A fresh look at the fossil evidence for early Archaean cellular life

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The rock record provides us with unique evidence for testing models as to when and where cellular life first appeared on Earth. Its study, however, requires caution. The biogenicity of stromatolites and 'microfossils' older than 3.0 Gyr should not be accepted without critical analysis of morphospace and context, using multiple modern techniques, plus rejection of alternative non-biological (null) hypotheses. The previous view that the co-occurrence of biology-like morphology and carbonaceous chemistry in ancient, microfossil-like objects is a presumptive indicator of biogenicity is not enough. As with the famous Martian microfossils, we need to ask not 'what do these structures remind us of?', but 'what are these structures?' Earth's oldest putative 'microfossil' assemblages within 3.4–3.5 Gyr carbonaceous cherts, such as the Apex Chert, are likewise self-organizing structures that do not pass tests for biogenicity.

There is a preservational paradox in the fossil record prior to *ca* 2.7 Gyr: suitable rocks (e.g. isotopically light carbonaceous cherts) are widely present, but signals of life are enigmatic and hard to decipher. One new approach includes detailed mapping of well-preserved sandstone grains in the *ca* 3.4 Gyr Strelley Pool Chert. These can contain endolithic microtubes showing syngenicity, grain selectivity and several levels of geochemical processing. Preliminary studies invite comparison with a class of ambient inclusion trails of putative microbial origin and with the activities of modern anaerobic proteobacteria and volcanic glass euendoliths.

Keywords: Apex Chert; Archaean; early life; endolithic microtubes; Strelley Pool Chert;
western Australia

1. INTRODUCTION

Three fundamental features about the Archaean Earth need to be borne in mind when discussing the setting for the origins of life. First, habitable surface environments following the late heavy bombardment (approx. 3.85 Gyr ago (Ga)) were very different from those in the Proterozoic and strongly influenced by volcanic and hydrothermal processes. Second, isotopically light carbonaceous matter, preserved largely in silica-rich chert, was not only widespread in surface environments, but also intimately connected to numerous, deep hydrothermal dyke systems. Third, there is an apparent preservation paradox: cellularly preserved and ensheathed microfossils and complex stromatolites (remarkably preserved from the late Archaean onward; e.g. Knoll 2003), are rarely found in the early rock record and all are controversial. This taphonomic paradox is surprising given the high fidelity of the Proterozoic microfossil record in cherts and carbonates (e.g. Knoll 2003) and the ease with which microbes can be silicified in modern settings (e.g. Konhauser *et al.* 2003). As we argue below, most reports of early microfossils and stromatolites (e.g. Hoffmann *et al.* 1999) are not readily distinguishable from self-organizing structures (SOS) and have yet to pass the null hypothesis, that microfossil- and stromatolite-like

structures older than about 3.0 Gyr should not be accepted as of biological origin until alternative hypotheses for their abiogenic origin have been tested and falsified (see Grotzinger & Rothman 1996; Brasier *et al.* 2005 and references therein).

This vestige of a primordial, *non-uniformitarian* world, in which life was yet to shape and coevolve with (bio)geochemical cycles, poses huge epistemological challenges and defies any easy consensus about the earliest signals for life (Rose *et al.* 2006). It requires us to approach the early Earth as we would a distant planet such as Mars and to take a calm, cautious, multidimensional and multidisciplinary approach to the evidence (e.g. Brasier *et al.* 2005; Westall 2005).

2. SETTING

The earliest Archaean (3.82–3.65 Ga) rocks of Greenland and Labrador are highly metamorphosed so that their potential for decoding the early biosphere now seems doubtful and extremely difficult (Fedo & Whitehouse 2002; Van Zuilen *et al.* 2002, 2003; Lepland *et al.* 2005; Moorbath 2005; Westall 2005). Better-preserved rocks outcrop in the *ca* 3.5–3.0 Gyr Pilbara craton of Western Australia and the Barberton region of South Africa and Swaziland. Here, they comprise basins of lavas and thin intercalated sediments known as greenstone belts, between supracrustal domes of granite. Evidence from these granite-greenstone belts now points towards an oceanic-like crust

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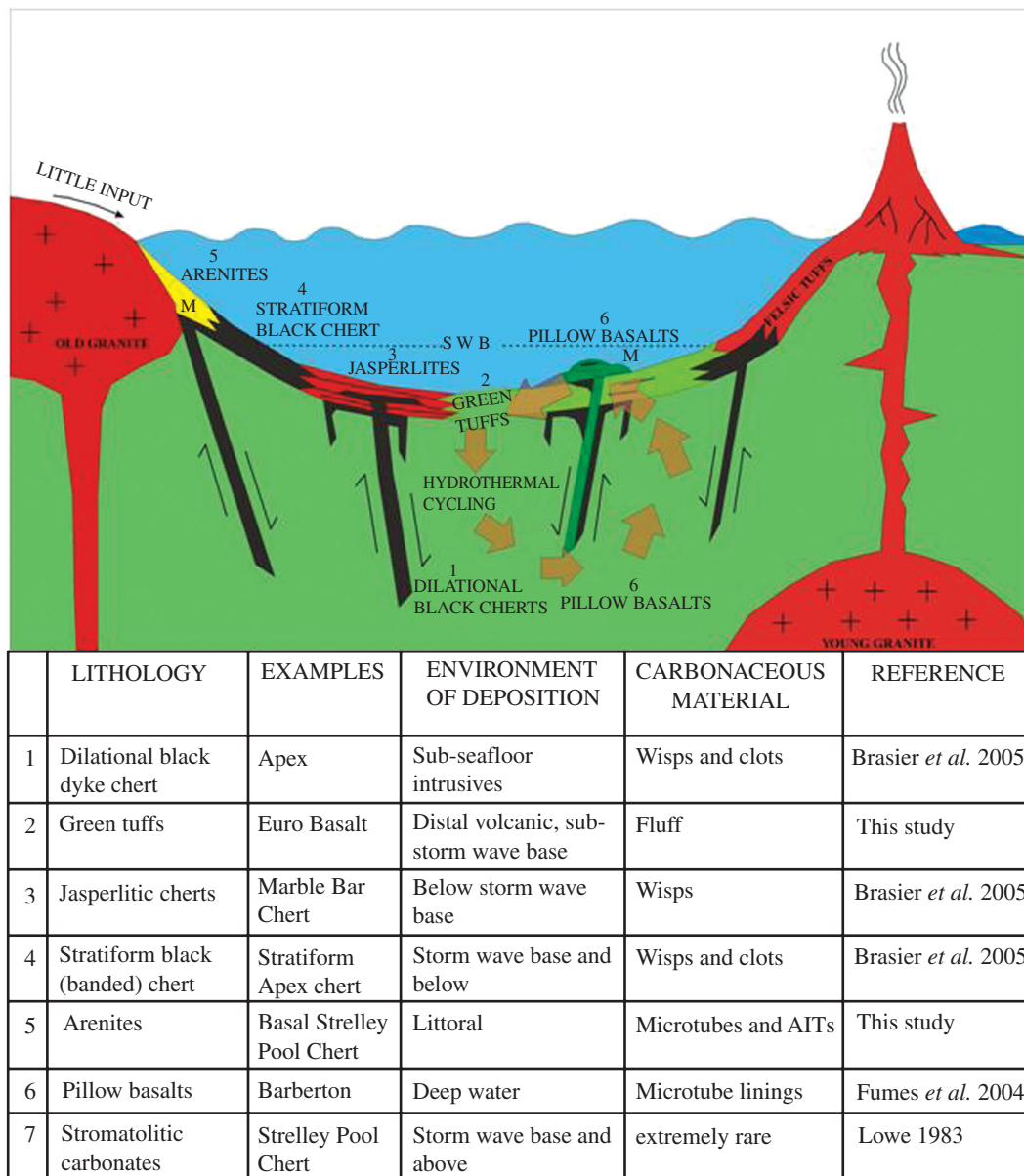|	LITHOLOGY	EXAMPLES	ENVIRONMENT OF DEPOSITION	CARBONACEOUS MATERIAL	REFERENCE
1	Dilational black dyke chert	Apex	Sub-seafloor intrusives	Wisps and clots	Brasier *et al.* 2005
2	Green tuffs	Euro Basalt	Distal volcanic, sub-storm wave base	Fluff	This study
3	Jasperlitic cherts	Marble Bar Chert	Below storm wave base	Wisps	Brasier *et al.* 2005
4	Stratiform black (banded) chert	Stratiform Apex chert	Storm wave base and below	Wisps and clots	Brasier *et al.* 2005
5	Arenites	Basal Strelley Pool Chert	Littoral	Microtubes and AITs	This study
6	Pillow basalts	Barberton	Deep water	Microtube linings	Fumes *et al.* 2004
7	Stromatolitic carbonates	Strelley Pool Chert	Storm wave base and above	extremely rare	Lowe 1983

