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# Archean tufted microbial mats and the Great Oxidation Event: new insights into an ancient problem

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The macroscopic fossil record of the Archean consists solely of stromatolites and other microbialites, which seldom offer compelling clues to the identities of the organisms that formed them. Tufted microbial mats are an exception because their formation is known to require a suite of morphological and behavioural characteristics from which the behavioural and biological affinities of early microbialite-constructing microbes can be inferred. Here, the oldest yet reported convincing fossil tufted microbial mats are described and discussed in the context of other ancient and modern examples. Significantly, cyanobacteria dominate all known modern occurrences and may also have been the builders of ancient examples, the oldest of which predate by several hundred million years the earliest convincing cyanobacterial microfossils and most geochemical evidence for an oxygenated atmosphere.

**KEY WORDS:** Archean, microbialite, stromatolite, Tumbiana Formation, tufted microbial mats, Australia.

## INTRODUCTION

### Archean Microbialites

The macroscopic fossil record of early life on Earth is composed solely of microbialites. Almost all little-metamorphosed Proterozoic limestones, dolomites and magnesites contain stromatolites (Walter *et al.* 1992), and a scant, yet still considerable 50 or so, stromatolitic formations of Archean age are known (Schopf 2006). Microbial mat structures have also been reported from siliciclastic sedimentary rocks of Archean age (Noffke 2010). The morphologies of Precambrian stromatolites are diverse and appear to show temporal variation (e.g. Semikhatov 1976), but interpreting this rich record has proven difficult due to the complexities of stromatolite morphogenesis. The relative contribution of the three principle forces involved in stromatolite formation, physical, chemical, and biological, is difficult to assess, and structures dominated by physical or chemical processes offer little in the way of biologically informative data.

The structures of some microbial mats are paleobiologically significant in that the predominant factors responsible for their morphology are overwhelmingly biological. Tufted and pustular microbial mats of Shark Bay, Western Australia are two such examples. The morphology of Shark Bay pustular mats likely reflects the process of cell division in coccoid cyanobacteria (Golubic 1976). Tufted mats are more complex and contain a variety of recurring structures, which protrude from otherwise flat surfaces; these are for the rest

of this paper referred to as 'tufted microbial mat structures.' The structures include centimetre-scale tufts, pinnacles and ridges arranged into radial, parallel and reticulate patterns. Similar structures are described from tufted microbial mats occurring in a variety of environments from around the globe (Table 1). All known modern examples of tufted microbial mats are structurally dominated by filamentous cyanobacteria, which are thought to construct the structures by way of undirected gliding motility (Walter *et al.* 1976; Shepard & Sumner 2010) and positive phototaxis (Walter *et al.* 1976). Significantly, the morphologies of tufted microbial mat structures are a direct reflection of the morphology and behaviour of the microbes that build them, and these characteristics are shared by a limited number of major bacterial groups. This information can be preserved in the rock record and may thus be used to infer the biological affinities of ancient microbialite-building micro-organisms.

### Great Oxidation Event

Archean tufted microbial mats have the potential to offer a new insight into an old problem: the timing of the origin of the cyanobacteria. There exists a discrepancy between the dates of the earliest paleobiological evidence for cyanobacteria and the earliest geochemical evidence for an appreciably oxygenated atmosphere (Figure 1). In recent years the discovery of the mass independent sulfur (MIF-S) isotope signal has significantly improved the resolution afforded by

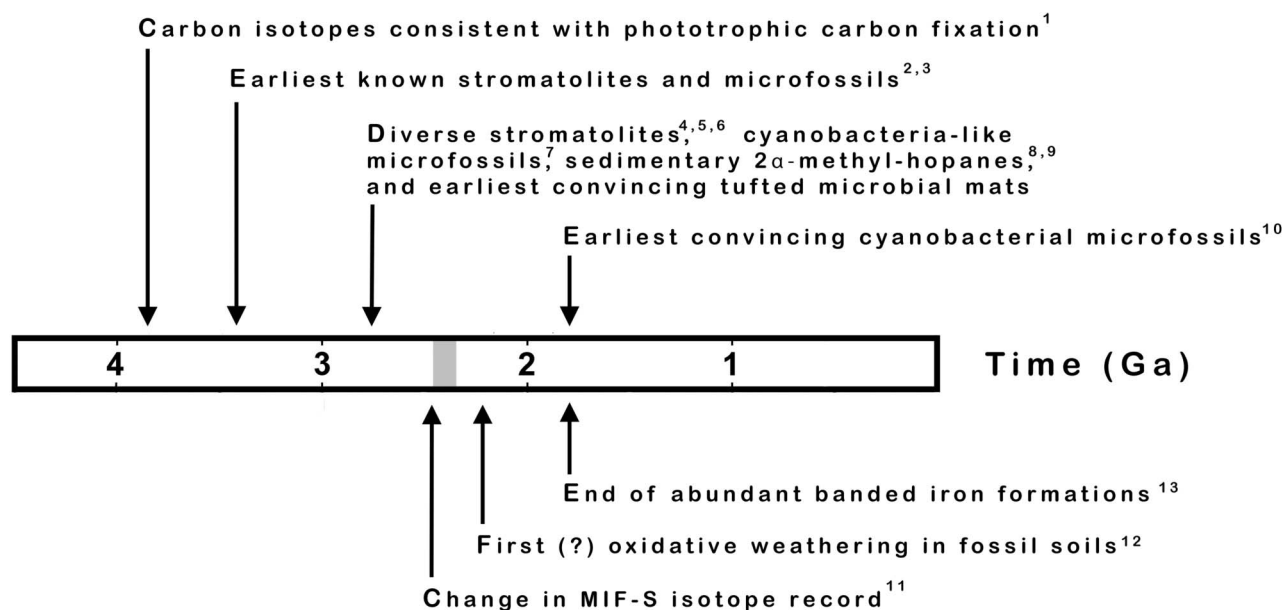
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**Table 1** Location and characteristics of some modern tufted microbial mats.

