clusters of unrimmed, hemispherical pits with smooth surfaces when they come to rest on a sediment surface. Cooper and Jackson (2001) documented how variation in the morphology of foam impressions was related to the speed of the wind transporting the foam and tidal elevation. However, the likelihood of foam impression formation depends on the balance between sediment and impresser properties — Fig. 11f shows an example of organic-rich foam on a modern beach that exhibits little interaction with the underlying sediment as the bubbles are not much larger than the sediment grains on which they rest. In this instance, stable clusters of 3–4 grains can support the bubbles without being compressed downwards.

The presence of a microbial mat can buffer against impression from rain, foam or ice such that there is less likelihood of a sedimentary surface texture developing: the presence of raindrop impressions in the rock record would be strong evidence for the absence of microbial mats on a particular surface (Schieber, 2004). However, the cohesive nature of the mat means that other, more forceful impressions (such as footprints or trackways) can leave higher resolution trace fossil trackways in the mat itself than on granular sediment (e.g., Buatois and Mángano, 2012; Dai et al., 2015). Furthermore, the imprint of tracks into a mat (or the later colonization of a trackway by a mat) can promote a higher preservation potential since the mat may be more efficient than bare sediment at withstanding later erosion (Marty et al., 2009; Carmona et al., 2012; Fernandez and Pazos, 2014). However, this can depend on the thickness of the mat or biofilm: in instances where thicker mats have developed, their elasticity can also buffer against a defined impression. Fig. 11g-h show actively forming mat roll-ups formed by wind shear on a thick supratidal mat in the High Arctic (Meighen Island, Nunavut). Where footprints (bird and human) have been left in the bare sediment under the mat (after the mat has been rolled away), the level of definition is far greater than in the mat itself; the material properties of the mat result in less defined footprints being rendered as the mat elastically reverses the deformation induced by the impression (Fig. 11g). Equally, the resolution and number of footprints translated through the mat into the underlying sediment is also diminished by buffering effects. No discernible sedimentary surface textures reflecting the former mat presence are apparent where the mat has been torn up, although the underlying sediment is reddened due to microbially-induced redox chemistry (Fig. 11h). If such an example of a matground were preserved in the rock record, potential preservation of roll-ups or biogeochemical signatures may occur, but microbial sedimentary surface textures would likely be absent and preserved track populations would be diminished.

Sedimentary surface textures formed by impression on bare substrates may thus create wrinkle-like structures that could appear as pseudo-MISS, while on substrates that are actually colonized, microbial mats may dampen the formation of many impression textures.

3.3.5. Textures formed by shear (Fig. 12)

Gingras (2002) noted that shear stress (either from wave orbitals, sediment creep or gentle hydraulics) could be instrumental in forming wrinkles (runzelmarken) within cohesive sediments (where cohesion could be provided by sediment, water or micro-organisms). Abiotic wrinkles may develop when wind exerts non-erosive shear on damp sediment or on a thin film of water on top of a substrate (Reineck, 1969; Singh and Wunderlich, 1978; Reineck and Singh, 1980; Kopaska-Merkel and Grannis, 1990). Fig. 12a-b shows how transverse wrinkles may also develop in both cyanobacterial and algal mats as a result of shear stress on the surface of the mat, imparted by a fluid (air or water). Such wrinkles reflect the innate survival strategy that is employed by mat- or biofilm-producing micro-organisms: namely that the elastic biofilm is able to survive in an environment precisely because it is able to absorb external mechanical stress through deformation (Shaw et al., 2004). As the features in Fig. 12a-b are within the

mat itself, if they were to be preserved in the rock record then the mat material itself would also need to be preserved (or at least not have decayed away until it had a chance to mineralize during diagenesis, cf. Gehling, 1999). Initially there may be potential for such structures to leave impressions on the base of overlying sediment, but such impressions would have limited preservation potential if the mats degraded away and the formerly impressed surface was compacted into the void vacated by the decayed mat.

Non-erosive shear, exerted on the surface of plastic muds by fluids moving under a transitional laminar-turbulent regime, can induce the formation of abiotic transverse wrinkles (Dzulynski and Walton, 1965; Dzulynski and Simpson, 1966) of comparable morphology to sedimentary surface textures commonly classed as MISS. Wrinkle lineations have been reported as forming due to shallow subsurface shear on surfaces within submarine slide deposits (Corbett, 1973; Gibling and Stuart, 1988).

Millimetre-scale ripples, with 5–15 mm-spacing, have traditionally been considered problematic due to the fact that waves with small orbital amplitudes (of below 16 mm) are not strong enough to move sand or silt. Mariotti et al. (2014) successfully showed that microbial aggregates could produce such ripples by rolling along a substrate, collecting grains through cohesion, and reorganising the substrate into millimetre-scale ripples. They suggested that microbial aggregates were the most likely mediators of such a process because potential abiotic mediators such as cohesive sediment flocs would not aggregate over 1 mm in size, and would likely shear apart in moving water. In conjunction with other putatively microbial sedimentary surface textures, millimetre-scale ripples may thus be indicative of former mat fragments. However, there are published examples of ripples of similar dimensions actively forming in fine sand and silt in extremely shallow water, apparently in the absence of microbial mats (Singh and Wunderlich, 1978; Theakstone, 1980). In these instances, the shape and density of certain sediment grains may permit the formation of anomalously small ripples (Theakstone, 1980) outside of the expected hydrodynamic thresholds for quartz grains, so the mineralogy of millimetre-scale ripples must first be considered before an interpretation as MISS can be determined.

In addition to wrinkles and millimetre-scale ripples, fluid flow over a substrate may encourage erosion or deposition in focussed locations, which may be misinterpreted as microbially-related without context. Examples of this include the formation of horseshoe-shaped current crescents (Fig. 12c), which may be preserved in the rock record while the original obstacle forcing their formation is not (Fig. 1s). Setulfs (Figs. 1p, 12d) arise from erosional wind shear in emergent substrates as small obstacles trap wind-deflated sediment in their lee (Sarkar et al., 2011), and are positive epirelief structures resembling inverted flute casts (hence their name; Friedman and Sanders, 1974), with their long axes oriented parallel with flow and first described from modern supratidal settings. Bottjer and Hagadorn (2007) called similar Cambrian features 'sand shadow structures' and suggested that they were formed where microbial bumps nucleated physically-transported leeward tails. Sarkar et al. (2011) noted modern setulfs nucleating from both microbial aggregates and other biogenic obstructions such as pellets and shells. Modern examples can also develop in the absence of biogenic material; in the instances shown in Fig. 12d the necessary obstacles appear to be incipient adhesion warts. Based on the occurrence of two Neoproterozoic and one Cambrian instance, Sarkar et al. (2011) suggested that there was a Precambrian and early Palaeozoic bias to the global stratigraphic of setulfs in the rock record. They suggested that although setulfs must have occurred throughout the Phanerozoic, they could not enter the rock record without microbial mats binding the surface and that such a situation was unlikely after the evolution of metazoan grazing. Fig. 1p shows an example of ancient setulfs within the Silurian Tumblagooda Sandstone of Western Australia, which is extensively bioturbated in adjacent beds (McNamara, 2014).
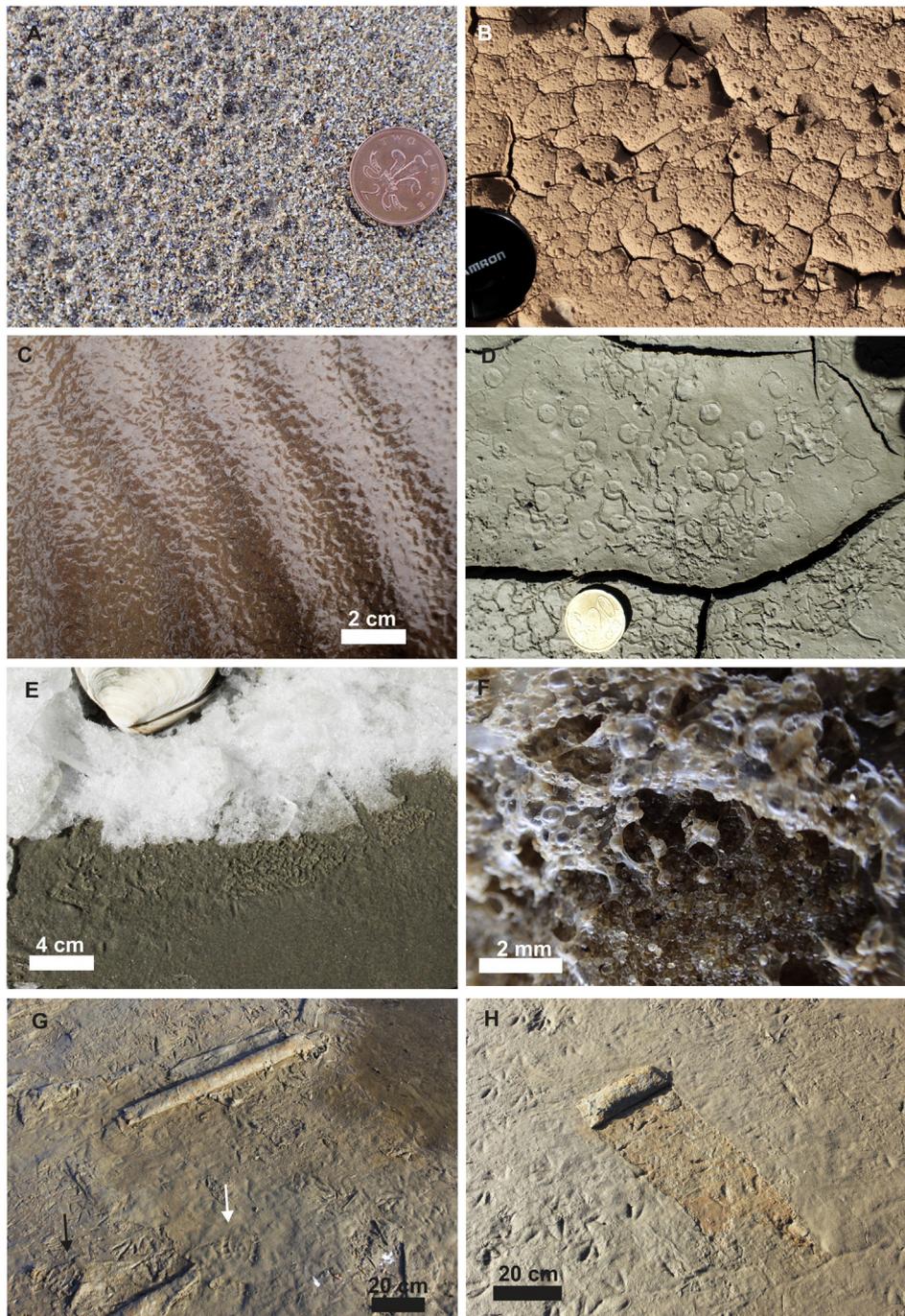
Fig. 11. Impression and sedimentary surface textures in modern sediments. (a) Fresh raindrop impressions in damp beach sand, resulting in clusters of craters separated by shared crater margins. Bamburgh, Northumberland, England. Diameter of coin is 26 mm. (b) Discrete raindrop impressions preserved in desiccated mud on floor of ephemeral stream. Boom Canyon, Kyrgyzstan. Diameter of camera lens cap is 62 mm. (c) Rain impact microtopography (R.I.M.) developed on wet sand on top of intertidal ripples immediately after heavy rain shower — note how R.I.M. blankets ripples on all sides. Bay of Fundy, Five Islands, Nova Scotia, Canada. (d) Drip impressions (and invertebrate trails) formed 2 m below a bridge from coalesced drops of water — note flattened discoidal shape and larger size than rain drop imprints. Mont Saint-Michel Bay, Normandy, France. Diameter of coin is 23 mm. (e) Wrinkle-like impressions in sand resulting from frozen beach foam. Clam Harbour, Nova Scotia, Canada. (f) Close-up of patch of organic-rich foam on tidal flat — although individual sediment grains are entrained in foam, there is little imparting of texture to the underlying sediment. Stiffkey Marshes, Norfolk, England. (g–h) Human and bird footprints on a supratidal algal mat in the High Arctic. Wind has created roll-up structures in algal mat, leaving patches of bare sediment. Where footprints are marked in bare sediment (black arrow) definition is greater than where they rest on mat (white arrow). However, mats appear to increase preservation potential of partial footprints (h). Meighen Island, Nunavut, Canada.