Figure 1. A generalized model for the occurrence of carbonaceous matter in Archaean cratons at *ca* 3.4 Gyr, based on field mapping in the Pilbara. SWB, storm wave base; M, known microtube localities; AIT, ambient inclusion trail. Isotopically light carbonaceous matter is not restricted to surface environments, it is also found within numerous deep, hydrothermal dyke systems.

that was hot and highly volcanic, with massive hydrothermal recycling of seawater through the upper layers (figure 1), leading to widespread silica super-saturation on the seafloor (cf. Kamber & Webb 2001) accompanied by white smoker like hydrothermal events where barite, jarosite and alunite were precipitated near the seafloor (cf. Nijman *et al.* 1998; Kato & Nakamura 2003; Sugitani *et al.* 2003; Van Kranendonk & Pirajno 2004). Hydrothermal activity seems to have been especially marked during intervals of major granitic emplacement. Thin sedimentary chert layers then formed intermittently on the seafloor from direct precipitation of silica and/or from the replacement and displacement of other rock types, especially near to the numerous hydrothermally influenced growth faults (e.g. Nijman *et al.* 1998). There is scant evidence for plate tectonics or subductive recycling of the crust at this time (McCall 2003), implying absence of this major carbon recycling mechanism.

Carbonaceous matter is found remarkably widely across Archaean cratons. A generalized model based on our field mapping in the Pilbara is presented here (figure 1). Carbon occurs in subsurface fissure-filling (dyke) cherts, in shallow sublittoral sandstones, through jaspilitic cherts deposited close to wave base and in deeper water green cherts associated with basic pyroclastic eruptions (figure 1; Nijman *et al.* 1998; Tice & Lowe 2004; Brasier *et al.* 2005). Carbon also occurs as migratory hydrocarbons at this time (e.g. Rasmussen & Buick 2000). By contrast, reports of carbonate are rare in sediments prior to *ca* 2.9 Ga, although high precision rare earth element (REE+Y) data have been used to infer a primary marine origin for dolomite within the *ca* 3.4 Gyr Strelley Pool Chert (SPC) and ankerite within the 3.49 Gyr Dresser Formation (Van Kranendonk *et al.* 2003). That said, carbonate is mainly confined to secondary dolomites around volcanic vents and to hydrothermal margins

around and within submarine mafic lavas. Evidence for photic zone conditions (e.g. oolite grains, wave ripples, tidal features) in marine carbonates is largely absent while evaporitic aspects have been taken to represent both hypersaline lagoons (e.g. Lowe & Worrell 1999) and supersaturation under hydrothermal white smoker conditions (cf. Nijman *et al.* 1998).

The source and nature of this early carbonaceous matter, especially that of the 'deep carbon', is of wide interest since it is invariably enriched in the light isotope ^{12}C, much like that from biological fractionation (e.g. Schidlowski 2001; Hayes & Waldbauer 2006). While such an isotopic record in younger rocks may be accepted as biogenic in origin, the earliest records deserve the same critical scrutiny as both morphological and other geochemical evidence. A number of hypotheses have been put forward for this deep carbon. An origin from light-independent hyperthermophilic microbes within the crust, like those around black smokers, has been suggested by the ubiquity of carbonaceous matter in hydrothermal dyke cherts (Nijman *et al.* 1998; Ueno *et al.* 2004). An origin from phototropic microbes at the sediment surface has been suggested by the presence of putative microbial mat fabrics and 'microfossils' (Schopf 1993; Tice & Lowe 2004), while an origin from pelagic microbial matter within the water column is raised by the presence of 'fluffy' carbonaceous grains in marine sediments close to storm wave base (e.g. Walsh & Lowe 1999).

A null hypothesis that needs to be falsified for each of the above, however, is an abiogenic origin for this light carbon, for example, from Fischer-Tropsch type (FTT) reactions between CO and metals (Horita & Berndt 1999; Sherwood Lollar *et al.* 2002) and/or from the metamorphic reduction of siderite (Van Zuilen *et al.* 2003), which can both result in carbon isotope fractionations that lie within the 'biogenic domain' (up to $-40‰$). An abiogenic source for some of this deep Archaean carbon is suggested by the ubiquity of light carbon in deep hydrothermal dyke cherts and by close association with hydrothermal carbonates, sulphates and metals (Nijman *et al.* 1998; Brasier *et al.* 2002, 2005; Lindsay *et al.* 2005). This scenario, that there was deep, abundant, hydrothermally generated abiogenic carbon like that found around some modern black smokers, urgently needs to be further tested, not least for its implications to the origins of life. Unfortunately, a single line of evidence, such as isotopically light carbon or laser Raman analysis (Schopf *et al.* 2002; Pasteris & Wopenka 2003; Schopf 2006), is insufficient to distinguish between these options.

3. BIOSIGNALS FOR CELLULAR LIFE

The burden of proof is great when considering the earliest claims for early cellular life. Such proposals require multiple, *in situ* and mutually supporting lines of evidence for a well-constrained age and context, evidence for a morphology unique to biology and more than a single line of geochemical evidence for metabolic cycling, *together with* falsification of the null hypothesis of plausible abiogenic origins (see Brasier *et al.* 2002,

2004; Altermann & Kazmierczak 2003; Cady *et al.* 2003; Westall 2005; Rose *et al.* 2006).

Geological context here implies mapping at scales from kilometres to metres, supported by mapping of petrographic thin sections in order to show that candidate structures are truly syngenetic and ancient (e.g. Cady *et al.* 2003; Brasier *et al.* 2005 and references therein). This can be tested by laser Raman spectra (Pasteris & Wopenka 2002) or atomic force microscopy (Altermann & Kazmierczak 2003), though both need to be coupled with careful contextural and petrographic mapping to falsify the 'null hypothesis' of an abiogenic origin (Brasier *et al.* 2002; see also Schopf *et al.* 2002; Tice & Lowe 2004). Morphological analysis requires *in situ* imaging and mapping of morphospace to distinguish the fields of biotic and abiotic morphology and to compare with self-organizing structures (see below). Geochemistry requires high resolution three-dimensional micrometre scale *in situ* mapping and analysis, using more than a single line of contaminant-free evidence. Examples include the study of C and S isotopes and oxidation states (e.g. House *et al.* 2000; Ueno *et al.* 2001), major and trace element mapping (cf. Kamber & Webb 2001) and biomarker analysis (cf. Summons *et al.* 1999) from putative microfossils and host rocks.

A hidden problem in early life studies concerns our reliance upon inductive lines of reasoning. This is inevitable, of course, in a historical science such as palaeobiology (Cleland 2001). But in the past, we have tended to rely too much upon evidence that is 'consistent with' microbial processes, without falsifying or rejecting (*sensu* Popper 1959) other possible non-biological scenarios that may likewise be consistent. We have tended to ask 'what do these structures remind us of' rather than 'what are these structures'? Recognition of the need for testing a null hypothesis of an abiogenic origin for the earliest fossil evidence forces us to face up to, and overcome, this very human tendency. And it prepares us for the coming debates that may yet arise on the return of rock samples from Mars.

4. SELF-ORGANIZING STRUCTURES

Morphological complexity has for long been taken as a keystone characteristic for the earliest fossils (e.g. Buick *et al.* 1981; Buick 1990; Schopf 1999). A basic understanding of SOS and complexity is therefore essential if the early fossil record is to be correctly decoded. Unfortunately, complex structures do not require complex causes, as shown nearly a century ago by Thompson (1917). They can arise naturally in physico-chemical systems within the realms of 'chaotic' behaviour as Grotzinger & Rothman (1996) showed a decade ago with reference to stromatolites. In figure 2, we draw attention to a range of physico-chemical gradients that can lead to the formation of macroscopic stromatoloids (figure 2*a*) and ripples (*b*) as well as to microfossil-like structures generated by the growth of dendrites (*e*), 'coffee-ring' effects (*f*), polygonal crystal rims (*g*) and spherulites (*h*).