Location	Description and primary constituents	Environment	References
Bahamas	Pinnacles, columns and tufts. Filamentous cyanobacteria <i>Lyngbya</i> and <i>Scytonema</i> .	Seasonal hypersaline lake	Monty (1972)
Shark Bay, Western Australia	Straight parallel ridges, straight ridged reticulate patterns, tufts and pinnacles up to 2 cm high. Filamentous cyanobacteria <i>Lyngbya aestuarii</i> and ' <i>Pseudophormidium</i> .'	Hypersaline embayment	Davies (1970); Golubic (1976); this study
Yellowstone National Park	Silicified ridges and cm-scale cones linked by regularly occurring interconnecting laminae. Filamentous cyanobacterium <i>Phormidium tenue</i> .	Hydrothermal springs	Walter <i>et al.</i> (1976); Petroff <i>et al.</i> (2010)
Laguna Mormona, Baja California, Mexico	1 cm high tufts. Straight and sinuous ridges, rings and columns. Filamentous cyanobacteria, primarily <i>L. aestuarii</i> with a secondary component of <i>Oscillatoria</i> sp., <i>Microcoleus chthonoplastes</i> and <i>Spirulina</i> .	Evaporate-flat/salt-marsh	Horodyski (1977)
Trucial Coast, Middle East	<6 cm high tufts Filamentous cyanobacteria <i>M. chthonoplastes</i> and <i>L. aestuarii</i>	Coastal sabka	Park (1977)
Laguna Guerrero Negro, Mexico	1 cm high tufts Filamentous cyanobacterium <i>L. aestuarii</i>	Hypersaline marshes and flats	Javor & Castenholz (1981)
Lake Vanda, Antarctica	<5 cm high tufts Filamentous cyanobacteria <i>Lyngbya</i> and <i>Phormidium</i>	Permanently ice-covered lake	Love <i>et al.</i> (1983)
Hainan Island, China	<2-3 mm high tufts and <2 cm high pinnacles. Filamentous cyanobacteria <i>Phormidium</i> .	Submerged in commercial salt ponds	Zhang & Hoffmann (1992)
Southern Tunisia Meta to hypersaline embayment	2-3 mm high tufts, ridges and reticulate patterns. Filamentous cyanobacterium <i>L. aestuarii</i> .	Meta to hypersaline embayment	Gerdes <i>et al.</i> (2000)
Ohaaki Pool, North Island, New Zealand	Silicified cm-scale cones linked by regularly occurring interconnecting laminae. Filamentous cyanobacterium <i>Phormidium</i> .	Hydrothermal pool	Jones <i>et al.</i> (1998)

previous geochemical proxies for atmospheric oxygen, and sets the date at which appreciable quantities of oxygen began to accumulate in the atmosphere at around 2.45 Ga (Farquhar & Wing 2003). The evolution of oxygenic photosynthesis in cyanobacteria is widely considered to have been the cause of this event, termed the Great Oxidation Event, or GOE (Holland 2002), yet some paleobiologists see evidence for the presence of cyanobacteria as far back as *ca* 3.5 Ga—in excess of one billion years prior to the GOE (Schopf & Packer 1987; Schopf 1993), and many see what they regard as convincing evidence for the presence of cyanobacteria at *ca* 2.7 Ga—some 270 million years earlier than the abrupt change in the MIF-S isotope record (eg. Schopf & Walter 1983; Walter 1983; Buick 1992; Brocks *et al.* 1999; Summons *et al.* 1999; Waldbauer *et al.* 2009). The

existence of, and reason for, such a delay is the subject of many recent publications and considerable debate. Proposed mechanisms include a change in the redox state of volcanic gases (Kump *et al.* 2001), a relatively sudden switch between two stable equilibrium states (Goldblatt *et al.* 2006), a decrease in levels of atmospheric methane (Zahnle *et al.* 2006; Konhauser *et al.* 2009) and increased nutrient flux to the oceans (Campbell & Allen 2008). The alternative hypothesis is that oxygenic photosynthesis evolved immediately prior to the GOE (Kopp *et al.* 2005). The discovery of tufted microbial mats reported here from the 2.72 Ga (Blake *et al.* 2004) Tumbiana Formation adds to the body of evidence suggesting that the ancestors of today's oxygen-producing cyanobacteria had evolved by *ca* 2.7 Ga.



**Figure 1** Diagram illustrating the discrepancy between the earliest palaeobiological evidence for the presence of cyanobacteria and the earliest geochemical evidence for an oxygenated atmosphere. Grey zone represents the GOE. (1) Rosing & Frei (2004). (2) Walter *et al.* (1980). (3) Schopf (1993). (4) Walter (1983). (5) Buick (1992). (6) Awramik & Buchheim (2009). (7) Schopf & Walter (1983). (8) Brocks *et al.* (1999). (9) Waldbauer *et al.* (2009). (10) Hofmann (1976). (11) Farquhar *et al.* (2000). (12) Rye & Holland (1998). (13) Holland (1984).