3.3.6. Textures formed by shrinkage (Fig. 13)

The drying of water-saturated sediments induces a delayed top-down shrinkage in sediment-water volume, inducing the formation of polygonal desiccation cracks as the topmost layer contracts (Fig. 13). The capability of the upper material layer of a substrate to shrink will be hindered by its attachment to a non-shrinking (wetter) layer below. This leads to the characteristic V-shape of desiccation

cracks in cross-section and, in plan-view, a clear temporal and geometrical hierarchy of cracks, with higher-order (later) cracks connecting with lower-order cracks at right-angles (Bohn et al., 2005) (Fig. 13a). In microbial surfaces, drying may also lead to varying degrees of desiccation cracking — completely, incompletely, or not at all if the mat retains elasticity (Plummer and Gostin, 1981). Microbial surfaces may crack in a "cauliflower" pattern (Fig. 13b) that differs from the sharp-
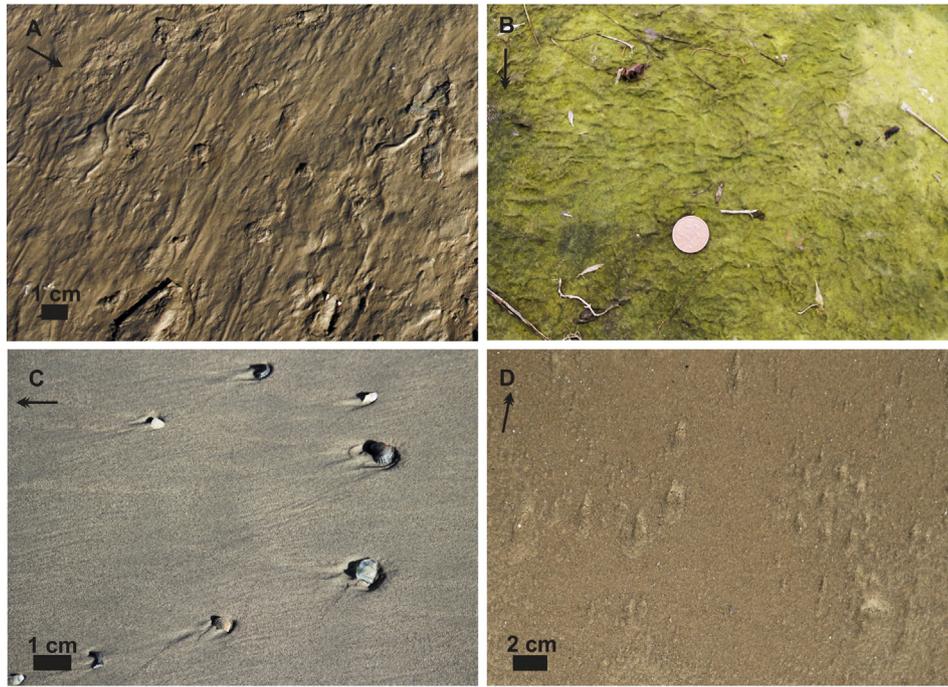
Fig. 12. Sedimentary surface textures arising from flow and shear in modern sediments: arrows indicate flow direction. (a) Transverse wrinkling of top of supratidal mat resulting from wind. Meighen Island, Nunavut, Canada. (b) Wrinkling in intertidal algal mat resulting from draining of tide from margins of salt marsh. Alnmouth, Northumberland, England. Diameter of coin is 23 mm. (c) Cuspate forms developing in the lee of shell material during ebb tide. Ostend, Belgium. (d) Setulfs developing through wind erosion (and associated with adhesion ripples in Fig. 7). Holkham, Norfolk, England.

edged form seen in mineral clays (Gerdes et al., 1993). The fact that microbial mats are ultimately a discrete material layer on top of a substrate means that they may detach from the substrate and curl or roll more readily (Fig. 13c) (Bouougri and Porada, 2012) — potentially forming curled microbial clasts if their elastic nature preserves the curled edges (Eriksson et al., 2007a). Desiccated lids that have curled in abiotic muds (e.g., Fig. 13d) are more likely to lose their fragile curled edges by attrition during subsequent transport, so are more likely to be preserved as plate-like intraformational mudclasts in the rock record.

Partial shrinkage of a sediment surface means that only incipient, isolated bifurcating or trifurcating cracks are formed (Shrock, 1948). Such cracks may be seen in both naked and microbial mat substrates. However, partial desiccation cracks in microbial mats may only be preserved if they are buried rapidly whilst in a state of desiccation, as the reintroduction of water promotes the reestablishment of the mat, and crack 'healing' by interlocking of microbial filaments. This can be seen in Fig. 13e-g, where a trifurcating partial crack can be seen to heal rapidly by microbial mat regrowth, and the extension of interlocking filaments, within only a few hours of resubmergence.

"Synaeresis" cracks are a third problematic class of shrinkage textures that are common in the rock record. These are partial, narrow linear to curved cracks, with tapering terminations and lacking V-shaped cross-sections (Fig. 1m-n). As similar cracks could be seen forming subaqueously in shallow water they were originally interpreted, through experimental analogue, as forming by synaeresis (i.e., the shrinkage of clay due to salinity changes in the ambient water column) (Jüngst, 1934). Although it has long been appreciated that the process of synaeresis is unlikely to actually account for these features in nature (Allen, 1982), the term "synaeresis crack" has become endemic in geological literature and is used here without inference of formative mechanism. Subsequent explanations for their formation include simple desiccation (Allen, 1982), seismogenic soft-sediment deformation (Pratt, 1998), evaporite pseudomorphs (Astin and Rogers, 1991) and microbial mediation (Pflüger, 1999; Harazim et al., 2013). Pratt (1998) proposed a universal model for the formation of "synaeresis" cracks where synsedimentary earthquakes injected liquefied sand into open fissures; however, the ubiquity of such features in the geological record militates against this explanation for all known instances, across multiple tectonic regimes. Astin and Rogers (1991) suggested that there was no clear evidence for subaqueous shrinkage in the rock record and that most geological examples arose from partial subaerial desiccation, sometimes in conjunction with, or nucleating around, evaporite pseudomorphs. Harazim et al. (2013) demonstrated a mechanism whereby such cracks could be formed intrastratally by burial, then shrinkage, of a mat-topped mud layer. Using geochemical evidence for microbial mat presence and an absence of deposit-feeding trace fossils under the "synaeresis" cracks, those authors demonstrated that such cracks in the Ordovician Beach Formation of Newfoundland could be reasonably considered as MISS. However, it should be noted that such a formative mechanism for "synaeresis" cracks is not universal. Examples of such cracks cross-cutting *Rosselia* and other burrows (Fig. 1m-n) indicate that they are not always restricted to unbioturbated matgrounds. "Synaeresis" cracks may therefore be polygenetic sedimentary surface textures for which multiple formative mechanisms, sometimes microbial and sometimes not, have been responsible. An exception may be the particularly sinuous variant of these cracks, known as *Manchuriophycus* (possible example in Fig. 1o), which appear to form only when the shrinking material has a very high strength and elasticity as would be expected in a mat (Koehn et al., 2014).

3.3.7. Textures with palimpsest, mimic and problematic origins

Certain sedimentary surface textures do not easily fit within the categories listed above, either because they develop due to a combination of two or more processes, or because their formative mechanism remains problematic.

Arguably the most problematic structure claimed as an example of MISS is "Kinneyia" (Fig. 1v-x), which informally retains the taxonomic name from its initial description as fossil algae (Walcott, 1914) and has been the focus of much discussion continuing to the present day (e.g., Fenton and Fenton, 1936; Martinsson, 1965; Singh and Wunderlich, 1978; Reineck and Singh, 1980; Hagadorn and Bottjer, 1997; Porada and Bouougri, 2007a, 2007b; Seilacher, 2007; Porada

Fig. 13. Sedimentary surface textures arising from shrinkage and drying. (a) Abiotic desiccation cracks with characteristic secondary cracks between major initial cracks, Kuzbas, Siberia, Russia. (b) Cauliflower-like polygonal cracks developed on surface of biological soil crust. San Rafael, Utah, United States. (c) Shrunken and curled polygons of cohesive mat within supratidal salt marsh pond, Stiffkey Marshes, Norfolk, England. (d) Curled lids of desiccation cracks forming abiotically on the banks of the Murchison River, Western Australia. e) Incomplete desiccation and "synaeresis" cracks on top of a microbial mat in a dried-out salt marsh pond, Stiffkey Marshes, Norfolk, England. (f–h) Close-up images of isolated trifurcating "synaeresis" crack in e, taken at different stages of a tidal cycle, showing rapid healing by microbial mat as soon as water is reintroduced to the pond — f taken when substrate was sub-aerially-exposed, on rising tide at 16:10 GMT on 16th May 2015 (137 min after low tide), g taken underwater at 16:19 GMT (146 min after low tide), h taken underwater at 12:52 GMT on 17th May 2015 (257 min after high tide).

et al., 2008; Thomas et al., 2013; Mariotti et al., 2014). The definition of "Kinneyia" offered by Porada et al. (2008, p. 65)) is followed here; namely "comparatively short, curved, frequently bifurcating, flat-topped crests, 0.5–1 mm high and 1–2 mm wide, which are separated by parallel, round-bottomed depressions. The crests are usually steep sided and may run parallel or form honeycomb-like patterns. The depressions frequently exhibit constrictions and may be reduced to isolated, round, or elongate pits. A problematical feature of the structures is the steep-to-almost-vertical flanks of the crests".