In each of the systems shown in figure 2, a move to the right results in a loss of symmetry, but a gain in morphological or temporal complexity towards the
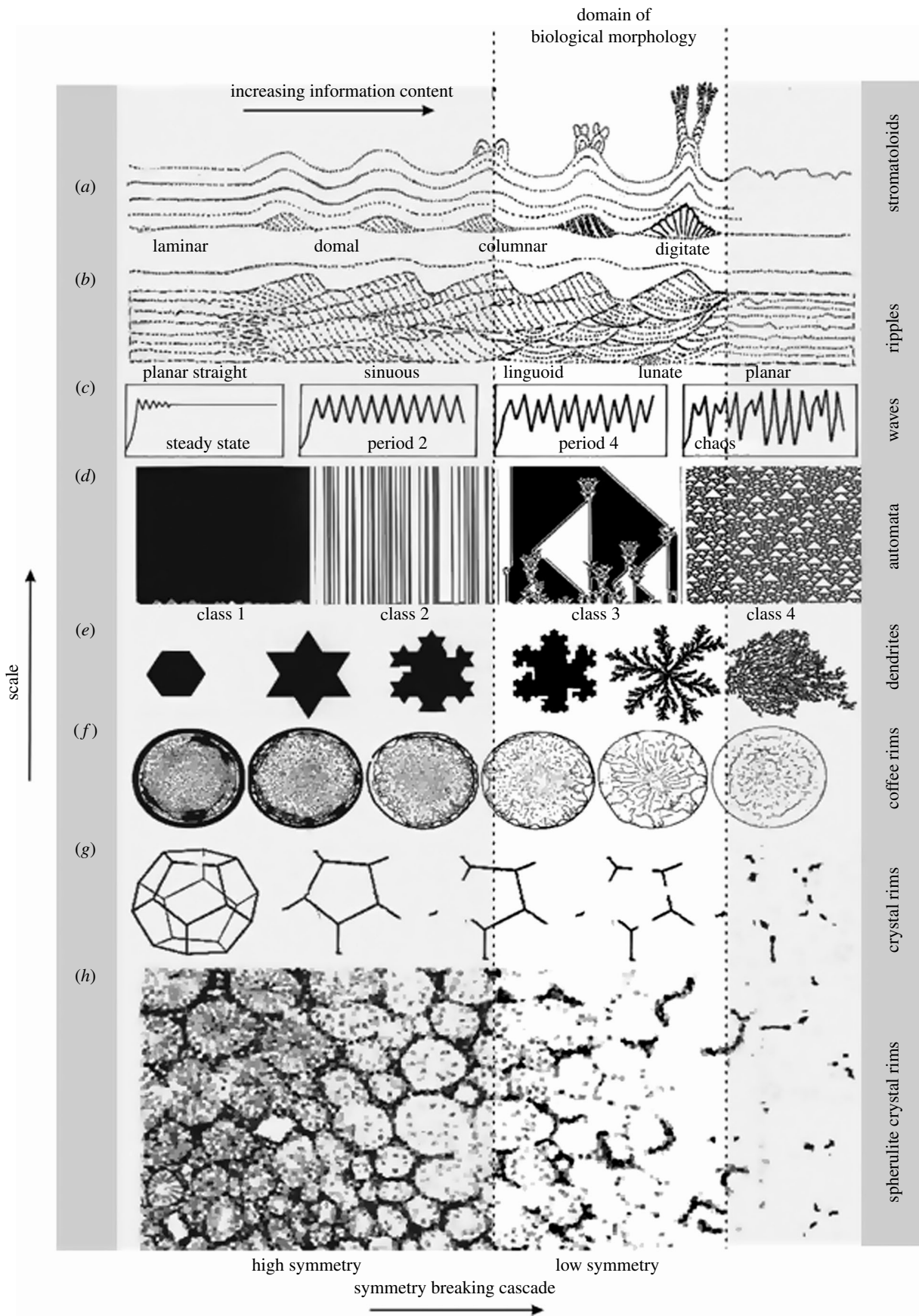
Figure 2. The range of self-organising structures (SOS) that can arise naturally in physico-chemical systems within the realms of chaotic behaviour. Symmetry is lost as one moves to the right, but morphological complexity increases. The size of the SOSs decreases down the figure. With stromatoloids (at *a* and *d*) some scientists believe that complex forms (within the 'domain of biological morphology') necessitate a biological component. But the full spectrum of forms is found in both biological and abiological stromatoloid systems; both result from the physics of viscous materials and neither result from behaviour of microbes alone. In well preserved and true microfossil assemblages, the morphological variation is usually less than co-occurring abiogenic structures (at *e–h*) and so will occupy a more restricted domain ('domain of biological morphology') within the morphospace.

Table 1. A critical evaluation of putative reports of early life based upon geological context, biology like morphology and geochemical processing. (✓, Arguably present; +, possibly biogenic, further testing necessary; SOS, abiogenic self-organizing structure; AIT, ambient inclusion trail, abiogenicity still to be falsified; h/t, hydrothermal; R D Si, replacive and displacive silica; met, metamorphic; ign, igneous; Bs, basalt; sed, sedimentary; prim, primary; fab.map, fabric mapping.)