## TUMBIANA FORMATION

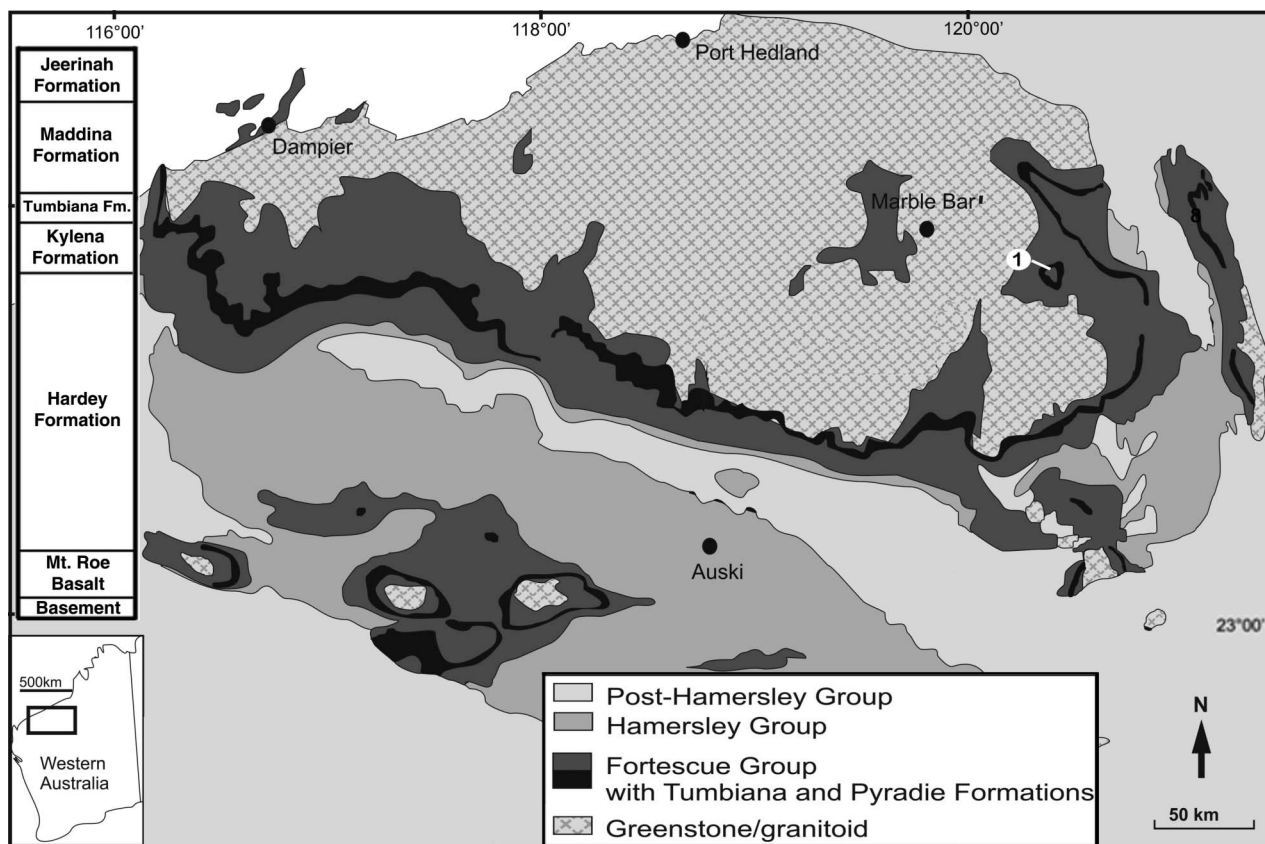
### Geological Setting

The *ca* 2.72 Ga Tumbiana Formation is part of the Fortescue Group, a succession of flood basalts, volcanoclastic, siliciclastic and carbonate sedimentary rocks lying unconformably upon an early Archean greenstone-granitoid basement in the Pilbara Craton of Western Australia (Figure 2). The group was deposited in lacustrine, fluvial and marine environments during the Neoproterozoic, when the basement was part of an emergent landmass in a continental rift setting (Thorne & Trendall 2001; Blake *et al.* 2004; Bolhar & Van Kranendonk 2007). Four Fortescue Group sub-basins have been recognised: the southern sub-basin, the Marble Bar Sub-basin, and the northeast and northwest sub-basins (Thorne & Trendall 2001). Subsequent regional metamorphism was limited to prehnite–pumpellyite to prehnite–pumpellyite–epidote facies in the northeast, Marble Bar and northwest sub-basins, and to actinolite facies in the south (Smith *et al.* 1982; Thorne & Trendall 2001; Thomazo *et al.* 2006).

The formation is an ideal location to investigate potential pre-GOE cyanobacterial communities in light of its Neoproterozoic age, diverse stromatolites, remarkable preservation, and prior reports of cyanobacteria-like microfossils (Schopf & Walter 1983), cyanobacterial biomarkers (Brocks *et al.* 1999; Eigenbrode *et al.* 2008), and inferred oligotrophic environment lacking in nutrients needed to power metabolisms other than oxy-

genic photosynthesis (Buick 1992). The formation also hosts kerogen with  $\delta^{13}\text{C}$  values of  $-57$  to  $-44\%$  VPDB indicative of methanogenesis and biomarkers suggestive of methanotrophy (Eigenbrode & Freeman 2006; Eigenbrode *et al.* 2008).

The Tumbiana Formation consists of the Mingah Member and the Meentheena Member. The Mingah Member is a  $\sim 150$  m-thick succession of tuff, accretionary lapilli, mudstone, siltstone, volcanoclastic sandstone and minor stromatolitic limestone considered to be of an intertidal or fluvial origin (Packer 1990; Sakurai *et al.* 2005). The Meentheena Member is a thinner but prominent succession of alternating siliciclastic and stromatolitic limestone beds deposited under either lacustrine or marine conditions. Stromatolites are widespread and abundant as well as diverse. Previous work on the Meentheena Member's paleobiology includes that of Walter (1983), Packer (1990), Buick (1992), Thorne & Trendall (2001), Sakurai *et al.* (2005), Bolhar & Van Kranendonk (2007) and Awramik & Buchheim (2009). Paleoenvironmental interpretation has long divided researchers. Early (Kriewaldt & Ryan 1967; Walter 1983; Buick 1992) and more recent (Blake *et al.* 2004; Bolhar & Van Kranendonk 2007; Awramik & Buchheim 2009) studies have proposed a lacustrine origin, but Packer (1990), Thorne & Trendall (2001) and Sakurai *et al.* (2005) considered the formation marine. The balance of probabilities now seems to favour a lacustrine interpretation, especially in light of facies relationships, non-marine REE+Y signals reported by Bolhar & Van Kranendonk (2007) and reinterpretation of herringbone



**Figure 2** Map showing the location of fossil tufted microbial mat outcrop in the Tumbiana Formation. (1) Meentheena. After Thorne & Trendall (2001).