At least since Martinsson (1965) described "kinneyian ripples" on bedding surfaces, the understanding of "Kinneyia" as a particular type of wrinkle on a bedding plane has been accepted. Recently, however, one of the current authors (RFM, in Stimson et al., submitted) has restudied Walcott's (1914) holotype specimen of "Kinneyia" (Smithsonian Institute USNM 60705) and discovered that it actually shows no bedding surface features of note. The bedding surface of the clast that forms the holotype is a nondescript limestone plane: the identified "Kinneyia" marks are actually found along two separate side

profiles of the same clast. This observation has been lost in the literature as misleadingly cropped images of the original material, appearing in Walcott (1914) and the Treatise on Invertebrate Palaeontology (Häntzschel, 1962, 1975), perpetuated the illusion that it was a surface feature. The observations made by Stimson et al. (submitted) support previous suggestions (Häntzschel, 1962, 1975) that the original "Kinneyia (Walcott, 1914)" is inorganic, and is no more than a recent chemical weathering artefact.

The name "Kinneyia" is thus clearly invalid, and (excepting morphological likeness) Walcott's (1914) holotype has nothing in common with features currently described by the term. However, as the term is now more commonly used to refer to bedding plane features (sensu Martinsson, 1965), and as those features are commonly referred to MISS, the term "Kinneyia" is temporarily used in the following review and discussion of the bedding plane features without inference of genetic origin, but with reference to the common understanding of "Kinneyia" as defined by Porada et al. (2008), above. This is in line with our use of the term "synaeresis crack" in the previous section, but we acknowledge that "Kinneyia" should ultimately be abandoned as a term to describe MISS (Stimson et al., submitted) and that there is a pressing need for a robust modernization of MISS terminology.

Most recent studies have stated that, although "Kinneyia" structures have never been found in association with modern microbial mats (Porada et al., 2008), they likely arise from interactions between microbial mats and physical processes (Hagadorn and Bottjer, 1997; Porada and Bouougri, 2007a, 2007b) and are exclusively marine features (Porada et al., 2008). Seilacher (2007) suggested an unlikely and convolute formation mechanism for "Kinneyia", whereby earthquakes triggered the formation of gas bubbles under a microbial mat. Experimental models have successfully recreated "Kinneyia"-like patterns in viscoelastic films, representing artificial biomats, by inducing Kelvin-Helmholtz instabilities (Thomas et al., 2013), but have been unable to satisfactorily explain how these could be translated into underlying sediments. Mariotti et al. (2014) successfully created "Kinneyia"-like wrinkles by means of microbial mat aggregates. Where a mat had failed, under increasing shear stress, low density fragments of the mat could be transported below the threshold required to move sediment grains. The rolling of these fragments, coupled with their adhesive qualities that permitted the 'plucking' of sand grains from the substrate, were demonstrated to produce a variety of wrinkles, including "Kinneyia".

Modern examples of "Kinneyia" are shown in Fig. 14, where they seem to have formed in the absence of microbial mats. Fig. 14a-b shows "Kinneyia"-like features actively forming in medium-grained sand on the margins of a small natural drainage channel on a beach at Holkham (Norfolk, England). These "Kinneyia" marks formed as ridges extending 1–2 mm above very shallow water. The ridges developed as abiotic adhesion structures grew through the accretion of wind-blown sand within a 2-mm-thick film of standing water, resulting in subparallel ridges of 1 mm width, with the characteristic steep sides of "Kinneyia" marks. Fig. 14c-d shows "Kinneyia" structures preserved in dried mud within an ephemeral stream channel near Sarytobe, Kazakhstan. No active microbial component was witnessed either on or adjacent to these particular structures, which were observed during dry conditions on the stream bed and were thus relict forms. The existence of these structures demonstrates that the previously-stated stratigraphic (Archean to Jurassic) and environmental (marine only) restrictions of "Kinneyia" found by Porada et al. (2008) are a sampling artefact. Additionally, they show that "Kinneyia" may be a further example of a polygenetic texture that can be formed by microbial and non-microbial processes in siliciclastic sediment (and the dissolution of carbonate rock).

Arumberia (Fig. 1t-u) is an enigmatic texture known from multiple Neoproterozoic and Cambrian strata (Bland, 1984). Originally described as a body fossil of an extinct soft-bodied organism (Glaessner and Walter, 1975), it was considered a pseudofossil arising from turbid water flow by Brasier (1979) due to its morphological similarity to

experimental structures produced by Dzulynski and Walton (1965). Bland (1984) suggested that Arumberia was restricted to a very specific stratigraphic range, indicating a more likely biological origin, and tentatively interpreted it as the body fossil of a colonial organism. McIlroy and Walter (1997) later suggested that the structures were formed by scouring currents creating flute marks on a microbially-bound surface, thus permitting them to be considered a variety of MISS, but also noted that they appeared to have a narrow stratigraphic range. Kolesnikov et al. (2012) suggested that the morphological complexity of Arumberia exceeds that which would be expected to have formed from interactions between fluids and microbial mats alone, alternatively proposing that they are the fossilized remains of a distinct biostabilizing organism particular to the Precambrian-Cambrian transition. The examples of Arumberia shown in Fig. 1t-u occur in rocks of likely lower Cambrian, but possibly Cambro-Ordovician, age. Their occurrence within emergent desiccated mudstone facies attests to their enigmatic nature, as such facies are not typically associated with flute mark formation in non-microbial settings. The presence of multiple problematic pits and mounds (Fig. 1u), dismissed as occurring coincidentally by McIlroy and Walter (1997) and McIlroy et al. (2005), appears to be an intrinsic characteristic of this particular Arumberia occurrence. The extensive spatial coverage of these structures over the same bedding plane, seems to suggest a 'mat-like' structure, but the exact formative mechanism (or organism) remains enigmatic.

Other anomalous sedimentary structures can be formed when fluid shear acts upon a third party, which temporarily changes normal thresholds for sediment movement and results in a class of sedimentary structures here grouped as 'mimic phenomena'. Mimic phenomena arise where a third party, often with limited or no preservation potential, has the capacity to move grains under flow conditions where such movement would not normally be expected. This may lead to the formation of anomalous sedimentary structures that cannot be used to determine palaeohydraulic conditions by assuming that the depositional fluid was acting on the sedimentary particles alone. Probably the most geologically common examples of mimic phenomena are the sinking of ice-rafted debris into fine-grained sediment as dropstones. Seaweed, fish, and terrestrial vegetation may also act as a buoyancy aid to transport gravel-sized sediment (Liu and Gastaldo, 1992; Frey and Dashtgard, 2012; Pledger et al., 2014). When analogous conditions persist at a much smaller scale, it may be possible that sedimentary surface textures could develop. Examples include the movement of sand by microbial aggregates (Mariotti et al., 2014), or by water tension on the edges of bubbles (Menard, 1950). A fundamental problem presented by mimic phenomena is that in the vast majority of cases it will be impossible to prove their existence in the rock record. However, as they must undoubtedly have occurred, they may in part be responsible for some problematic sedimentary surface textures.

3.4. Pseudo-MISS

Certain sedimentary structures illustrate the need for documented uncertainty when interpreting other MISS, whether or not they can be classed as sedimentary surface textures. Multi-directed and palimpsest ripples are bedding surface structures commonly classed as MISS (Fig. 15; Noffke, 1998). It has been suggested that ripples in different directions in successive layers require a covering of microbial mats that enable such palimpsest ripples to develop without the reworking of earlier rippled surfaces; such that the older generations of ripples can be preserved in one direction while younger generations develop in another (e.g., Eriksson et al., 2010). Multi-directed ripples on the same surface have been observed to be colonized by microbial mats in modern tidal environments (Noffke, 1998) and have been claimed to be a class of MISS (Noffke, 2010). However, it is crucial to note that multi-directed ripples also commonly form in modern tidal environments without any microbial mats (Fig. 15a-b): in these instances they simply reflect different oscillation directions in shallow water, with ponds of water
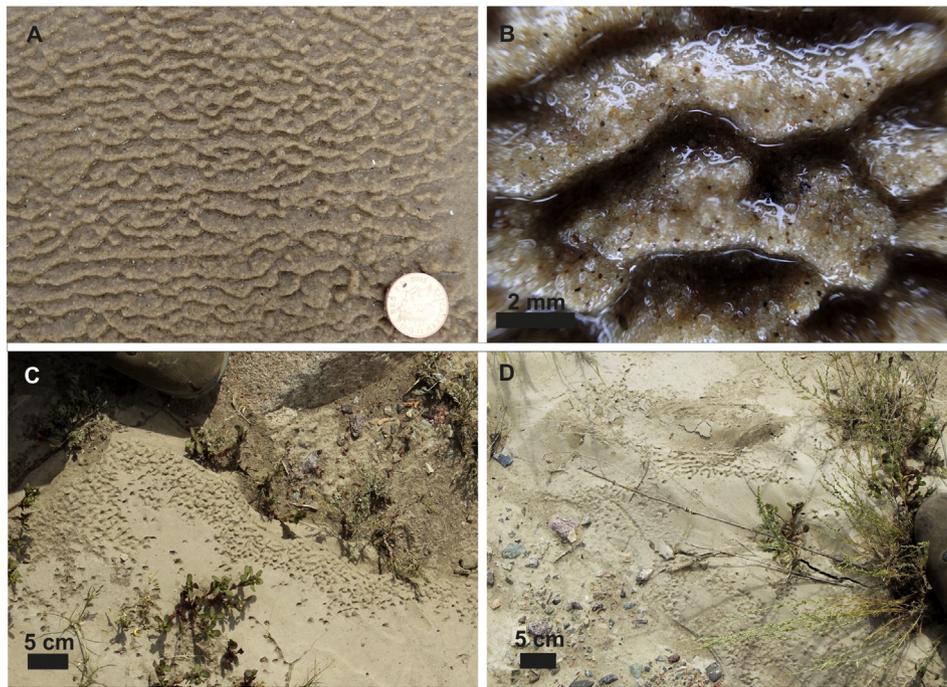
Fig. 14. Modern "Kinneyia" wrinkles in the absence of microbial mats. (a,b) "Kinneyia"-like form developing in very shallow (<2 mm) water in ponded water adjacent to a small channel on a beach at low tide. Wind is transporting sediment in arrowed direction and ridges of "Kinneyia" accrete above level of water by adhesion from water tension, retaining steep sides. Holkham, Norfolk, England. (c,d) Patches of "Kinneyia"-type form within clayey silt on the dried floor of an ephemeral stream in an endorheic basin, near Sarytobe, Kazakhstan.