| site | reference | age | context | | preservation | steps | | morphology | | | | | | | | |
			fab. map	setting		elements	zones	clusters	tubes	spheroids	filoids	septate	sheaths	wisps	fluffs	stroms
W. Greenland	Mojzsis et al. 1996	>3750		met. ign.	heavily met	C?										
	Rosing 1999	>3700		met. sed	heavily met	C										
North Pole	Ueno et al. 2001	3490		h/t chert	R D Si	C			AIT			SOS				SOS
Awramik B	Awramik et al. 1983	3490		h/t chert	R D Si	C		✓	AIT			SOS			SOS	
Barberton	Furnes et al. 2004	3480	✓	pillow Bs	R titanite	C		✓	AIT?	+						
Awramik A	Awramik et al. 1983	3460		h/t chert	R D Si	C			AIT			SOS			SOS	
Apex dyke	Brasier et al. 2005	3460	✓	h/t chert	R D Si	C				SOS	SOS	SOS		SOS	SOS	
Apex stratiform	Brasier et al. 2005	3460	✓	sed.	prim. Si	C				SOS	SOS	SOS		+	+	
Barberton	Walsh 1992	3445	✓	sed.	prim. Si	C		✓	AIT?	SOS	+	SOS		+	+	
Barberton	Westall et al. 2001	3445		sed.	prim Si	C				SOS	+	SOS		+	+	
SP arenite	current study	3435	✓	sed.	prim. Si	CN S FeP	✓	✓	AIT			+				
SP chert	current study	3430	✓	sed.	R D Si	C					SOS	SOS				SOS
Barberton	Tice & Lowe 2004	3416	✓	sed.	prim. Si	C			AIT?		+			+	+	
Eurobasalt	current study	3400		sed.	prim. Si	C									+	
Sulphur springs	Rasmussen 2000	3235	✓	h/t chert	prim Si	C FeS		✓			+					
Mozaan	Noffke et al. 2003	2900		sed.	prim. Si	C					+	+		✓		✓
Fortescue	Schopf & Walter 1980	2768		sed.	prim. Si	C			AIT			+				✓
Campbelr.	Altermann & Schopf 1995	2600		sed.	prim. Si	C, CaCO₃		✓		✓	✓	+	+	✓		✓
Gunflint	Barghoorn & Tyler 1965	1878	✓	sed. +/− h/t chert	prim. Si	CN S		✓	AIT	✓	✓	+		✓		✓
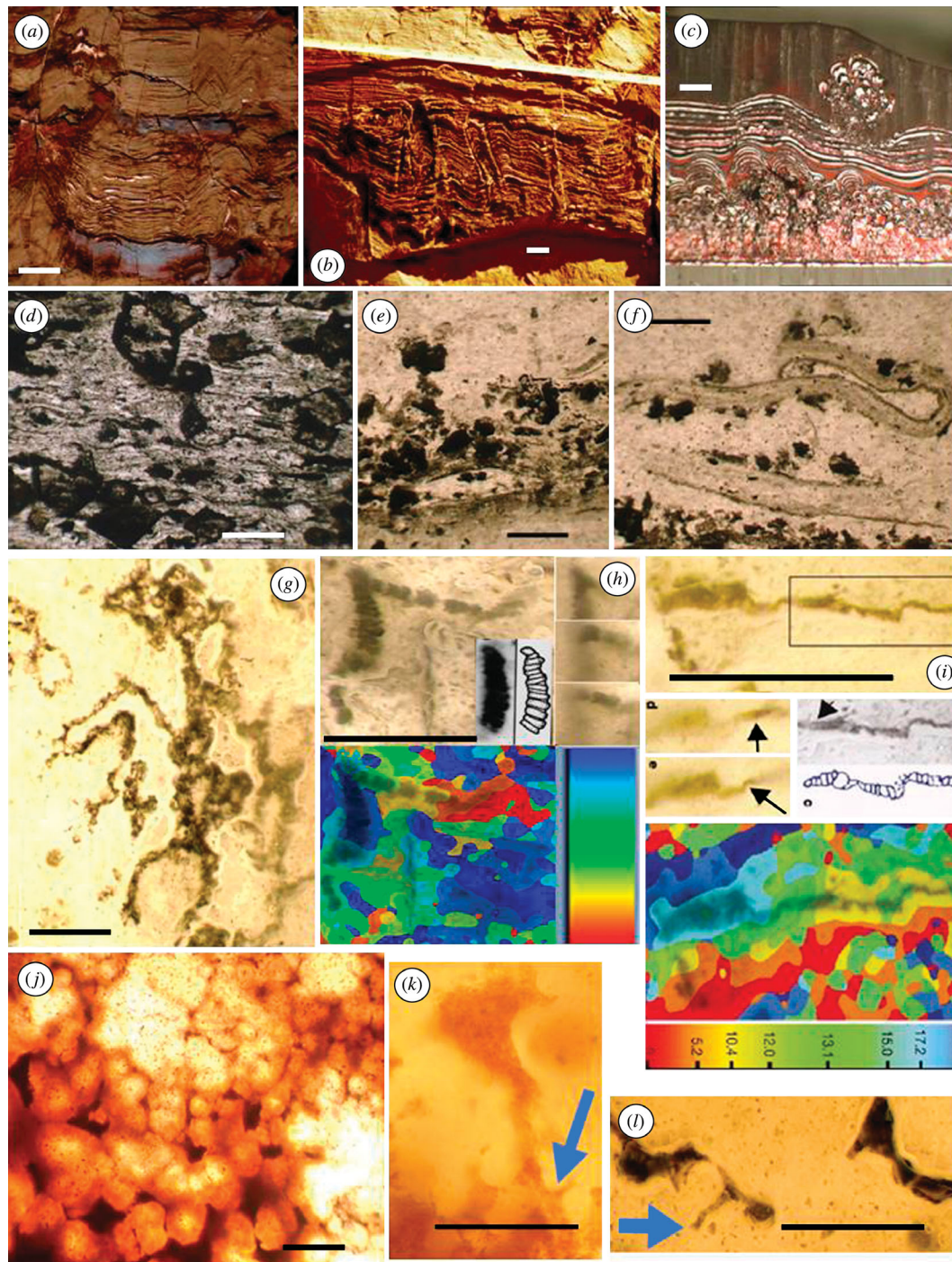
Figure 3. (*a*) Conical and (*b*) pseudo-columnar 'stromatoloids' from the Strelley Pool Chert, Pilbara, Western Australia. (*c*) Stromatoloid produced by physical discontinuities between polymeric layers of different viscosities in experiments with synthetic polymers (McLoughlin *et al*. submitted). (*d*) Carbonaceous 'wisps' in the Apex Chert. Note also, carbonaceous matter concentrated around rhombic crystal growths. (*e*) Rounded grains of carbonaceous 'fluff' from the Buck Reef Chert, Barberton, South Africa. (*f*) Laminar, carbonaceous 'fluff' from mat fragments from the Buck Reef Chert, Barberton, South Africa. The presence of bends and rollover structures has been interpreted to represent the plasticity of early microbial mats. (*g–i*) Automonatages of microfossil-like artefacts from the Apex Chert. (*g*) Pseudo-septate and branched filamentous artefacts from vein chert generated from the growth of dendrites, polygonal crystal rims and spherulites. (*h*) Image of putative cyanobacterium *Archaeoscillatoriopsis disciformis* Holotype and (*i*) image of putative beggiatoan *Eoleptonema apex* Holotype (Schopf 1993) both here explained as a SOS structures resulting from the breaking of polygonal symmetry during crystal growth (false coloured images in *h* and *i* represent depth profiles within the thin section using Automontage software). (*j*) Spherulitic SOS from the Gwna Chert. (*k*) Abiogenic septate dendritic fringe of a spherulite mass, Apex Chert. (*l*) Abiogenic septate carbonaceous filament shown branching off spherulitic mass from the Apex Chert. Scale bar: 2 cm *a,b*; 1 mm *c*; 40 μm *d–l*.

'chaotic domain' (see Stewart & Golubitsky 1992). This leads to a 'symmetry breaking cascade', wherein the 'symmetry group' falls and the level of information rises. Symmetry breaking is a particularly conspicuous phenomenon during the growth and recrystallization of

spherulites, leading to natural assemblages of structures that can range from spheroidal (broadly rotational symmetry), to dendritic (reflectional to slide symmetry), to arcuate (no clear symmetry; figure 2*h*). Such symmetry-breaking cascades appear to arise when
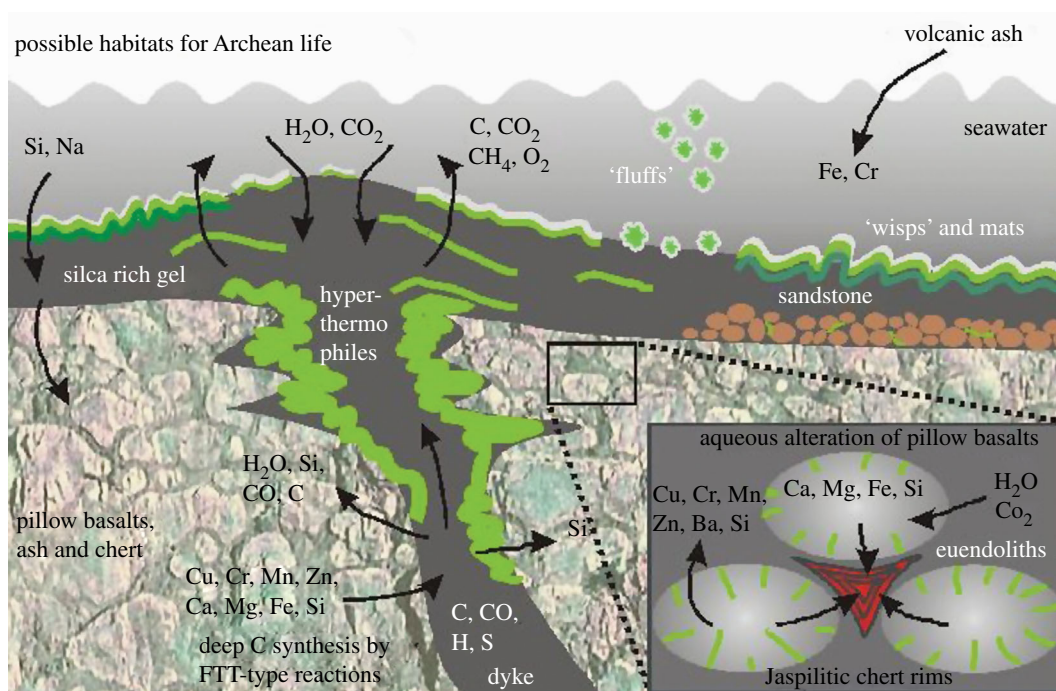
Figure 4. Schematic diagram showing the possible habitats for life (here shown in green) and suggested cycling of major elements in the Archaean ocean. Ecological tiering includes: planktonic cell aggregates or 'fluffs', benthic 'wisps' and mats, intraterrestrial euendoliths within sandstones and pillow basalt rims (inset at right) and hyperthermophilic microbes in hydrothermal settings.

localized changes in the ionic concentrations of the constituent chemicals (e.g. iron oxide, carbon) fall below a critical threshold, so that the higher levels of symmetry became unstable. In this way, the margins of crystal growth can provide a rich harvest of pseudo-fossil structures, ranging from polygonal to dendritic to filamentous (e.g. snowflakes, moss agate, pyrolusite 'moss'; figure 2*e–h*) and from spherulitic/ botryoidal to dendritic to filamentous (e.g. hydrothermal cherts and jaspers; figure 2*h*). Such complex systems have also been simulated by computational experiments and digital automata (figure 2*c,d*), replicating the self-organization seen within stromatolites and dendrites (Grotzinger & Rothman 1996; Wolfram 2002). Below, and in table 1, we briefly review the main types of SOS: spheroids, filoids, septate filoids, stromatoloids, wisps and fluffs; and the challenges that they present for decoding the earliest fossil record.