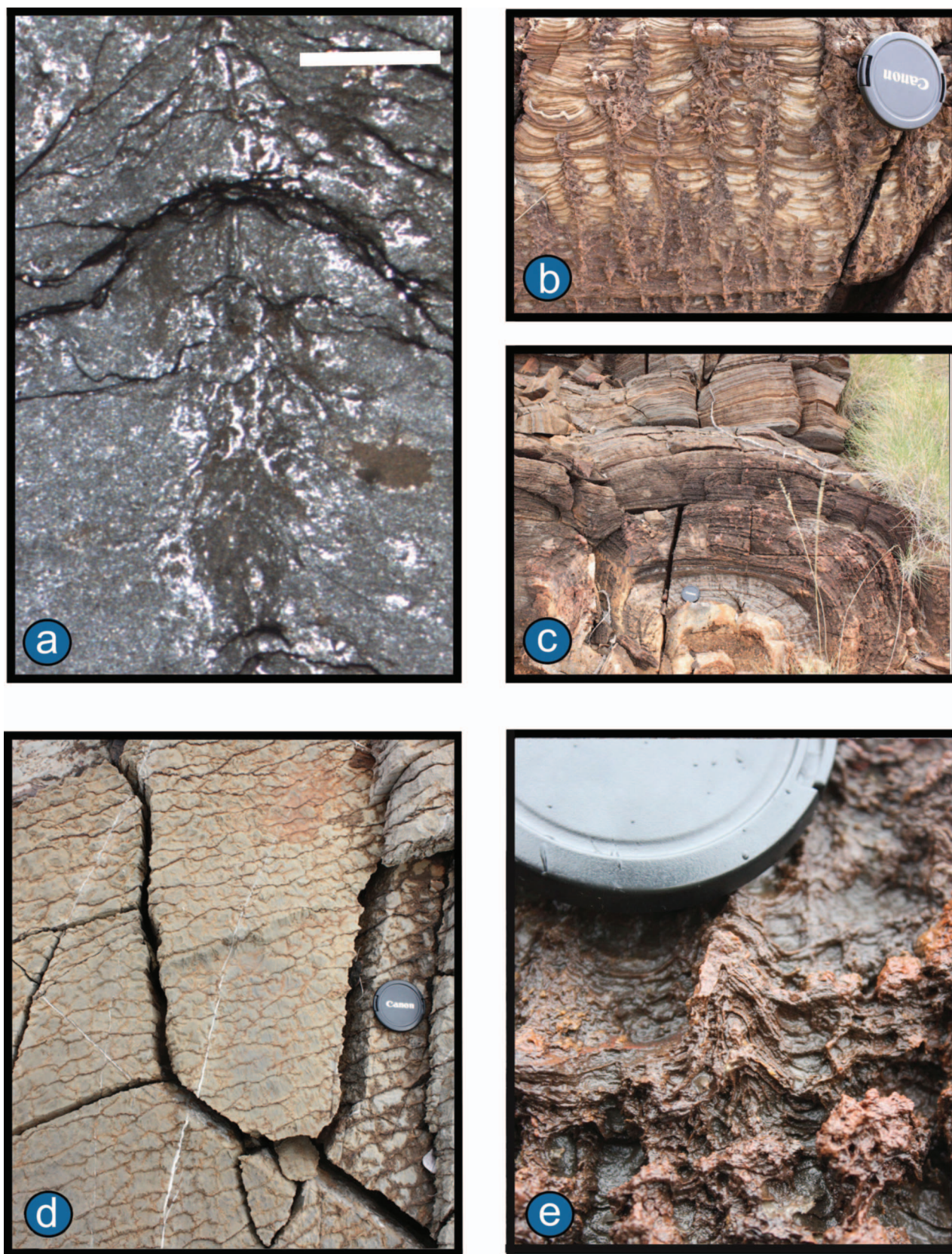
cross-stratification reported by Packer (1990) and Sakurai *et al.* (2005) (these observations have not been confirmed and appear to be misidentifications of trough cross-stratification). The presence of tufted microbial mats favours neither interpretation—modern examples are known from marine, lacustrine and hydrothermal pool environments (Logan *et al.* 1974; Walter *et al.* 1976; Love *et al.* 1983).

Lithofacies of the Meentheena Member consist of an edgewise-flat pebble conglomerate, a ripple cross-laminated calcarenite, and laminated siltstone and shale. Lithofacies often occur in a repeating succession, are typically not laterally continuous and may change abruptly over metre-scale distances. Significant sedimentological features include tepee structures, rosettes, climbing ripple cross-stratification, desiccation cracks and fenestrae. Ooids and oncolites are also present. Stromatolites of the member are diverse, with examples of domical, pseudocolumnar, columnar, branching columnar, nodular, bulbous, coniform, turbinate and cumulate forms, and metre-scale simple and complex bioherms and biostromes containing many of the above. Microstromatolites including *Alcheringa narrina* (Walter 1972) are present in bioherms, as isolated individuals, and in small stromatolitic buildups within the ripples of ripple-cross laminated calcarenite.