that have different forms and orientations developing and persisting disharmonically as the water drains. Illustrated examples of 'microbial' palimpsest or multi-directed ripples in the literature (e.g., Pflüger, 1999, Fig. 4B; Petrov, 2014, Figs. 8e, 9c) are often simply misidentified ladder ripples (Fig. 15b), which form as very shallow water ponds and oscillates laterally in ripple troughs during drainage. Furthermore, it is often hard in field investigations of sedimentary rocks to firmly ascertain whether multiple-directed ripple marks are indeed on the same surface, or whether they occupy successive millimetre-spaced layers (Fig. 15c-d). As such, although specific instances of multiple-directed ripples could have formed due to patchy microbial mats, abiotic explanations are widely applicable, and multiple-directed ripples need not necessarily be MISS.

Petee ridges were first defined by Gavish et al. (1985) from modern sabkhas in the Red Sea, where wetting (mat development) and drying (desiccation) of microbial substrates generated undulating ridges on the sediment surface. They were named as a counterpoint to tepee structures, purely abiotic features of almost identical form resulting from desiccation and halite precipitation. In the first description of petee structures, Gavish et al. (1985, p. 192) note that "petee structures (biogenic) and tepee structures (abiogenic) are very difficult to distinguish and even a very experienced ecologist or geomicrobiologist will find it difficult to distinguish between the two possible origins of a surface in a continental or marine sabkha, when he sees it during completely dry conditions, which is the normal situation for 980 out of 1000 days in a desert environment". However, as with wrinkles, this crucial uncertainty has largely been lost in subsequent literature, and petee structures are now routinely described as definitively MISS from strata as old as the Archean (Bouougri et al., 2007).

3.5. Preservation of sedimentary surface textures

It has been claimed that certain sedimentary surface textures, normally seen to form abiotically, 'must' have been bound by microbial mats because otherwise they 'should not' have been preserved in the rock record (Bottjer and Hagadorn, 2007; Eriksson et al., 2010; Sarkar et al., 2011; Petrov, 2015). For example, where a sedimentary surface

texture exists in the rock record that has morphological similarities to both MISS and adhesion marks, the former has been considered the most likely explanation due to the 'low preservation potential' of the latter (Porada and Bouougri, 2007a, 2007b; Petrov, 2015) — although adhesion marks can be and are preserved through early consolidation and burial by windblown sand (Figs. 6h, 7; Hunter, 1969, 1973; Dott et al., 1986, their Fig. 2). Similar claims have been made regarding features such as setulfs (Sarkar et al., 2008, 2011), palimpsest ripple marks (Eriksson et al., 2010) and arthropod trackways (Seilacher, 2008).

There is little or no evidence to support such claims, which are based on an argument that conflates taphonomy, in a palaeontological sense, with the innate nature of sediment deposition and preservation. The sedimentary rock record is almost entirely composed of "frozen accidents": bedforms and structures that 'should not' have been expected to be preserved (see detailed discussion in Miall, 2015). The natural state for many common bedforms is that they are innately transient features: for example, ripple marks migrate under flowing water, actively 'destroying' themselves as they do so, yet it is common to find ripplemarked bedding planes in the rock record. Even on a modern beach at low tide, the ripple marks exposed at low water are highly anomalous, preserved momentarily for a few hours in the sedimentary record, when considered amongst the multiple-magnitude-greater populations and iterations of ripples that migrated during high water (Miall, 2015). Their occurrence, either in a beach or a Precambrian sandstone, would only require a special 'glue' holding them in place if the external hydrodynamic forces acting upon them were operating with a perpetually constant intensity: in the natural world, this is never the case. In fact, the only thing that bedform preservation (of any duration) requires is a perturbation in those external forces. Well-established bedform stability diagrams attest to this, and numerous papers are emerging that are starting to look at how bedform preservation happens under aggrading conditions — something which has not traditionally been considered in the study of dynamic bedforms (e.g., Fielding, 2006; Miall, 2015). All that is required for a substrate to enter the sedimentary record is a combination of sufficient accommodation space and a change in hydrodynamic conditions, such that the flow that deposits the overlying layer
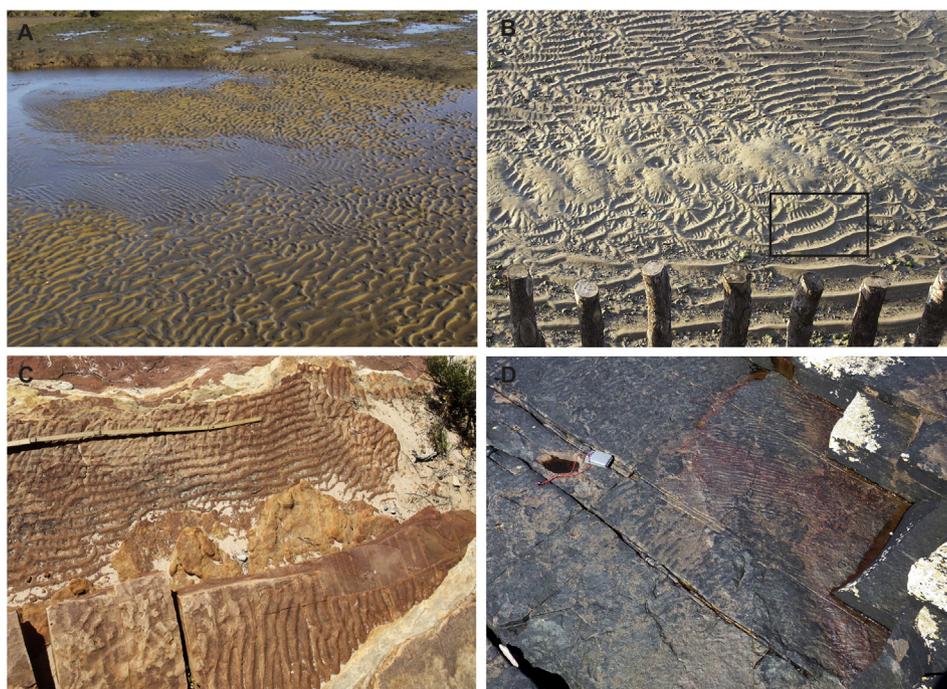
Fig. 15. Multiple-directed ripples on modern tidal flats and in the rock record. (a) Ripples with multiple orientations developed abiotically as ebb tidal water drains from puddles of progressively changing dimensions, Stiffkey Freshes, Norfolk, England. (b) Multiple directed ripples, including ladder ripples (highlighted in box), formed during falling tide in the absence of microbial mats. In this instance, multiple ripple directions were accentuated by wave reflection into the corner of an artificial sea-wall, extending parallel to the bottom and right of the photograph. Saint-Malo, Brittany, France. (c) Multiple ripple directions in Silurian tidal facies, Tumblagooda Sandstone, Kalbarri, Western Australia. Stick is 1 m long. (d) Multiple ripple directions in successive layers of Precambrian fluvial sediments, Applecross Formation, Torridon, Scotland. Length of compass is 90 mm.

is unable to erode the preceding sediment. Regular allogenic (e.g., waning flow) and autogenic (e.g., changes in water depth as sediment builds up) shifts in fluid flow regime are so ubiquitous in natural systems that it is conceptually unlikely that a fraction of all the sediment surface markings that ever existed would not end up preserved in the rock record. Even delicate features such as raindrop impressions enter the rock record (Fig. 1l, Metz, 1981) and, as discussed above, these are less likely to form on an elastic biomat. As this is clearly evident in the rock record, there is no need to invoke the presence of biomats for the preservation of other delicate impressions such as arthropod trackways (contra Seilacher, 2008), particularly as (unlike raindrops) these can leave undertraces well below the original substrate surface.

Evaluating preservation potential is arguably as problematic for true MISS as it is for abiotic bedforms, because the reintroduction of water to dormant mats may fundamentally change their morphology very rapidly. In Fig. 13f-h, the returning tide into a dried high intertidal pond can be seen to induce rehealing of partial desiccation cracks by microbial filaments within a matter of hours. In Fig. 10c-d, the impressions of gas escape bubbles formed by a respiring mat in a dried puddle were eradicated and resealed rapidly after the puddle refilled with rain water.

It is inherently problematic to understand the link between a modern sedimentary surface texture and an ancient one, as the erosional effects that may accompany the deposition of a succeeding layer cannot be observed in the field. Where modern bedforms develop in non-cohesive and aggrading sediment, the bedding plane expression of buried (preserved) surficial forms cannot be directly observed until the sediment is lithified and the former substrate surfaces can be re-exposed. However, the rock record clearly demonstrates that, even when complete preservation is unlikely, there is often the opportunity for partial preservation of bedforms and sedimentary surface textures (e.g., the preservation of undertraces in trace fossil trackways, or adhesion ripple lamination (Fig. 7)). The precise nature of how sedimentary surface textures (abiotic and microbial) enter the rock record remains poorly understood, and warrants being the focus of future investigation to permit better interpretation of the relict features that clearly do exist in the rock record.