5. CANDIDATE MORPHOTYPES

Spheroids are simple microscopic spheres of carbonaceous matter that can resemble simple coccoid or baccilate cells. Commonly encountered in Archaean carbonaceous cherts, some have been regarded as microfossils (table 1; figure 3; see also Schopf 2006). The problem here is that spheres have a high level of symmetry and are readily generated abiogenically by physico-chemical systems in the form of fluid inclusions, vesicles (bubbles), globules, rings and spheroidal crystallites (figure 2*h*; see Folsome 1977; Deegan 2000; Brasier *et al.* 2005). With such low levels of information and complexity, it is therefore hard to demonstrate biogenicity for solitary (e.g. Walsh 1992; Schopf 1993) or clustered spheroids (e.g. Schopf & Packer 1987; Sugitani *et al.* 1998; Westall *et al.* 2001).

Microscopic carbonaceous filaments referred to here as filoids have been widely reported from early to middle Archaean cherts and compared with younger prokaryotic microfossils (e.g. Schopf 2006). Unfortunately, filaments provide one of the commonest SOS from the breaking of polygonal, spheroidal or circular symmetry during crystal growth (figure 2*f–h*; e.g. Buick 1988; Deegan 2000). Complex filaments that resemble the earliest Archaean microfossils have been generated experimentally by the precipitation of metallic salts in silica gels (e.g. Garcia-Ruiz *et al.* 2003). Dendritic artefacts (cf. figure 2*e*) are also common in hydrothermal jaspers and carbonaceous cherts (Brasier *et al.* 2005); and hollow, bacteria-like filaments can be generated by spark-discharge or FTT-like synthesis of organic polymers in prebiotic experiments (Folsome 1977; Baker & Harris 1978). As discussed above, FTT-like processes may have operated in Archaean hydrothermal systems, while spark discharges are likely to have accompanied all major volcanic eruptions, though neither have yet been unambiguously demonstrated from the Archaean rock record.

Of considerable interest are 'septate filoids'. These are microscopic, subdivided carbonaceous structures that resemble cellular prokaryotic microfossils owing to the presence of cell-like septation (figure 2*h*). They have been reported from several localities in the early Archaean of Western Australia (table 1) where they have been interpreted as the remains of bacteria (figure 3*h*), and at times compared with photosynthetic cyanobacteria because of their size range (Awramik *et al.* 1983; Schopf & Packer 1987; Awramik 1992; Schopf 1992*a*, 1993, 1999; Ueno *et al* 2001). The formation of cell-like structures from crystal growth, however, has long been known (Baker & Harris 1978; Horodyski 1981; Garcia-Ruiz *et al.* 2003). We find that

the famous early Archaean, Apex Chert examples are associated with the recrystallization of amorphous glassy silica to spherulitic chalcedony and other hydrothermal fabrics (see below). They arise within the complex conditions found along the boundaries of crystals within jaspilitic and carbonaceous cherts, volcanic glass and rhyolite (figure 2h), and are part of a symmetry breaking cascade from spheroidal-dendritic-arcuate artefacts preserved in these rocks (see Brasier *et al.* 2002, 2004, 2005). Some of these septate filoids can also be highly angular when associated with polygonal or rhomboid crystal casts (figure 2g; Brasier *et al.* 2005). Although such forms have been interpreted as biogenic, for example, *Beggiatoa*-like microfossils (e.g. Schopf 1992a, 1993), we find that they clearly intergrade with other SOS filaments along the margins of growing quartz, carbonate or sulphate crystals (figure 3g–i). All the early Archaean examples outlined by Schopf (2006) are in need of further investigation.

Although structures optimistically regarded as cells in the process of division have been used to argue for their biological origin (Schopf 1993, 2006), this ignores the fact that such structures can arise naturally within complex self-organizing systems, such as mineral growths (Brasier *et al.* 2005) and even soap bubbles. We are aware of no convincing examples of cell division from the Archaean. Carbonaceous composition is effectively irrelevant to morphological arguments.

Stromatolites are macroscopically layered structures comprising wrinkled surfaces, domes, cones and columns (figure 3a,b) that accrete upwards from a point or surface of initiation and have been defined in terms of either requiring (Krumbein & Werner 1983) or not requiring (Semikhatov *et al.* 1979) microbial mediation. In table 1 we adopt the non-genetic term 'stromatoloid' and make no assumptions about the presence or absence of microbial mats. The diversity of Archaean stromatoloids is much lower than in subsequent Proterozoic examples (Hofmann 2000), and their morphologies, we argue, tend to be less complex over a range of scales. It is widely inferred in the literature that many early Archaean stromatoloids record microbial trapping and binding of detrital sediment and or microbially mediated chemical precipitation (e.g. Walter *et al.* 1980; Awramik *et al.* 1983; Hofmann *et al.* 1999). Additionally, there have been arguments for the presence of oxidative photosynthesis by 3.5 Ga (e.g. Awramik 1992; Schopf 1999) and phototrophic behaviour by stromatoloids (Hofmann *et al.* 1999). But we caution that macroscopic SOSs resembling stromatolites are readily generated by abiogenic processes (Lowe 1994) that include: diffusion limited aggregation of synthetic colloids in laboratory experiments (figure 3c and McLoughlin *et al.* submitted), computer simulations using the Kardar Paris Zhang equation (Grotzinger & Rothman 1996), and cellular automata (cf. figure 2d; Wolfram 2002). Abiogenic numerical modelling experiments using the SRK equation have also generated conical stromatoloid-like structures (Jogi & Runnegar 2005), for long taken to represent a distinct class of phototactic structures. This tells us that the morphospace occupied by most stromatoloids need not be shaped by biological behaviour or by natural

Table 2. Comparison of the mathematical compressibility (cf. Corsetti & Storrie-Lombardie 2003) of digitally imaged assemblages of microfossil-like structures in petrographic thin sections. (Obtained from the following Precambrian sediments: *ca* 1900 Myr Gunflint Chert of Canada, containing clusters of possible iron bacteria filaments (slide D$_3$; see Barghoorn & Tyler 1965; Knoll 2003); *ca* 800 Myr Boorthanna chert of Australia, containing colonies of coccoid cyanobacteria-like cells (cf. Schopf & Fairchild 1973) that can degrade to pseudofilaments (slide WPM 18/6; cf. Kazmierczak & Kremer 2002); *ca* 560 Myr Gwna Group jaspilitic cherts from Newborough Warren, Wales containing questionable microfossil-like structures (slide CG4; see Muir *et al.* 1979) formed from abiogenic spherulites (figure 3j herein); *ca* 3460 Myr Apex Chert, Australia, containing questionable microfossil-like structures (slide V.63165; see Schopf 1993) formed from abiogenic spherulites (figure 2H and 3g–l herein); *ca* 3430 Myr Strelley Pool Arenite, Australia, containing microtubes (slide SP9a; see figure 5 herein). Stratigraphic horizons (column 1), number of filaments (column 2), mean filament width in micrometres (column 3), standard deviation of filament width in each population (column 4) and percentage compression measured using lossless compression algorithm (column 5), in petrographic thin sections. An England Finder Slide was used to pick out a traverse line across the slide. Maximum linear length and maximum width (90° to the length) measurements were also made, and coordinates recorded, of filaments and other structures in all thin sections. Multiple traverses were taken across each slide to gain statistically significant ($n = 100$) readings. Each filament or structure that crossed this line then had its maximum linear length and maximum width (taken to be 90° to the length) measured and recorded. Two JPEG images were chosen at random and their percentage compressibility calculated using a lossless compression algorithm 'gzip' available at www.astrobio.net/cgi-bin/compare.cgi. All slides are stored in the Palaeobiology Laboratories at Oxford.)

	n	mean	s.d.	compress
Gunflint	299	2.33	1.23	2.531
Boorthanna	302	1.51	0.53	0.172
Gwna	304	9.19	10.94	0.909
Apex	200	4.7	4.8	0.378
SPA	200	5.9	3.1	1.01

selection. It arises directly from the thermodynamics of viscous materials, much like ripples in sand. Given the absence of compelling microbial mat or microfossil remains in many early Archaean stromatoloids and their close association with non-equilibrium hydrothermal systems, questions unfortunately remain as to whether, alone, they have anything useful to tell us about microbes or early biology. We agree with Schopf (2006), that 'it is perhaps impossible "to prove beyond question" that the vast majority of reported stromatolites…are assuredly biogenic'.