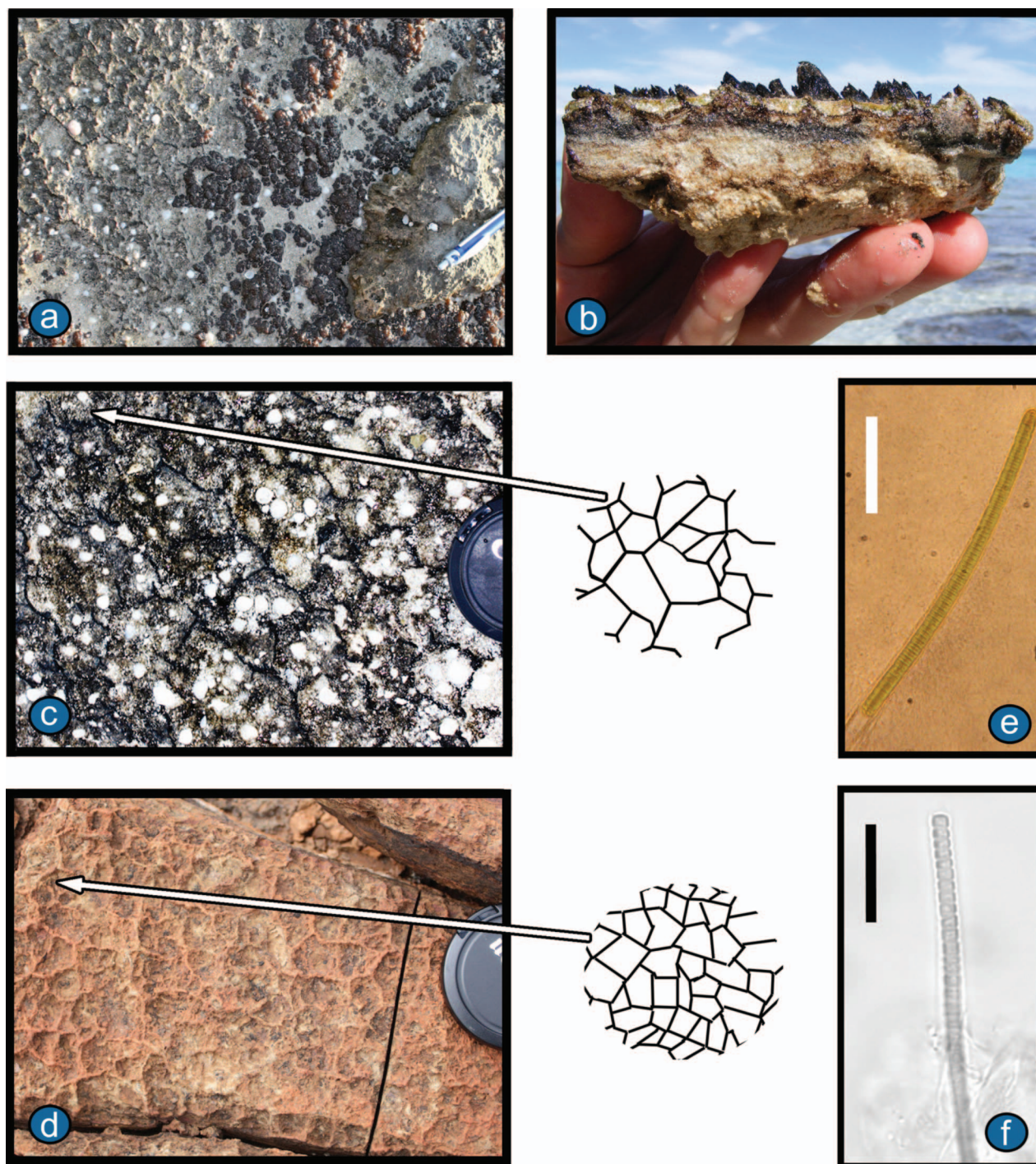
### New observations

Tufted microbial mat structures are described from the laminated calcilutite and calcisiltite lithofacies of the Meentheena Member. The structures occur as coniform pseudocolumnar and columnar (Figure 3b) stromatolites composed internally of strongly inherited steeply convex to conical laminae linked by laterally continuous inter-column lamination occurring every few centimetres (visible in Figure 3b).

Apical zones extend in one, two or three dimensions, producing conical, ridged (Figure 3d) and reticulate (Figure 4d) plan view surfaces. The columns lie conformably upon metre-scale roughly equidimensional domical stromatolites with up to 45 cm of synoptic relief (Figure 3c). The width of polygons comprising reticulate patterns is ~1–1.5 cm. The junctions of ridges in reticulate patterns are higher than the ridges themselves, which sag slightly to form straight saddles between junctions. Steeply convexly laminated tufts and ridges are an average of ~5 mm in diameter with ~6 mm of synoptic relief (Figure 3e). Large, vertically orientated, squiggle-shaped calcite filled voids (fenestrae), and dark, straight and sinuous palimpsest fabrics (Walter 1983) are features of apical zones (Figure 3a). Styrolites are common and typically follow original lamination, which is generally poorly preserved (Figure 3a). Laminae and surrounding sediments consist of xenotopic 3–10  $\mu\text{m}$  grains of



**Figure 3** Microbialites of the Tumbiana Formation. (a) Thin-section photomicrograph showing the internal structure of reticulate ridges shown in Figure 4d. Note filamentous palimpsest fabrics and fenestrae in the apical zone. Scale bar = 1 mm. (b) Vertical outcrop section through conformably laminated columns connected by regularly occurring inter-column laminae. (c) Large Domical stromatolite underlying b. (d) Plan view of conformably laminated columns terminating in ridges. (e) Partially silicified conformably laminated column showing lamination in outcrop.