4. Distinguishing biotic and abiotic sedimentary surface textures in the rock record

The determination of a biotic or abiotic origin for certain sedimentary features by morphological comparison has traditionally been a cause of debate amongst sedimentary geologists, with even sedimentary structures created by complex metazoans being confused with inorganic structures (and vice versa; see discussions in Frey, 1970; Cameron and Estes, 1971; Boyd, 1975). When combined with consideration of the examples listed in Section 3, it should not be surprising that microbially-induced structures (arising from the 'passive' presence of a mat) can sometimes be morphologically indistinguishable from wholly inorganic structures (e.g., Menon et al., 2016). In active sedimentary environments, the role of micro-organisms and microbial mats in the formation of sedimentary surface textures can be easily identified or refuted through observation (e.g., Figs. 6 and 8). However, in the geological record, supporting contextual evidence for the formation of sedimentary surface textures may be lacking, particularly during initial field observation. This can be problematic in instances where there is convergence of form between microbial and abiotic structures. For example, "Kinneyia"-like forms may be created by capillary adhesion (Fig. 14a-b) or microbial activity (Mariotti et al., 2014), or where erosion or compaction diminishes the preserved form of a sedimentary surface texture.

Sedimentary surface textures that are preserved in the rock record and can be taken in isolation as absolutely diagnostic of ancient microbial activity are extremely rare (and possibly non-existent). The interpretation of microbial activity must only be made by building up multiple lines of evidence, placing the structures within a clear sedimentological context, and even then only diagnosing microbial activity with a caveat of reasonable uncertainty. Such descriptions were common in the past (Schieber, 1998) but appear to have become less so. The following sections discuss considerations and practical approaches for distinguishing abiotic and microbial sedimentary surface textures in the geological record.

4.1. Association of biotic and abiotic textures

The problem of similarity of form is accentuated by the fact that many MISS often occur alongside purely abiotic surface textures. For example, the respiring microbial community shown in Fig. 10a was observed in a stagnant pool of water above the high tide line in a coastal landslip. Significantly, in immediately adjacent ponds that had already drained or dried out, there were no clear MISS present; however, the wet cohesive mud in these dried-up ponds had developed adhesion warts through trapping of windborne sand from the adjacent beach. Thus these stagnant ponds exhibited MISS during wet intervals, but the sedimentary surface textures left behind when they dried were dominantly abiotic. A similar close spatial and temporal association between MISS and abiotic structures arising from drying or cohesive sediment can also be seen in ephemeral fluvial deposits and modern intertidal areas — the images in Figs. 6c-f, 10e (inset), 11f, 12d, 13c, 13e-h, 14a-b and 15a were all taken within an area of a few square kilometres in the same back-barrier tidal system (the north Norfolk coast in eastern England). This close association of MISS and morphologically-similar abiotic textures is clearly apparent in modern environments, but is less well identified in the rock record. In studies where MISS have been documented, even from non-marine or intertidal environments, abiotic sedimentary surface textures are rarely recorded in association with them. This is possibly a bias arising from the mistaken identity of certain more likely abiotic forms as microbial in instances where other more convincing MISS are already known to be present. For example, Petrov (2015) illustrated a series of sedimentary features within mixed fluvial-sabkha facies in the Mukun Basin of Russia. Whilst many of the sabkha facies features can more convincingly be described as MISS (his plate 10), features claimed as microbial-related in the fluvial facies (his plate 9) included adhesion marks, ladder ripples, accretionary dunes and possible soft-sediment deformation. Modern and Phanerozoic examples of all of these structures can be demonstrated to form and be preserved in the absence of biofilms and, without accessory evidence to the contrary, the null hypothesis for their formation should be that they are abiotic. With such a reinterpretation, Petrov's (2015) succession would record a patchy distribution of microbial mats, with a preference for their accumulation and preservation in relatively quiescent sabkhas as oppose to neighbouring higher energy sandy rivers: a situation with clear analogy to present day sedimentary environments and less requirement for non-actualistic explanation.

4.2. Criteria for biogenicity and thin section evidence

Noffke (2009) introduced a series of "criteria for biogeneicity" [sic] which she suggested could be used to recognise true MISS in the rock record. These were: (1) MISS occur in rocks of not more than lower greenschist facies, (2) in stratigraphic sections, MISS correlate with turning points of regression–transgressions, (3) MISS correlate with a characteristic depositional facies recording clear water, moderate wave energy and quartz sand, (4) MISS have a distribution that reflects local hydrodynamic conditions (i.e., MISS are patchy and have different morphologies depending on localised processes), (5) fossil MISS have modern analogues, and (6) the MISS include specific textures in thin section.

Noffke (2009) suggested that if (and only if) all six of these criteria are met, then a sedimentary surface texture in the rock record is MISS. However, there are issues with these criteria. Criterion (1) is unnecessary as it should be self-evident for the study of sedimentary surface textures, and criterion (2) cannot be proven with certainty from most MISS occurrences known in the rock record: stating it as a definitive criterion would require a level of resolution more commonly found in basin-scale analyses (or sequence stratigraphy textbooks) than the isolated outcrops from which many MISS are reported. Further, once it is accepted that MISS are not restricted to shallow-marine and tidal environments, and that photoautotrophic cyanobacteria are not the only organisms that may create MISS (Flood et al., 2014), the valid criteria for

the biogenicity of MISS suggested by Noffke (2009), Fig. 5) can be whittled down to numbers 4–6. However, these remaining criteria are not necessarily diagnostic as they do not account for the fact that abiotic processes may create similar forms that also fulfil those criteria.

Where sedimentary surface textures are suspected to be MISS, thin sections of the suspected MISS can be used to good effect to provide supporting evidence. Ulmer-Scholle et al. (2015) illustrate how dark-coloured wavy–crinkly carbonaceous laminae, sometimes internally draped with clastic grains, may be identified as in situ microbial mats in thin section (Fig. 16a). Shreds of such material, with evidence for cohesiveness such as curling or fraying, may be regarded as reworked mat fragments (Fig. 16 b-c). However, in some instances, thin section evidence may be less compelling. Fig. 16d illustrates a thin section of "Kinneyia" from the Silurian Tumblagooda Sandstone of Western Australia, shown in the field photograph in Fig. 1x. The thin section reveals no evidence of carbonaceous material, in contrast with other thin sections of "Kinneyia" (Porada et al., 2008). This could suggest that the Tumblagooda "Kinneyia" are abiotic features (similar to those in Fig. 14a-b), or were formed by rolling microbial aggregates that did not get preserved (Mariotti et al., 2014), but it is not possible to distinguish which of these possibilities is more likely, nor rule out the original presence of a microbial mat that was not preserved.

Fig. 16e shows a thin section of mudstone from the Cambrian of northern France. The mudstone occurs as a thin (<20 cm) band and is the only such occurrence of mudstone within an extensive succession of "sheet-braided"-style alluvium in the Fréhel Formation (Davies et al., 2011). Although the thin section shows a large proportion of reworked microbial mat fragments, the macroscopic form of the mudstone bed exhibits no evidence of MISS (Fig. 16f). Although this may, in part, be due to limited bedding plane exposure, it emphasises that even where microbial mats were present they may not necessarily leave any indicative sedimentary surface textures (for example, also see the untextured substrate beneath the modern microbial mats in Fig. 11g-h).

The above examples show that combining suspected microbial sedimentary surface textures with thin section evidence may in some instances provide strong evidence for the textures being MISS. However, there is an important caveat that not all microbial mats will have left preserved organic material, and not all sedimentary surfaces that do preserve microscopic mat material will exhibit MISS.

As an alternative, analytical techniques including scanning electron microscopy have been successfully used to identify microbial fossils or the biological activity of micro-organisms in association with textured sedimentary surfaces and, in such instances, may be clearly indicative of former microbial mats or microbial presence (e.g., Bailey et al., 2013; Wacey et al., 2011, 2015; Brasier et al., 2015). SEM still cannot account for potential preservation issues, however, and the technique may be impractical or inappropriate for studies that are not specifically searching for MISS in the rock record.

4.3. Interpreting sedimentary surface textures in the field — a practical classification

We consider that in most instances the best approach to interpreting a microbial origin for sedimentary surface textures from morphology alone remains a pragmatic one, reliant on building up localised circumstantial evidence in support of the interpretation on a case-by-case basis. The need for a new classification scheme that is inclusive of microbial, abiotic and problematic forms has become apparent for two prominent reasons: (1) Whilst the criteria for biogenicity (Noffke, 2009) discussed in the previous section are for the most part scientifically sound, there are clearly practical problems with their application. Satisfying definitive criteria (identifying internal textures, mineralogical compositions, geochemical signatures, etc.) is research-expensive and is simply less likely to be applied to suspected MISS from rock successions where the end product is unlikely to yield a high-profile output (e.g., the oldest life on Earth, life after extinctions, life on other planets).
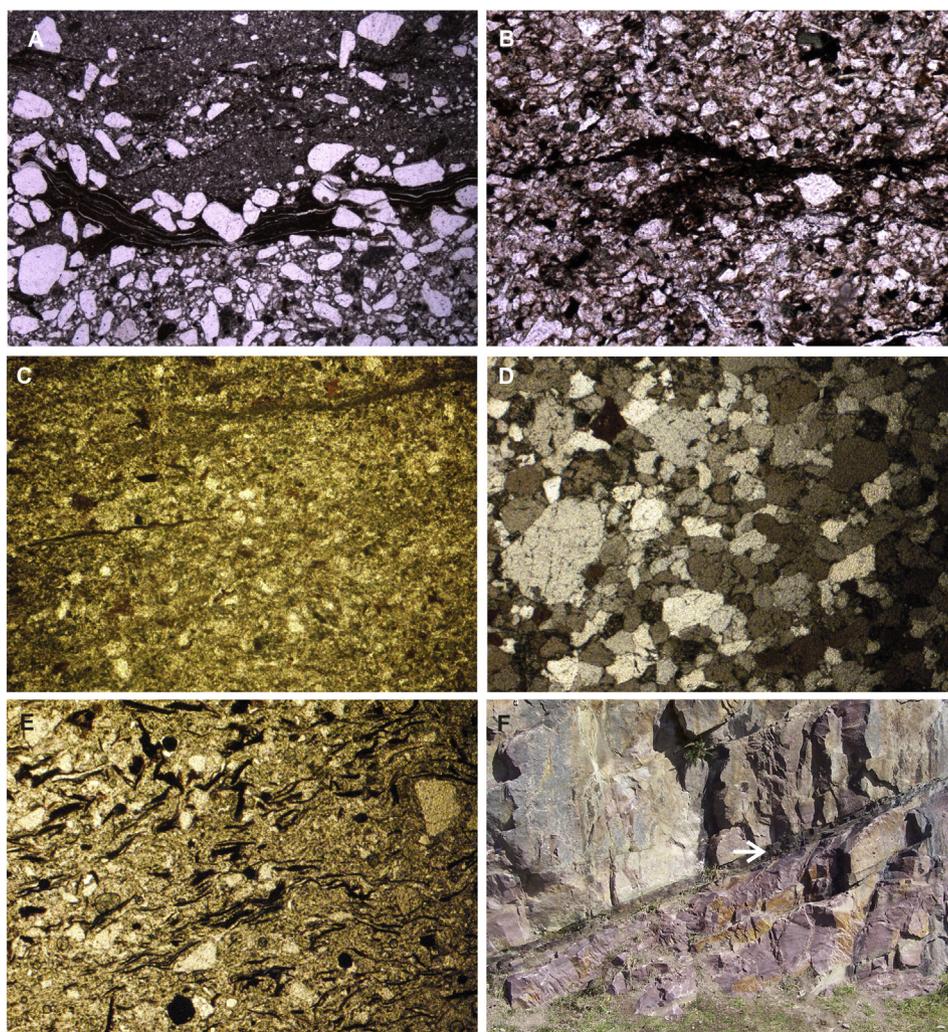
Fig. 16. Thin section images of suspected MISS. (a) Thick organic layers draped over mounds of large quartz grains with twisted and recumbent pieces, implying original cohesion, and sand grains apparently imbedded within the organic layer. Mississippian Horton Bluff Formation, Blue Beach, Nova Scotia, Canada (see Fig. 1c for larger scale structure). Field of view = 2.5 mm. (b) Dark organic lenses splitting and fraying, but not exhibiting lateral continuity. Pennsylvanian Tynemouth Creek Formation, New Brunswick, Canada (see Fig. 18e). Field of view = 2.5 mm. (c) Thin section of Arumberia, cut perpendicular to bedding, with thin wisps of organic material. Cambro-Ordovician Port Lazo Formation, Brittany, France (Fig. 1t). Field of view = 3.1 mm. (d) Thin section of "Kinneyia" wrinkles, cut perpendicular to bedding, exhibiting no evidence for organic material. Silurian Tumblagooda Formation, Western Australia (Fig. 1x). Field of view = 3.1 mm. (e-f) Thin section with abundant organic microbial mat fragments that comes from mudstone horizon in 16f, where there is a total absence of sedimentary surface texture or any other macroscopic features that would suggest a microbial presence. Cambro-Ordovician Frehel Formation (correlative with Port Lazo Formation in 16d), Brittany, France.