'Wisps' are microscopic carbonaceous wrinkled laminae that can be found in many modern to late Archaean 'mats' whose biological origin is largely undisputed (e.g. Knoll 2003). Wisps are often assumed to have formed from microbial biofilms of extra-cellular polymeric substances (EPS; Noffke *et al.* 2003) and occur *in situ* within the stratiform Apex Chert of the Pilbara (figure 3d, Brasier *et al.* 2005) and at several

levels in the Barberton (Westall *et al.* 2001), where they have been interpreted as the remains of photosynthetic mats, albeit anaerobic (Walsh & Lowe 1999; Tice & Lowe 2004). The original plasticity of these mats is suggested by bends and rollover structures (figure 3*f*; see also Walsh & Lowe 1999) and is a major line of evidence used to infer their biogenicity. It is important to note however, that wisps and 'microfossil-like structures' are absent from the earliest stromatoloids (approx. 3.5–3.0 Gyr; Lowe 1994; Hoffman *et al.* 1999). Care is also needed to avoid confusion of wisps with other secondary phenomena, such as compaction wrinkles, evaporitic wrinkles and pressure solution wrinkles or even volcanic fabrics: they need to be carbonaceous and lacking in evidence for association with tectonic strain, pressure solution or authigenic clay mineral or iron oxide growth. Even then, further notes of caution are needed. Our own experiments with synthetic polymers (figure 3*c*; McLoughlin *et al.* submitted) confirm that wrinkled laminae can arise from physical discontinuities between polymeric layers of differing viscosities. This means that wispy laminae can arise without the intervention of vital processes, let alone photosynthesis. Hence, while wrinkles and wisps may provide potential indications for the former presence of EPS secreted by microbes, that is not a unique explanation; wispy laminae may also be produced by the polymerization of 'oily' layers that form around oil slicks, cold seeps or even from pre-biotic processes (see Folsome 1977). One way forward perhaps will be to determine whether the composition of the organic material in roll-ups included carbohydrates or other polymers consistent with EPS.

Diffuse carbonaceous matter known as 'fluffs' (table 1) can occur in discrete layers (figure 3*d*) or as grains within laminar to rippled Archaean sediments (figure 3*e*). Fluffs might be compared with flocculent grains known as 'marine snow' that form from the action of bacterial (heterotrophic) decomposition when planktonic matter settles down through the water column, to settle loosely on the seafloor. In the Archaean, such fluffy grains can behave as sediment grains when entrained within deep-water traction currents (see Lowe 1999). Such fluffy grains are also abundant, however, in subsurface dyke cherts, where they form layers of bush-like shrubs within hydrothermal cavern systems (Brasier *et al.* 2005). These bushes arise from dendritic, soot-like growths, meaning that self-organization cannot yet be disproved for their origin.

6. LIFELINES
How can we hope to distinguish the morphology of complex but unquestionably abiogenic structures, of the kinds outlined above, from putatively biological structures? Although the situation is difficult there are some 'lifelines', namely emerging techniques and approaches that hold potential for verifying the earliest fossil record on Earth and beyond.

The first of these lifelines involves the exploration of potential morphospace; i.e. size-and shape independent mapping of morphology both within microfossils and in the relationship between them. For example, in well-preserved microfossil assemblages, morphological variation within natural populations is usually less than that of comparable abiological structures and they will therefore occupy a more restricted domain within figure 2. There is tentative evidence to support such a view, given that the standard deviation of 'filament' widths (table 2) is larger for the abiogenic Apex Chert structures when compared with the biogenic Gunflint Chert assemblage (Barghoorn & Tyler 1965). The degree of biological patterning or 'information content' of such assemblages can also be approximated using compression algorithms (e.g. Corsetti & Storrie-Lombardie 2003). Initial studies applying this technique to stromatoloids have suggested that biogenic stromatolites are more compressible relative to the surrounding rock matrix than are abiogenic stromatoloids (Corsetti & Storrie-Lombardie 2003), but questions of standardization and calibration hamper this technique. The compressibility of assuredly biogenic (Gunflint Chert, Boorthanna Dolomite, table 2) material was compared with that of the assuredly abiogenic (Gwna Group) and disputably biogenic material (Apex Chert) by applying similar tests to images taken at the same magnification (see table 2). We find least compressibility in the Apex Chert and highest compressibility in the Gunflint Chert. Abiogenic spherulites of the Gwna Group (figure 3*j*) and the Strelley Pool microtubes occupy intermediate values. This test may therefore prove to be a valuable tool given careful calibration, although in our investigations it failed to recognize fossilized coccoidal colonies (table 2, Boorthanna Chert) as biogenic. Additional information may also come from mapping the areal distribution of putative microfossil filaments. 'Clusters' of filaments (see table 1) that overlap and intertwine are common for microbial communities (e.g. Gunflint Chert) but seem to be rare or lacking in comparable abiogenic assemblages (e.g. Apex Chert).

A second 'lifeline' involves geological and petrographic mapping and the investigation of whether morphological transitions correlate with environmental gradients at a range of scales. For example, if the morphology of the stromatolites is controlled by biologically relevant factors such as water depth and nutrient levels, then a biogenic origin seems at least plausible. If on the other hand, the candidate fossil structures form part of a morphological continuum that is independent of such biological factors and/or controlled entirely by abiogenic parameters such as crystal size or energy levels, then their biogenic origin remains unproven. (The Apex Chert microfossils explained below are an excellent illustrative example of the latter.)

A third lifeline concerns the preservation of 'zones' of microbial processing (table 1) and or evidence for microbial tiering within ecosystems (figure 4). By this we mean geochemical or morphological evidence for microbial stratification within the putative fossil remains; or evidence for microbial processing by heterotrophs; or perhaps evidence for biologically induced precipitation in and around EPS. In the Proterozoic, for example, S and C isotopes and also REE patterns within stromatolitic and non-stromatolitic sediment from the Belingwe Greenstone Belt,

Zimbabwe, have been used to argue for the presence of diverse microbial ecologies that included anoxygenic photosynthesis, methanogenesis and methanotrophy by bacterial and archaeal consortia (e.g. Grassineau *et al.* 2001). Comparable geochemical data is yet to be reported from *ca* 3.5 Gyr old rocks. New, high resolution secondary ion mass spectrometer capable of working on the nanometre scale (nanoSIMS) and FIB-TEM (focused ion beam transmission electron microscopy) techniques now offer the opportunity to map such elemental and isotopic patterns at fine scales and low concentrations not previously measurable and may thereby illuminate ancient cellular processes. For example, a concentration of biologically significant metals such as Cu and Pb in and around putative fossilized mat fragments from the Archaean could bolster current petrographic arguments (cf. Westall *et al.* 2000). Such techniques should also help to further elucidate any metabolic pathways.

7. THE APEX 'MICROFOSSIL' DEBATE

The world famous Apex microfossils have been described in a series of papers (Schopf & Packer 1987; Schopf 1992*a*,*b*, 1993, 1994; Schopf *et al.* 2002). Hitherto, these objects have held their key position in Archaean palaeobiology because of a supposedly excellent state of preservation and their wide acceptance by the scientific community (e.g. Buick 1990; Knoll & Walter 1996; McClendon 1999; Schopf 1999). This contrasts with preliminary reports of other presumed microfossils from the Warrawoona Group, dismissed as either unreliable or unreproducible (Buick *et al.* 1981; Buick 1984; Schopf & Packer 1987, 1988, 1990; Schopf 1993). Eleven putative species of microfossils from the Apex Chert have, hitherto, provided the oldest accepted morphological evidence for life on Earth. These structures are nearly a billion years older than putative cyanobacterial biomarkers (Summons *et al.* 1999), genomic arguments for dating the appearance of cyanobacteria (Hedges *et al.* 2001) and an oxygenic atmosphere (Catling *et al.* 2001), and are more than 1500 Myr older than any comparable suite of microfossils so far described (Knoll 2003). If accepted, this must imply that high levels of biological diversity were achieved at a very early stage in Earth history (Schopf 1993), remarkably soon after the end of massive meteoritic bombardment of the inner solar system at *ca* 3.8–3.9 Ga (cf. Kamber *et al.* 2002), with little evidence for further diversification in the fossil record until the emergence of widespread eukaryotes nearly two billion years later (Knoll 1994, 2003). While acknowledging the similarities to other more primitive bacteria, the size range of the supposed cells (less than 20 μm in diameter) has been taken to suggest that oxygen-releasing cyanobacteria may have been present at least 3.45 Ga (Schopf 1992*a*,*b*, 1993, 1994, 1999), implying an early start for the contribution of photosynthetic oxygen to the atmosphere.

The security of these reports is now open to question. This is in part because major aspects of the preservation and context of this potentially important evolutionary benchmark have received little independent or detailed study and in part because new techniques of analysis are now available. Brasier *et al.* (2002, 2005) have taken a fresh look at Earth's oldest microfossils, following an integrated and collaborative programme of research involving field mapping, multiple sampling, petrography, optical and electron microscopy coupled to computer-controlled digital image analysis plus surface analytical and geochemical techniques. Petrographic slices of all microfossil-bearing type material deposited at the Natural History Museum (NHM) in London (Schopf 1993) have been compared with new slices and thin sections of material recently re-collected from the same horizon (deposited at the NHM and the Geological Survey of Western Australia, GSWA). Fabrics and mineralogy in both the original and the recollected samples are similar and both contain comparable microfossil-like structures.