**Figure 4** Modern tufted microbial mats of Shark Bay, Western Australia. (a) Contact between pustular microbial mat comprised mostly of unicellular cyanobacteria (right) and reticulate tufted microbial mat (left) comprising mostly motile filamentous cyanobacteria. Mechanical pencil for scale. (b) Section of tufted microbial mat showing vertical relief of coniform structures and underlying endobenthic mats. Photo credit: J. Coffey. (c) Reticulate ridges in tufted microbial mat at Carbla Point, Shark Bay, Western Australia. (d) Reticulate ridges of the Tumbiana Formation. (e) *Lyngbya aestuarii* filament—the primary constituent of Shark Bay tufted microbial mats. Scale bar = 100  $\mu\text{m}$ . (f) '*Pseudophormidium*' filament—this cyanobacterium also occurs in Shark Bay tufted microbial mat structures. Scale bar = 10  $\mu\text{m}$ .

carbonate, with rare tabular crystals of carbonate, shards of volcanic glass (now chert) and other detrital grains occurring within coniform laminae and in the surrounding laminated and unlaminated sediments. Sub-mm euhedral crystal pseudomorphs, of what appear to be goethite after pyrite, occur along bedding planes.

## DISCUSSION

### Modern tufted microbial mats

Modern tufted microbial mats are restricted to a handful of 'extreme' environments, including hypersaline

embayments, hydrothermal springs and permanently ice-covered Antarctic lakes (Table 1). In hypersaline sabkas and embayments of the Bahamas, Western Australia, Mexico, Tunisia and the Middle East, tufted microbial mats are a thin but cohesive, dark green to black, periodically desiccated mat that cover a gelatinous stack of variously coloured endobenthic microbial mats arranged in a vertical stratification reflective of different pigments, minerals and metabolisms (Figure 4b).

The tufts and larger coniform structures (often termed pinnacles), which protrude from these mats, are composed almost exclusively of vertically aligned bundles of filamentous cyanobacteria. The ridges found in association with coniform structures consist of tangles of the same filamentous cyanobacteria as found in tufts and ‘pinnacles.’ Ridges may coalesce to form centimetre-scale reticulate (polygonal) patterns, sometimes with tufts and pinnacles present at ridge junctions and an absence of dark-coloured mat in the centres of polygons, which may instead host a reddish-coloured mat dominated by unicellular phototrophic bacteria. The height of intertidal ridges and coniform structures rarely exceeds 2 cm, but pinnacles of up to 6 cm in height have been reported from the Trucial Coast (Park 1977). Tufted cones forming in some hydrothermal pools are silicified *in situ* and are known to attain heights of up to 10 cm, internal lamination, and true axial zones (Walter *et al.* 1976; Jones *et al.* 1998), which have not been reported from intertidal pinnacles. ‘Fairy rings’ were described from Laguna Mormona tufted mat by Horodyski (1977); they consist of <2 cm high ridges arranged in 5–20 cm diameter rings composed of higher filament densities than surrounding mat.

Several different classes of filamentous cyanobacteria are associated with the structures of intertidal tufted microbial mats; large ensheathed single filaments of *Lynbya aestuarii*, bundles of trichomes of *Microcoleus chthonoplastes* organised into single filaments and sheathless filamentous cyanobacteria such as *Oscillatoria limosa* (Table 1). A minor component of unicellular cyanobacteria, diatoms and foraminifera has also been reported but is typically much less common in tufted microbial mat structures than in surrounding areas of stratiform mat (Logan *et al.* 1974; Horodyski 1977; Gerdes *et al.* 2000). More than one type of filamentous cyanobacteria may be found within a single tufted structure, as is the case at Carbla Point, Shark Bay, Western Australia (personal observation), and in Laguna Mormona of Mexico (Horodyski 1977).

### Morphogenetic mechanisms for tufted microbial mat structures

The mechanism behind the morphogenesis of ‘fairy rings’ is unclear, although Horodyski (1977) suggested that their formation may be related to shallow waters being unable to penetrate the interiors of wide, flat-topped mounds of filamentous cyanobacteria. Gerdes *et al.* (1994) outlined an alternative mechanism involving concentric nutrient fronts propagated by escaping gas bubbles, but neither explanation is backed by a strong observational framework. Potential morphogenetic mechanisms involving chemotaxis, phototaxis,

space competition, nutrient diffusion or possibly even quorum sensing (Decho *et al.* 2010) are plausible.

At intertidal localities tufted microbial mats are subjected to periodic desiccation, and it has been suggested that this repeated wetting and drying of the mats is the mechanism responsible for the formation of tufts and pinnacles (Horodyski 1977), yet the discovery of permanently submerged mats of filamentous cyanobacteria exhibiting the same structures (Walter *et al.* 1976; Love *et al.* 1983) indicates that this explanation is inadequate for at least some examples. Experimental studies have instead shown the tendency of some filamentous cyanobacteria to move and tangle via gliding motility, and possibly subsequent phototaxis, to be key factors in the initiation and continuation of growth of tufted microbial mat structures. Such results were first widely publicised by Castenholz (1967, 1968), then by Walter *et al.* (1976), and more recently by Shepard & Sumner (2010). The cones and ridges forming in tufted microbial mats growing in the hydrothermal springs of Yellowstone National Park are particularly significant, as the waters exiting in the hydrothermal vents are supersaturated in silica, entombing microbial filaments as they cool, and precipitating silica onto the pool floor. Similar *in situ* precipitation of minerals and early lithification is thought to have led to the accretion and preservation of many stromatolites (including by definition tufted microbial mats) in Precambrian times. The pools are thus a rare modern analogue for ancient stromatolites and were extensively studied by Walter *et al.* (1976) who favoured a multi-step model for tuft and cone formation. This model features gliding motility and filament tangling at its core: undirected motility, collision, and tangling of cyanobacterial filaments leads to the formation of small bumps on the surface of otherwise smooth mats composed of the cyanobacterium *Phormidium tenue* and the sulfur-oxidising bacterium *Chloroflexus auranticus*; after the initiation of this topographic irregularity, filaments of *P. tenue* glide up and over the bump, seemingly preferring areas of raised topography, and consequently shading out filaments entangled within bumps; these filaments then also begin to migrate upwards in what Walter *et al.* suggested was a display of positive phototaxis. In this way, an erect tuft of filaments begins to aggregate on the apex of the steepening topographic irregularity. The tuft will grow larger, and if *in situ* precipitation of minerals is taking place, the structures will be stable enough for filaments to build structures with a synoptic relief higher than the length of one or two individual trichomes. Periods of horizontal growth then result in the linking of these cones at regular intervals. Support for this interpretation was lent by a series of laboratory experiments performed by Walter *et al.* (1976) who recreated tufts in culture and largely ruled out the possibility that *C. auranticus* plays a significant role in the formation of tufts and cones. Important for the interpretation of fossil examples, Walter *et al.* also noted a distinct axial zone and internal coniform lamination composed of alternating layers of prostrate and erect microbial filaments.