This means that the 'normal' intervals of Earth history are more likely to be overlooked as a focus for MISS studies than the exceptional ones. Compounding this, the relative youth of the study of MISS means that it lacks the extended archive of investigations into a full gamut of strata (of highly variable 'importance') that is afforded to the neighbouring research fields of sedimentary facies analysis, ichnology and palaeontology. Without an anchor in the mundane, there is less opportunity to judge the merit or significance of the exceptional, and bias will (and arguably already has) become developed. (2) There already exists a growing precedent of published instances where criteria for biogenicity have not been applied and where the terminology of 'MISS' has been applied following comparison of morphology alone.

The classification scheme proposed here addresses these issues, and allows for the fact that sedimentary surface textures are commonly encountered during field investigations of siliciclastic strata, whether or not MISS are being searched for. In certain instances a suspected microbial origin arising from the morphology of sedimentary surface textures may be augmented with more conclusive evidence from internal structures or geochemical signatures (Schieber et al., 2007a), but in many

instances the textures themselves form the only point of reference for interpreting the conditions of formation (at least in the first instance). For such cases, the umbrella nomenclature in Fig. 17 introduces a semi-quantitative shorthand classification scheme whereby the likely formative mechanism is referred to an upper or lower case letter. Such a classification will be beneficial; both for recording initial field observations of sedimentary surface textures and for those studies where such features occur, but are not investigated in greater detail due to falling outside of the scope of the research at hand. Category A structures are demonstrably abiotic in origin and Category B are demonstrably biotic (microbial). Where there is uncertainty, the sedimentary surface textures may be classed as Ab (where circumstantial evidence suggests the structures may be abiotic, but a microbial origin cannot be ruled out), Ba (for the converse situation) or ab, where there is no clear evidence to support either origin. This descriptive approach brings wrinkles and other sedimentary surface textures in the rock record firmly back into the fold of geological agnosticism. Its scientific merit lies in the fact that it leaves open the possibility of multiple explanations, biogenic or abiotic, prosaic or sensational, until one or the other can be corroborated with certainty through other lines of investigation.
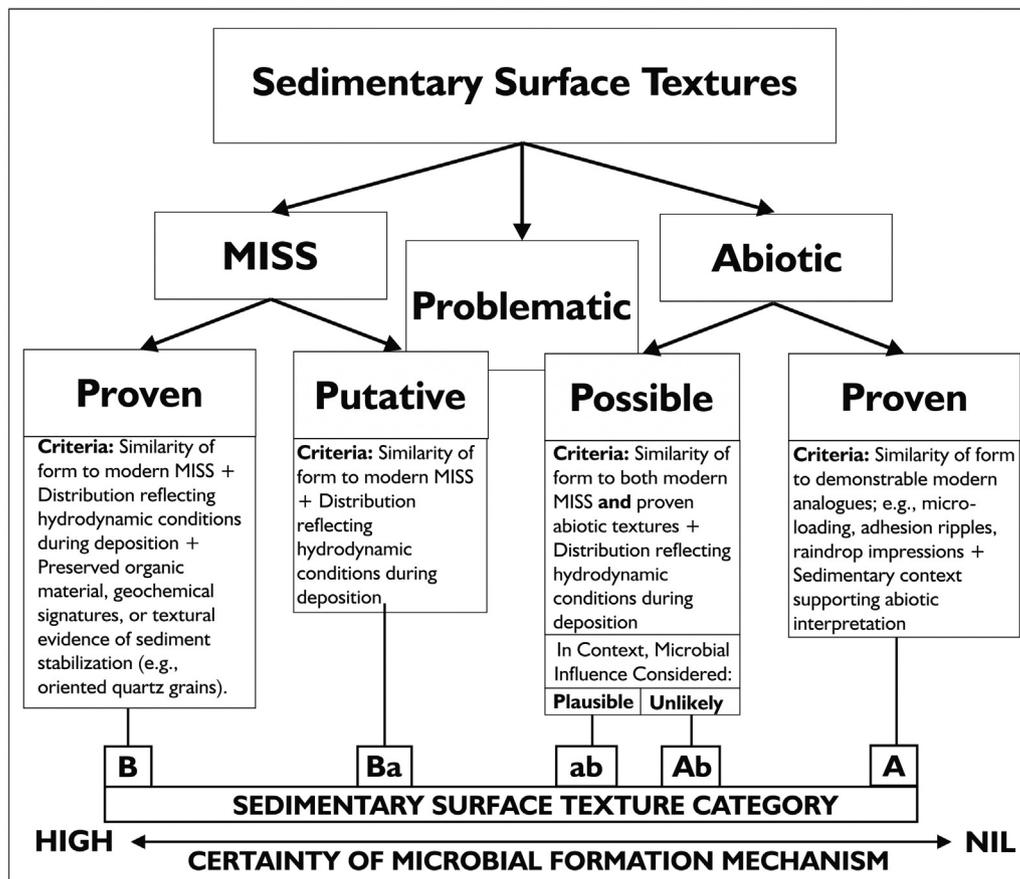
Fig. 17. Proposed umbrella classification of Sedimentary Surface Textures, incorporating true MISS as well as problematic and abiotic textures, and the shorthand approach for initial field classification.

An abundant and diverse array of putatively microbial or problematic sedimentary surface textures in a rock unit may add weight to an interpretation of the former presence of microbial mats (e.g., Schieber, 1999; Gehling and Droser, 2009). An isolated category 'ab' texture is weak evidence for the former presence of microbial mats; however, multiple different varieties of 'ab' structure within a limited sedimentary section may suggest that at least some had a microbial origin. The reason for this is simply that microbial mats significantly broaden the potential range of interactions between physico-chemical processes and a sedimentary substrate (Fig. 17). The increased variety of interactions promoted by the presence of a mat is significant, but the potential resultant signatures in the rock record are even greater, due to temporal variation in mat properties (Figs. 10c-d, 13f-h). This is because the instant of interment into the rock record (as a 'frozen accident', sensu Miall, 2015) may occur at any stage of microbial mat development. Throughout a given sedimentary succession, the presence of multiple microbial mats, each frozen during different developmental stages of thickness or cohesion, or composed of different successions of communities (e.g., filamentous and non-filamentous) will leave a large range of potential sedimentary surface textures. Thus, if a sedimentary succession is replete with abundant and very diverse sedimentary surface textures of problematic origin, a microbial interpretation may be more reasonable than one where purely physical processes were in such flux that they alone could account for the diversity. This understanding was clearly advocated in the past by Schieber (1999), who noted that although individual indicators provided only circumstantial evidence, "the larger the number of different microbial mat indicators that are found in a given sediment horizon, the better the chance that the sediment was indeed microbially colonized" (Schieber, 1999, p. 9).

An example of such a situation is illustrated in Fig. 18, with a series of sedimentary surface textures from the Pennsylvanian (Bashkirian)

Tynemouth Creek Formation from the Maritimes Basin in New Brunswick, Canada. The Tynemouth Creek Formation contains an abundance and wide variety of sedimentary surface textures, preserved on a significant proportion of siltstone and sandstone bedding planes throughout its 700-metre thickness. The formation was deposited as an aggradational megafan of seasonally-active, distributive fluvial channels that were locally sourced from the uplifted Cobequid Highlands to the south, and consists of a generally coarsening-upwards succession of mudrocks, sandstones and conglomerates (Plint and Van de Poll, 1982; Bashforth et al., 2014). Palaeobotanical work has confirmed that most of the seasonally-inactive channels on the megafan were colonized by a "dryland" cordaitalean-rich flora, with a "wetland" flora dominated by pteridosperms and calamitaleans occupying waterhole environments where standing water remained in channels throughout the year (Bashforth et al., 2014). The formation yields ichnological evidence for a diverse faunal community with common vertebrate trackways of amniotic and amphibious tetrapods (*Baropezia*, *Batrachichnus*, *Megapezia*, *Pseudobradypus*) and diverse invertebrate tracks and burrows, including decimetre-scale *Diplichnites* (Briggs et al., 1984; Falcon-Lang et al., 2015).