The mode of origin for the Apex microfossils is more fully discussed by Brasier *et al.* (2005). The context is now seen to be a chert breccia that lay some 100 m down a hydrothermal dyke system and well below the palaeosurface (i.e. not from a surface, stratiform unit). The microfossil-like structures often occur in recrystallized, late stage hydrothermal fabrics and are not confined to a single class of clasts. Stromatolite-like clasts are reinterpreted as hydrothermal cavity fillings. The microfossils are chaotic and incoherent, not simple and unbranched. They occur randomly and do not occur in mat-like clusters. We can find no correlation between 'cell shape', filament diameter and taxon-specific terminal cell morphology. Instead, we find that filament shape, septa and subdivisions can be parsimoniously explained as SOS resulting from silica recrystallization from glass to spherulitic chalcedony that caused displacement of amorphous carbonaceous matter towards spherulitic margins. This creates a morphological spectrum of arcuate to dendritic microstructures that include microfossil-like artefacts (figure 3 *g–i,k* and *l*). Our findings have therefore led us to reject the biological nature of these putative fossils and to accept the null hypothesis of their abiogenic origin.

8. ENDOLITHS AND THE WARRAWOONA 'MICROTUBES'

As a second example, we here report remarkably preserved endolithic microtubes from within *ca* 3.4 Gyr old sandstone grains of the SPC and from stratiform chert of the 3.46 Gyr Apex Chert. While we find such microtubes in both the Apex Chert and SPC units, we here concentrate on the latter, whose occurrence in sandstones enables both their mode of formation and diagenetic histories to be more readily interpreted.

Endoliths are micron scale cavities created in rocks and biological substrates by the corrosive activities of microorganisms that include archaea and cyanobacteria (e.g. Bromley 2004). They can preserve evidence for cellular morphology, microbial behaviour, ecology and metabolism in their selection and modification of rock substrates. Endolithic microborings are well known from silicified carbonate sediments younger than *ca* 1650 Myr (e.g. Zhang & Golubic 1987) and have been reported from the glassy margins of pillow basalts in modern settings (Fisk *et al.* 1998; Banerjee
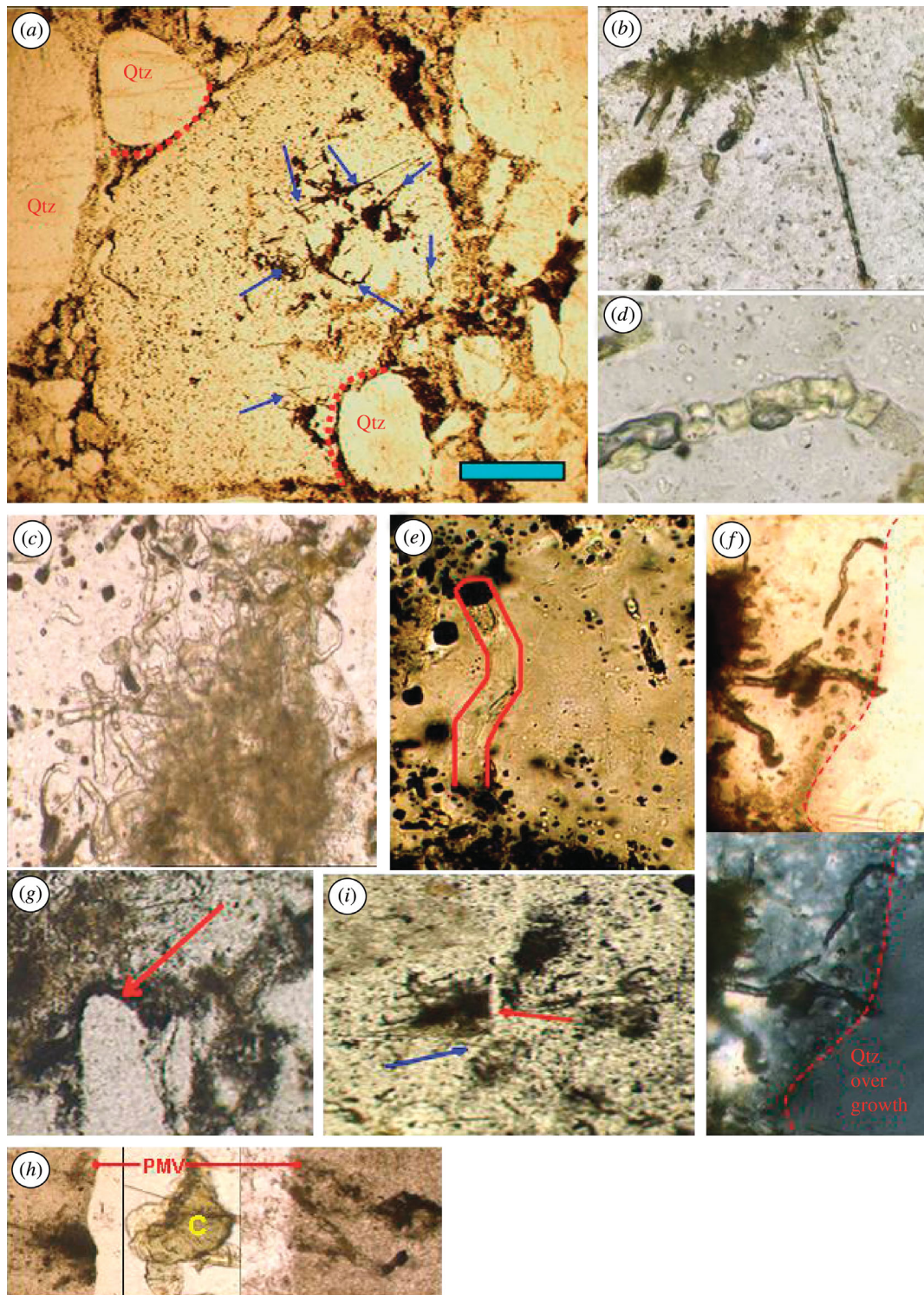
Figure 5. Microtube morphology and context in the Strelley Pool arenite. (*a*) Microtubes demonstrating grain selectivity. The microtubes (blue arrows) are predominantly found in inclusion-rich crypto-crystalline silica grains/clasts, such as the one shown here in the centre of the image and are truncated at the grain margins. Note the impaction fronts (dotted red lines) caused by adjacent rounded quartz (Qtz) grains producing pressure solution fronts. (*b*) Type A microtubes exhibiting parallel clustering plus radiation away from a clotted mass of phosphate and sericite in a 'starburst' pattern. (*c*) Tangled mass of Type B microtubes associated with clotted mass of phosphate. (*d*) Type B microtube partially infilled with cubic crystals of jarosite creating a pseudo-septate appearance. (*e*) Rare example of a Type B microtube with a euhedral pyrite crystal at the upper termination of the hollow tube (outlined in red). (*f*) Dark, phosphate filled Type B microtubes in microcrystalline silica seemingly terminating at compaction- or pressure solution-induced epitaxial quartz overgrowth (top, plane polarized light; bottom, cross polarized light); the junction is shown by a dotted red line. (*g*) Quartz grain (arrowed) impacting and intruding a larger microcrystalline silica clast causing compression and dissolution of a clot of microtubes above. (*h*) Cluster of Type B microtubes (left and right) from Apex Chert, seemingly cross cut and truncated by pre-metamorphic vein of clear megaquartz (PMV) containing a green grain of synmetamorphic chlorite 'c'; vein width has been compressed for ease of illustration. (*i*) Late stage fracture (red arrow) penetrating from the top of the picture to the blue arrow, here cross cutting a mass of Type A and Type B microtubes. Scale bar: 250 μm for *a*: 100 μm for *b*, *g*, *i*: 60 μm for *c*: 25 μm for *d*, *e*: 40 μm for *f*, *h*.

et al. 2004). Putative microbial endoliths have recently been described from the margins of subaqueous basic pillow lavas in the *ca* 3.5 Gyr Hoogenoeg and Kromberg Formations of the Barberton (Furnes *et al.* 2004). The challenge here is that the same kinds of morphological structure can be produced by ambient inclusion trails (AITs), especially those of pyrite (Tyler & Barghoorn 1963; Knoll & Barghoorn 1974), and an abiogenic origin needs to be falsified (Brasier *et al.* 2004). Such AITs are considered to form when pyrite (or other inclusions) are impelled to migrate through silica under raised fluid/gas pressures, possibly generated by biological decay.