Bosak *et al.* (2010) describe the preservation of gas bubbles enmeshed in mats of filamentous cyanobacteria cultured from microbial mats growing in Sentinel Meadows and Fairy Creek, Yellowstone National Park. They suggest a link between these features and the fenestrae occurring in the axial zones of some Proterozoic *Conophyton* (e.g. Donaldson 1976; Bosak *et al.* 2009). This is one explanation for the fenestrate axial zones described here; however, these are not spherical, nor are they enclosed by organic-rich laminae—characteristics by which Bosak *et al.* (2010) suggest fossil bubbles may be recognised. Buoyancy and lifting of modern cyanobacterial mats due to trapped gas bubbles evolved during oxygenic photosynthesis is known (e.g. Vopel & Hawes 2006), and such bubbles may have assisted in the initiation of topographic irregularities that seem to be required for the genesis of conical stromatolites, yet the morphologies of the stromatolites described here are unlike the small tubular structures observed by Bosak *et al.* (2010) and are more consistent with the morphologies of stromatolites and the mechanism described by Walter *et al.* (1976) during their study of stromatolites forming in thermal pools in Yellowstone National Park.

The role of phototaxis in the formation of tufted microbial mat structures is contested by Shepard & Sumner (2010), who investigated the role of phototaxis in the genesis of reticulate patterns produced by motile filamentous cyanobacteria. Multiple substrates were inoculated with slurries of the cyanobacterium *Pseudonabaena* under a variety of laboratory conditions, after which the authors found that reticulate patterns such as those seen in tufted microbial mats arose within a few hours on all substrates inoculated with a sufficiently dense slurry of cells. Whether cultures received light from directly above the mat, from a very low angle or from directly below transparent substrates seemed to have very little effect on the formation of reticulate patterns, and the patterns were also observed forming in complete darkness. Shepard & Sumner (2010) thus suggest that reticulate patterns arise solely from the random gliding motility and tangling of bacterial filaments, and that the presence of reticulate patterns alone is insufficient to infer that microbial builders of such structures are capable of phototaxis. In addition, Shepard & Sumner (2010) suggest that the earlier work of Walter *et al.* (1976) falls short of establishing a requirement for phototaxis in the genesis of coniform tufted microbial mat structures. To date, the role of phototaxis in the formation of tufts and cones has not been reinvestigated in the detail required to distinguish between phototaxis and other possible factors such as chemotaxis and nutrient diffusion (e.g. Petroff *et al.* 2010). Further experimental work in the area is clearly needed, yet previous studies have at least provided a minimum of three constraints on the identities of ancient tufted microbial mat-building organisms, and a potential fourth. These are (1) a filamentous form, (2) gliding motility, (3) the tendency to tangle upon contact with other members of the colony and (4) possible positive phototaxis.

Additional constraints may be elucidated by future experimental studies. For example, Gerdes *et al.* (2000) have suggested that the additional extracellular poly-

meric substances (EPS) provided by participating unicellular cyanobacteria are important in the stabilisation of intertidal tufts and pinnacles.

### Tufted microbial mats in the geological record

There are several reports of fossil tufted microbial mats from sediments of Proterozoic and Archean age, and several additional reports of similarly aged stromatolites not originally described as products of tufted microbial mats but which bear features suggestive of a similar origin (Table 2).

Park (1977) noted that the structures of tufted microbial mats have only a poor preservation potential, and indeed such delicate and informative structures can be preserved only if they grow in an environment characterised by *in situ* mineral precipitation. However, this is the case for most Proterozoic and Archean stromatolites, which are generally thought to have been preserved through this process. The oldest putative tufted microbial mat consists of 3 mm high ‘pin-like’ protuberances associated with shallow water microbially induced sedimentary structures (MISS) in tidal flat sandstones of South Africa’s 2.9 Ga Pongola Supergroup (Noffke *et al.* 2008). No distinct ridges or vertically continuous successions of strongly inherited coniform laminae are reported, a result perhaps of the original protuberances having been distorted by post-burial compaction and their occurrence in siliciclastic sediments where finer detail is not preserved. The circumstances have resulted in very limited preservation of relevant features and consequently preclude extensive analysis. The report is nonetheless significant in regards to its age and association with other shallow water microbial mat-related sedimentary features.