The sedimentary surface textures associated with this diverse community of higher animal and plant life were likely formed by a variety of mechanisms. Although there is some evidence for frayed carbonaceous films in thin section (Fig. 16b), the abundance of textures mean that it is impractical to section each example and the categorization shown in Fig. 17 proves useful. Certain forms appear to be likely abiotic whilst also having resemblance to features described as MISS in previous literature. The seasonally wet nature of the environments – determined from sedimentological and palaeobotanical evidence — provides a framework for the interpretation of some structures as adhesion warts (Fig. 18b, category Ab). Other textures include concave circular marks on the tops (or
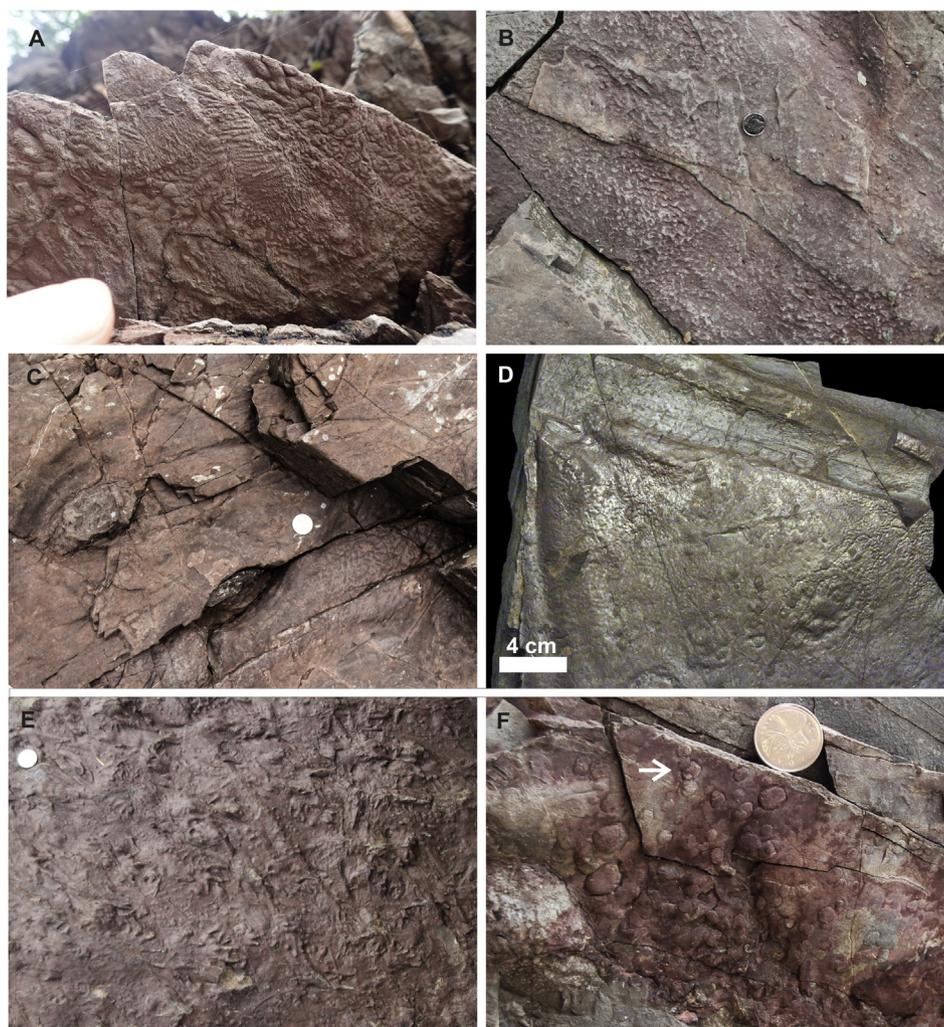
Fig. 18. Diverse sedimentary surface textures within Pennsylvanian alluvium of the Tynemouth Creek Formation, New Brunswick, Canada. (a) Oriented wrinkles on base of ephemeral channel sandstone. Category Ba. (b) Wrinkles resembling poorly preserved adhesion warts. Category Ab. Diameter of coin is 21 mm. (c) Patches of wrinkles associated with surface colonized by standing *Calamites*. Category ab. Diameter of coin is 24 mm. (d) Wrinkles and bubble-like structures in abandoned channel facies, associated with well-preserved *Cordaites* fronds. Category Ba. (e) Wrinkles and bubbles on layer associated with tetrapod tracks, but no good thin section evidence. Category ab. Diameter of coin is 24 mm. (f) Bubble like marks in positive hyporelief in abandoned channel facies that bear a strong resemblance to casts of drip marks. Category Ab. Diameter of coin is 24 mm.

convex marks on the base) of abandoned channel deposits (Fig. 18f). These features bear resemblance to the 'lizard-skin' microbial textures of Eriksson et al. (2007a), formed by gas-escape blistering of microbial mats. However, they also overlap, have a converse relief to that expected from gas doming, and bear a strong resemblance to the 'drip marks' figured by Twenhofel (1921) that arise from impression when water drips onto damp sediment (compare with Fig. 11d). Their occurrence in abandoned channels, with randomly oriented litter of *Cordaites* fronds, supports the idea that trees were growing in the vicinity and would have provided a locus for the inception of falling drips. However, as such shallow stagnant water environments would also promote microbial communities (e.g., Fig. 10a-d) a microbial origin cannot fully be ruled out, meaning that these textures also fall into category Ab. Patchy wrinkles (Fig. 18c) and bubble-like marks (Fig. 18e) directly associated with in situ *Calamites* stems and tetrapod trackways are classed as category ab, due to no definitive visual comparison with abiotic or microbial structures (in part because later erosion – prior to lithification – has seemingly diminished the resolution of the surface textures). Abandoned channel floors exhibit wrinkles that show highly irregular and tightly curved transverse forms (Fig. 18a), or very tightly spaced wrinkles and enigmatic circular forms associated with well-preserved leaf litter (Fig. 18d). In such instances the structures occur in sub-environments likely to have been colonized by microbial mats and have little resemblance to abiotic

textures, so a microbial origin is deemed more likely and the forms are classified as category Ba.

The above case study highlights how the presence of possibly or putatively microbial sedimentary surface textures in a sedimentary unit may be interpreted using the classification in Fig. 17. The interpretation does not preclude the possibility that future work will prove that all the structures are or are not microbial, but subdivides interpretations of the structures with reference to other sedimentological or ichnological clues. Other examples of this approach can be seen in Figs. 19 and 20. Fig. 19 shows the interaction of certain wrinkles with other sedimentary structures. In Fig. 19a, a drag mark (likely from woody debris — see Ielpi et al. (2014)) within Pennsylvanian alluvium of the Boss Point Formation of Nova Scotia can clearly be seen to have distorted a series of transverse wrinkles as the tool scraped through the sediment. The distortion of these wrinkles implies that they must have been cohesive at the time that the drag mark was carved — if they were simply small ripples, the drag would have carved a straight line through them without distorting their crests. Thus these wrinkles must have been made within a cohesive film on top of the substrate and, further, the resultant sedimentary structure must be a cast of the original surface form of the mat. The organisms responsible for this mat may have been cyanobacterial or algal, but it would be reasonable to classify this sedimentary surface texture as Category B. Fig. 19b-c show two images of turbidite tops in
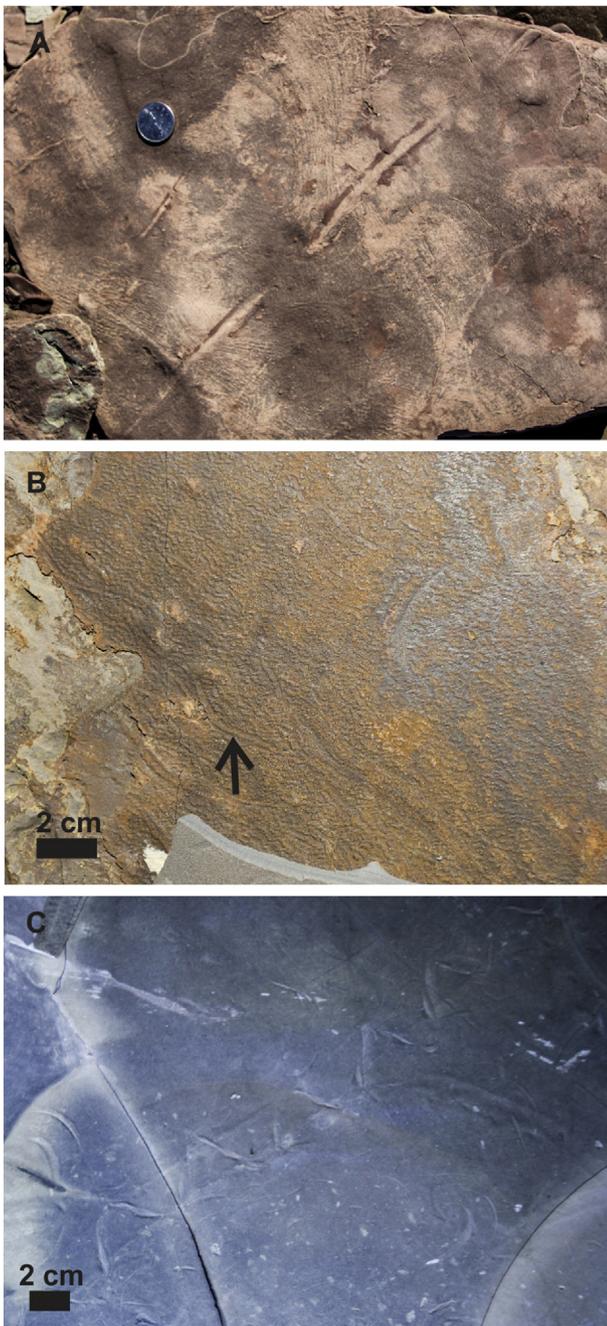
Fig. 19. Circumstantial evidence of former mats preserved as impressions due to interaction with other structures. (a) Drag mark on bedding surface, seen to distort transverse wrinkles. Result of object (likely woody debris, in context) dragging through cohesive veneer on top of sedimentary substrate. Alluvial facies of the Pennsylvanian Boss Point Formation, Little River, Nova Scotia, Canada. Diameter of coin is 24 mm. (b,c) Fish trails (*Undichna*) with different preservation depending on substrate. In (b), trails have levee margins, interpreted as indicative of fish fins dragging in 'sludge' of suspected microbial mat (also iron-rich and exhibiting millimetre-scale ripples and wrinkles). In (c), where the turbidite sandstone surface exhibits no sedimentary surface textures, the trails are preserved as sharp scratches without levees. Pennsylvanian Bude Formation, Cornwall, England.