The SPC microtubes occur in a silicified sandstone unit (approx. 85% quartz, 15% lithic grains) at the base of the succession, in the Pilbara region, Western Australia. The SPC is not dated directly; it outcrops conformably below the 3.35–3.325 Gyr Eurobasalt Formation (Smithies *et al.* 2005) and is separated by a regional unconformity from the underlying 3.45 Gyr Panorama Formation (Van Kranendonk *et al.* 2004). Hence we can assign an age of *ca* 3.4 Gyr for the SPC. In addition this basal sandstone contains two populations of detrital zircons dated at 3.502 Gyr ± 3 Myr ($n=33$) and 3.479 Gyr ± 8 Myr ($n=5$) (Nelson, personal communication) and at the sample site lies unconformably on basaltic volcanics and cherts of the *ca* 3.515 Gyr Coucal Formation of the Coonterunnah Group (Buick *et al.* 1995; Van Kranendonk 2000). The unit is 1–5 m thick here, resting on an unconformity surface that records the earliest preserved episode of subaerial exposure and deep chemical weathering *ca* 3.45 Ga in the rock record (Buick *et al.* 1995). The occurrence of low angle cross-bedding and channel bedforms, plus the relatively high textural and compositional maturity of the sandstone, indicates deposition during a relatively high energy, shallow marine transgression (Lowe 1983). Subsequently, the unit has experienced only low-grade metamorphism between *ca* 200–400 °C (prehnite-pumpellyite to lower greenschist facies; Van Kranendonk 2000) allowing good preservation.

The spatial distribution of the microtubes within the SPC is strongly controlled by clast composition. The majority occur within rounded clasts of well-preserved crypto-crystalline silica (less than 5 μm crystal diameter) that typically contain small cubes of pyrite (FeS_2) and needles of arsenopyrite (FeAsS) in their matrix (figure 5a). These sulphide crystals tend to be best preserved within clast cores and may be pseudomorphed by iron (III) sulphate (i.e. jarosite group, $KFe_3(SO_4)_2(OH)_6$) towards the clast margins. The pyrite crystals show wide variations in diameter, consistent with Ostwald ripening and unlike the more uniform, framboidal products of bacterial sulphate-reduction (cf. Kobluk & Risk 1977; Kawano & Tomita 2001). Most microtubes are also associated with fans of sericite and patches of fibrous iron (II) phosphate and aluminium phosphate around the clast margins, along resealed microzfractures and within the matrix. Fabric mapping and hot cathodoluminescence indicates up to four distinct phases of silicification in the arenite, including re-sealed fractures.

The morphology of our Australian microtubes ranges between two end-members. Type A is linear and narrow (1–10 μm width, modal width 5 μm; and up to 200 μm long) with near constant diameter and pointed to blunt terminations (figure 5b). These are often partially infilled by fibrous phosphate and now lack any pyrite or arsenopyrite crystals. Arrays of type A tubes commonly occur in parallel or radiating clusters directed away from clots of phosphate and sericite along clast margins and early fractures (figure 5b). More rarely type A tubes also occur at or near clast margins orientated almost perpendicular to the clast margins. They are seldom seen within the matrix or the megaquartz. Type B microtubes are more abundant and more varied in shape and size (2–15 μm width, modal width 9 μm; and up to 100 μm long). They can be straight, curved or twisted, occurring singularly or as tangled associations (figure 5c). Dense clusters of type B microtubes occur around the margins of the felsic 'glass' clasts and commonly pass into small masses of phosphate and sericite. Type B tubes may be hollow or partially infilled with fibrous phosphate or partially infilled with later, equant crystals of jarosite that confer a pseudo-septate appearance (figure 5d).

A subpopulation of type B tubes invites comparison with microtubes known as AITs (figure 5e). These have been thought to form when metallic inclusions are propelled in some way through glassy silica or an organic mush (cf. Tyler & Barghoorn 1963; Knoll & Barghoorn 1974; Xiao & Knoll 1999) leaving behind a hollow tubular trail, which may remain empty or be infilled by a secondary mineral phase. They can be recognized by: (i) presence of a mineral grain (e.g. a metal sulphide or oxide) at the end of a microtube of constant diameter, which may be pseudomorphed by later minerals (e.g. silica, metallic oxide or phosphate); (ii) longitudinal striations created by facets of the propelled mineral grain, which may also be obscured by later mineral infill; (iii) curved or twisted paths, particularly towards their ends, probably due to the increasing impedance of the host grain; and (iv) tendency of microtubes to crosscut or branch (i.e. where the impacting mineral becomes fragmented or a second grain is intercepted) and to make sharp turns. Hitherto, AITs have been explained by high gas/fluid pressures during metamorphic degradation of ubiquitously associated organic matter (Knoll & Barghoorn 1974; Xiao & Knoll 1999).

Detailed micro-mapping can reveal the timing and growth history of microtubes. A pre- to syn-depositional age may be indicated by: (i) truncation of microtubes at the margins of microcrystalline silica clasts (e.g. figure 5a); (ii) truncation of microtubes by compaction induced pressure solution fronts and quartz overgrowths (figure 5f,g); and (iii) truncation of microtubes by veins containing metamorphic mineral growth (figure 5h). Post-Archaean alteration or contamination is inferred for some of the microtubes, however, because of their hydrous (jarosite) mineralogy.

This new microtube assemblage shares features with those recently reported from pillow basalts from the Barberton Greenstone Belt of South Africa (Furnes *et al.* 2004). They are of similar size and shape, predate growth of chlorite and are etched into volcanic

protoliths. Our microtubes differ, however, in the following respects: (i) preservation in microcrystalline chert (rather than in metamorphic chlorite); (ii) a shallow marine sedimentary context (rather than deeper marine volcanic); (iii) a succession of early (pre- and syn-) to clearly post-depositional and modern microtube phases; (iv) show preferential selection for lithic grains; (v) demonstrate geochemical tiering (rather than uniform titanite); and (vi) infilled with biolimiting nutrients of phosphate and sulphate (rather than metamorphic or hydrothermal titanite).

Our ongoing research involving detailed fabric mapping combined with state of the art imaging and geochemical analysis continues to follow the rigorous criteria for biogenicity set out in Brasier *et al*. (2004). Once the pre- to post-depositional and abiogenic mechanisms have been carefully decoded, endolithic microtubes may yet provide a promising new avenue for research into early life.

9. CONCLUSIONS

Early geologists like James Hutton (1790) famously reported finding 'no vestige of a beginning'. In recent years, however, we have begun to obtain a much better understanding of the early Earth, with its remarkably widespread distribution of carbonaceous material (figure 1). Controversies currently rage over these earliest claims for cellular life. These controversies are helping the new science of astrobiology to develop criteria for testing new and existing claims for Archaean life (table 1). Such debates also provide the essential testing ground for future debates in the scientific community about the evidence for life elsewhere in the solar system, especially if the planned sample return missions from Mars are indeed successful.

We here propose that an appreciation of self-organizing structures (SOSs, figure 2) provides the essential unifying framework within which to study these early morphological remains. We also point to lifelines that may help to further elucidate the origins of cellular life on Earth: analysis of morphospace, geochemical evidence for ecological tiering and the correlation between environmental and morphological gradients.

From the perspective of geologists working on some of the world's oldest rocks we draw the following conclusions relating to the appearance and evolution of cellular life.

(i) The predominance of volcanic and hydrothermal rocks between greater than 3.5 and 3.0 Gyr supports the hypothesis that hyperthermophiles were amongst the earliest life forms (e.g. Stetter 1996; Rasmussen 2000).

(ii) Reliable fossil evidence for cyanobacteria and other oxygenic photoautotrophs is currently lacking between greater than 3.5 and 3.0 Ga, but these had probably emerged by 2.6 Ga. Anaerobes probably dominated the early biosphere and any mats formed in the photic zone are likely to have utilized anaerobic photoautotrophy (Tice & Lowe 2004; Westall 2005) or chemosynthetic metabolisms.

(iii) Rock dwelling, endolithic and perhaps deep intra-terrestrial microbes may yet prove to have been a significant component of the early biosphere at about 3.5 Ga.

(iv) Evidence for the presence of planktonic microbes at 3.5 Ga is scant as yet, but anoxygenic photoautotrophs and perhaps heterotrophs cannot be excluded.

In summary, we may perceive a 'vestige of a beginning', with endolithic, anaerobic and perhaps hyperthermophilic life at *ca* 3.5 Ga, but there is 'no prospect of an end', as yet, in terms of improving our understanding of the nature and evolution of the early biosphere.

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