Prior to this publication, the oldest fossil tufted microbial mats exhibiting the full array of features commonly observed in modern examples dated from *ca* 2.52 Ga. These are the perplexing microbialites of South Africa’s Campbellrand Subgroup, described in detail by Beukes (1987) and Sumner (1997). Both Beukes (1987) and Sumner (1997) suggested a relationship between these ancient microbialites and modern tufted microbial mats, specifically the permanently submerged *Phormidium* mats of ice-covered Antarctic lakes and Yellowstone hydrothermal springs, and the periodically exposed *Lyngbya* mats of Laguna Mormona, in Baja California. Corresponding features include millimetre-scale ‘supports’ comprising filmy laminae, millimetre-scale tufts with coniform laminae, ‘draping’ regularly occurring interconnecting laminae, and reticulate and parallel ridges on plan view surfaces. If analogous to the structures of modern tufted microbial mats, the central ‘support’ of many Campbellrand microbialites represents the column of coniform lamination formed by the vertical migration of microbial filaments. ‘Draped’ laminae then represent the regularly occurring laterally continuous laminae formed during periods of horizontal mat growth (cf. Walter *et al.* 1976; Jones *et al.* 1998). A completely different interpretation for these structures was proposed by Gandin *et al.* (2005), who considered the ‘cusped’ microbialites to be compressed organic matter trapped within folds of enterolithic gypsum. This

**Table 2** Putative Precambrian tufted microbial mats.

Age	Formation/group	Details	References
ca 2.9 Ga	Pongola Supergroup, South Africa	Poorly preserved 3 mm high protuberances on a surface associated with shallow water MISS. No microstructure.	Noffke <i>et al.</i> (2008)
ca 2.72 Ga	Tumbiana Formation, Fortescue Group, Western Australia	Well-preserved millimetre-scale coniformly laminated pseudocolumnar and columnar stromatolites linked by regularly occurring interconnecting laminae. Coniform, ridged and reticulate patterned plan surfaces.	This study
ca 2.52 Ga	Campbellrand Subgroup, Transvaal Supergroup, South Africa	Well-preserved millimetre-scale coniformly laminated tented, cusped and columnar stromatolites linked by regularly occurring interconnecting laminae. Straight and reticulate patterned ridges on plan surfaces.	Beukes (1987); Sumner (1997)
ca 1.8 Ga	Lower Albanel Formation, Canada	Millimetre-scale coniformly laminated columns linked by regular, interconnecting laminae	Hofmann (1978)
ca 1.55 Ga	Satka Formation, Southern Urals, Russia	Millimetre-scale coniformly laminated columns linked by regular, interconnecting laminae. Peaked, saddle ridged and reticulate patterned plan surfaces.	Vlasov (1977)
ca 1.2 Ga	Stoer Group, Scotland	Reticulate patterned ridges and distorted peaked structures	Upfold (1984)

explanation fails to account for several important features of the structures, including the asymmetrical nature of draping laminae and reticulate patterned horizontal surfaces. Several microbialites of the Campbellrand Subgroup are very similar in morphology to those found in the Tumbiana Formation, yet Campbellrand structures are considerably smaller than the Tumbiana examples; the width of some of the supports described by Sumner is only 50  $\mu\text{m}$ , and individual laminae are as thin as 3  $\mu\text{m}$ —indicating the organisms responsible for lamination were at least that small. This does not preclude a tufted microbial mat interpretation for the microbialites of either formation. Potentially, some of the structures of the Tumbiana Formation were constructed by filaments the size of *Lyngbya* (which constructs similarly sized structures in Shark Bay today; see Figure 3b, e), while the columnar supports described by Beukes (1987) & Sumner (1997) were constructed by much smaller filaments, something perhaps the size of *Phormidium*, which can have cells <1  $\mu\text{m}$  wide and is known to construct modern analogues in low-energy environments (Walter *et al.* 1976; Love *et al.* 1983; Jones *et al.* 1998). The Campbellrand Subgroup also preserves domal, columnar and stratiform stromatolites, laminated cherts, laminoid fenestrae, ooids, oncolites and tepee structures, all of which also occur in the Tumbiana Formation.

Two examples of previously described Precambrian stromatolites, which may be re-interpreted as the products of tufted microbial mats, are *Straticonophyton* and the Thyssagetids. *Straticonophyton* was described by Hofmann (1978) from Canada's ca 1.8 Ga Lower Albanel Formation and consists of millimetre-scale, conically laminated columns linked by regularly occurring interconnecting laminae. Morphology and microstructure is thus similar to both the Tumbiana Formation and Campbellrand Subgroup examples, and to modern stromatolites constructed by tuft-building cyanobacterial colonies (cf. Walter *et al.* 1976). *Mistassinia* described alongside *Straticonophyton* is similar in scale and morphology to columnar *A. narrina*, which is a stromatolite occurring in association with the Tumbiana Formation tufted microbial mat structures (see Walter 1983). The Thyssagetaceae family was named by Vlasov (1977) for an assemblage of several stromatolites of the Mesoproterozoic Satka Formation of the Southern Ural Mountains, which bear an unmistakable resemblance to the structures of modern tufted microbial mats. These stromatolites include millimetre-scale coniform peaks and reticulate patterned plan surfaces, sagging saddle ridges, radially ridged small cones and <1 cm wide coniformly laminated columns linked by 'draping' interconnecting laminae.

Also of note, Upfold (1984) interpreted upward-thinning, reticulate-patterned ridges and distorted peaked

structures from the ca 1.2 Ga Stoer Group of Scotland as fossilised tufted microbial mats. The tufts have been heavily distorted by post-burial compaction, and microstructure is not preserved, but other explanations for the features seem unlikely.

## CONCLUSIONS

The discovery of tufted microbial mat structures in the Tumbiana Formation provides significant insights into the nature of life in the Archean. Experimental work has shown that a filamentous form, gliding motility and the tendency to tangle upon contact are key characteristics of microbes capable of generating tufted microbial mat structures. The builders of ancient tufted microbial mats probably also produced large volumes of extracellular polymeric substances and were capable of phototaxis, but further experimental work is required to confirm these additional constraints.

Today, cyanobacteria seem to be the only prokaryotes capable of forming tufted microbial mat structures, possibly as a result of advantages conveyed to them by their unique metabolism. If cyanobacteria are indeed alone in their ability to produce such structures, a minimum date for their origin may then be based on the first appearance of tufted microbial mats in the fossil record, a date now set at 2.72 Ga. There then remains the dilemma of why it took more than 200 million years for oxygen to accumulate in the atmosphere.

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