Pennsylvanian deep lacustrine facies of the Bude Formation in Cornwall. In both instances, the turbidite tops are traversed by fish swimming trails of the ichnogenus *Undichna*, but the example in Fig. 19b also contains a large number of transverse wrinkles. Where wrinkles are absent, the *Undichna* trails are sharply defined in the underlying sand, but where wrinkles are present, the trails are bounded by two levees suggestive of fin-drag through a cohesive film, which also disrupts the wrinkles themselves. Again, such circumstantial evidence suggests

that the wrinkles may be Category B, or at least Category Ba. Notably, the Bude Formation also contains multiple Category A textures, attributable to abiotic loading (Fig. 9).

Fig. 20 shows further diversity in wrinkles and other sedimentary structures within alluvial facies rich in dinosaur footprints (Early Cretaceous Ashdown Formation in the Wealden Basin of southern England). In this instance, many of the sedimentary surface textures could be MISS, loading structures, or dinosaur skin impressions. Fig. 20a shows how textures occur both inside and outside of iguanadont footprints, indicating that not all the structures are likely to be skin impressions. However, Fig. 20c shows how the slip marks made by the ornamented dinosaur heel (compare Fig. 20d) match the potential in-foot impressions by size, potentially suggesting that they are skin impressions. Impressions of the folds in toes (Fig. 20b) show that skin impressions are possible. In such an instance, where initial field evidence is contradictory or ambiguous, a classification of ab fits the surface textures.

The sedimentary surface textures illustrated in Fig. 1a-x are classified, with explanation, in this new scheme in Table 2.

5. Conclusions

The recognition of MISS in modern and ancient environments (Noffke et al., 2001) unveiled valuable new insights into the role that microbiota may play in sculpting sedimentary textures, and has provided a plausible explanation for many previously enigmatic sedimentary structures in the rock record. The focus of early MISS studies has, however, resulted in a number of misconceptions regarding their stratigraphic and environmental distribution and, in some cases, biogenicity. From a survey of existing literature, field investigations of Precambrian and Phanerozoic rocks, and comparison with modern microbial and abiotic structures, we conclude that:

1. The recognition of MISS in modern and ancient environments has provided a plausible explanation for many enigmatic sedimentary structures in the rock record. The understanding of the full importance of microbiota and their secretions to sedimentary bedforms is still nascent. It appears that micro-organisms have left indirect, and sometimes indecipherable, signatures in the rock record from the Archean onwards. Their ever-presence suggests that previous indications that they were more common in the Precambrian, or after extinction events, may result from collection and publication bias. Although microbial mats may have produced some of the only biotic signatures of any note during such intervals, the same signatures are also present when lifeforms are more diverse and abundant during 'unexceptional' intervals of Earth history. Such occurrences remain under-reported and may be less familiar to workers focussed primarily on geomicrobiology or Precambrian studies. Reasons for this include MISS being overlooked in the Phanerozoic, where studies may concentrate on a greater diversity of fossils and sedimentological features besides MISS, and being considered too prosaic to warrant high profile publication.

2. MISS may provide crucial evidence for life on other planets or the oldest life on Earth, so their visual recognition is of great value. However, purely or predominantly abiotic processes are also capable of imparting intricate and organised textures onto sedimentary surfaces, and these commonly have a closely similar morphology and environmental distribution to microbial structures. Contrary to some claims, features including wrinkles, "Kinneyia" and multiple-directed ripple marks can form in the absence of microbial mats in modern environments. The rise of studies into MISS has increasingly overshadowed earlier research into these abiotic processes, which remains valid and should not be ignored. Bearing this morphological similarity in mind, many reported microbially-induced sedimentary structures in the rock record would more accurately be described as problematically-induced sedimentary structures. To resolve this, considering MISS as one subset of an umbrella group of biotic and
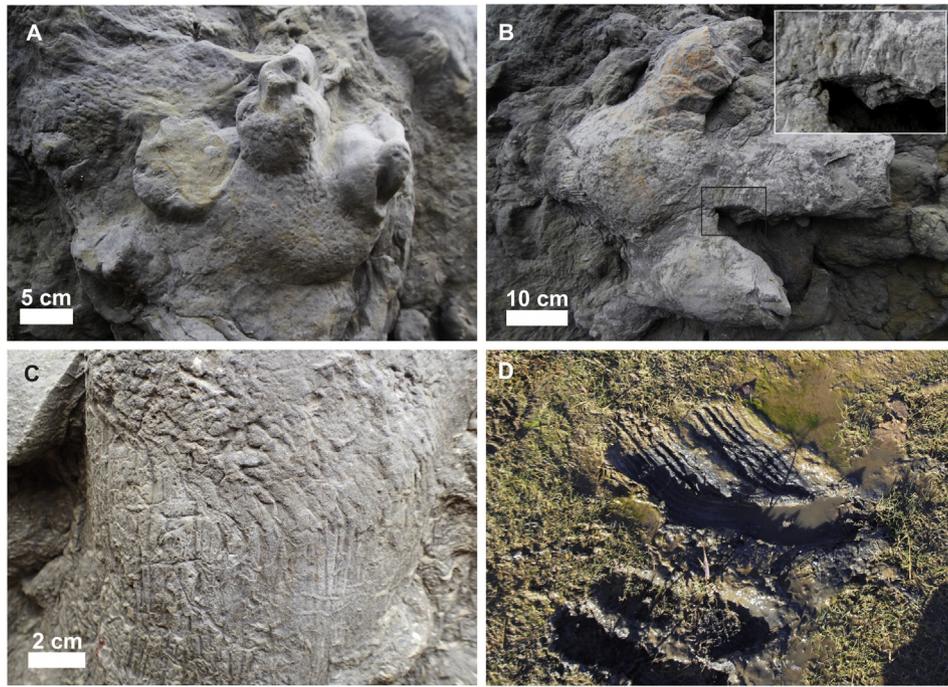
Fig. 20. Sedimentary surface textures associated with dinosaur footprints, Early Cretaceous Ashdown Formation, Fairlight Cove, Sussex, England. (a) Well-preserved iguanadont footprint with claw mark and wrinkles preserved on both base of footprint and outside of footprint. (b) Iguanadont footprint with heel slip marks and skin impressions around toe joints (inset). (c) Heel slip marks on iguanadont footprint with same dimensions as diamond shaped sedimentary surface texture internal to foot: possible skin impression. (d) Analogue for heel slip impression made by ornamented hiking boot soles on modern salt marsh, Stiffkey, Norfolk, England.

abiotic sedimentary surface textures provides a practical means by which such textures may be approached and interpreted when encountered in the rock record, divorced from their formative mechanism by millions or billions of years.

3. Studies into sedimentary surface textures, and inferences of microbial influence, should be couched within a reasonable degree of uncertainty. Smoking guns for microbial involvement (fossil evidence, geochemical signatures) are the exception rather than the rule, either due to the geological nature of the stratum, or academic constraints surrounding the purpose of the study that discovered them.

However, as the absence of such secondary clues may be a preservational artefact, and as microbes may also have been present where they left no textural signature in the sedimentary rock record, there is merit in interpreting microbial origins from other secondary evidence in a given rock succession. Reliably ascribing a microbial or physical origin to sedimentary surface textures requires careful holistic analysis of other associated sedimentological features, and often must be regarded as an interpretation rather than an absolute diagnosis. From a sedimentological perspective, the activity of microorganisms remains a plausible and sometimes even likely part of

Table 2
Re-evaluation of sedimentary surface structures shown in Fig. 1 using proposed classification scheme. Note that, in most instances, these designations are determined from visual interpretation alone and are therefore not permanent: further testing could support or dismiss these.

Fig. 1 Part	Classification	Reasoning
A	ab	Transverse wrinkles may have abiotic or microbial origins
B	Ba	Sharp lateral transition from dimpled texture to transverse wrinkles
C	Ba	Marked variation in transverse wrinkle orientation may suggest former mat
D	ab	Transverse wrinkles may have abiotic or microbial origins
E	Ba	Reticulate markings have modern microbial analogues due to filament tangling — compare Fig. 8
F	A	Bubble trains cross-cut ripples so likely load casts (Brasier et al., 2013)
G	Ab	Preferential orientation and form resemble abiotic adhesion marks — compare Fig. 6
H	ab	Large features appear to be abiotic load casts (compare Fig. 9c) but superimposed small wrinkles are enigmatic
I	ab	Enigmatic feature (see Section 3.3.3.)
J	Ba	Raised bumps suggest gas or air trapped under a film and are coupled with elongated reticulate texture
K	ab	Resembles both abiotic bubble sand and microbial sponge pore fabric — though questions remain regarding preservation mechanism
L	A	Strong similarity to modern raindrop impressions in mud — compare Fig. 11b
M	A	"Synaeresis" cracks cross cut Rosselia burrow: unlikely to be burrowed mat
N	A	"Synaeresis" cracks in same horizon as bioturbation: unlikely to be burrowed mat
O	ab	Curved shrinkage cracks within ripple mark troughs: some resemblance to Manchuriophycus, but no clear evidence of mat stability
P	Ab	Setulfs do not require microbial mats to form, but can occur in microbial settings — compare Fig. 12d
Q	Ba	Millimetre ripples cover crests and troughs of ripples oblique to crestline — possible mat cover
R	Ab	Resemblance to rain impact microtopography (compare Fig. 11c), but unclear why ripple crests are unornamented
S	A	Original cause of scour crescents absent, but null hypothesis has no reason to invoke microbial origin — compare Fig. 12c
T	Ba	Extensive coverage of Arumberia and fine detail lack convincing abiotic explanation
U	Ba	Extensive coverage of Arumberia and fine detail lack convincing abiotic explanation
V	Ba	"Kinneyia" in multiple directions: may have abiotic or microbial origins, but patchy nature (without topographic reasons) may suggest MISS
W	ab	"Kinneyia" may have abiotic or microbial origins
X	Ab	"Kinneyia" may have abiotic or microbial origins, but thin section shows no evidence of microbial mat — compare Fig. 14a

the explanation for the formation of any given texture, but identifying true MISS in the geological record can require piecing together a suite of circumstantial evidence to make a convincing case for the former presence of microbial mats. The nomenclatural classification scheme we propose offers a simple and effective way of recording the uncertainty associated with distinguishing abiotic and biotic sedimentary surface textures, which in many strata may occur together, and is applicable to both modern and ancient features.

Acknowledgements

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