Chapter 3
Microbes and the Fossil Record: Selected Topics in Paleomicrobiology

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Abstract The study of microbial fossils involves a broad array of disciplines and covers a vast diversity of topics, of which we review a select few, summarizing the state of the art. Microbes are found as body fossils preserved in different modes and have also produced recognizable structures in the rock record (microbialites, microborings). Study of the microbial fossil record and controversies arising from it have provided the impetus for the assembly and refining of powerful sets of criteria for recognition of bona fide microbial fossils. Different types of fossil evidence concur in demonstrating that microbial life was present in the Archean, close to 3.5 billion years ago. Early eukaryotes also fall within the microbial realm and criteria developed for their recognition date the oldest unequivocal evidence close to 2.0 billion years ago (Paleoproterozoic), but Archean microfossils >3 billion years old are strong contenders for earliest eukaryotes. In another dimension of their contribution to the fossil record, microbes play ubiquitous roles in fossil preservation, from facilitating authigenic mineralization to replicating soft tissue with extracellular polymeric substances, forming biofilms that inhibit decay of biological material, or stabilizing sediment interfaces. Finally, studies of the microbial fossil record are relevant to profound, perennial questions that have puzzled humanity and science—they provide the only direct window onto the beginnings and early evolution of life; and the methods and criteria developed for recognizing ancient, inconspicuous traces of life have yielded an approach directly applicable to the search for traces of life on other worlds.

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3.1 Microbial Fossils: A Vast Field of Study

Knowledge of the microbial fossil record has expanded tremendously in more than 50 years since early discoveries (e.g., Tyler and Barghoorn 1954; Barghoorn and Tyler 1965), both in depth—geologic time—and breadth—types of organisms, modes of preservation, and types of fossil evidence. Along with the new discoveries of fossil microbes and microbially induced structures, and keeping pace with technological advances in analytical tools, the paleontological community developed and expanded the set of methods used to study these fossils and refined the types of questions addressed, as well as the criteria applied to them. At the same time, the community of scientists itself broadened its scope and expanded its ranks to include paleobiology, geobiology, geochemistry, taphonomy, and other areas of research in its sphere of investigation. As a result of this explosive growth, paleomicrobiology is today just as vast an area of science as its "neo" counterpart and could itself be the subject of a multivolume book. That is why for this chapter, we had to select only some of the topics of major interest in paleomicrobiology which we review to summarize the current state of the art.

One of the topics is the recognition of microbial fossils and the criteria used for it (Sect. 3.3). These provide the foundation of all work involving microbial body fossils and are especially relevant to the search for the earliest traces of life. The development of these criteria over time, by discovery and critical scrutiny of increasingly older Precambrian microbial fossils, provides a telling example of the workings of science, in general, and paleobiology, in particular, as an objective empirical approach to questions about nature. As a logical follow-up on the criteria for recognition of microbial body fossils, we discuss microbially induced sedimentary structures and other traces of microbial activity (microbially induced structures), their classification, and criteria of recognition. These provide a powerful complement to the study of the microbial fossil record, even in the absence of body fossils, and are active and growing fields of inquiry. This section is prefaced by a review of microbial fossil preservation (Sect. 3.2), which provides a broader context for the different aspects comprising the recognition of the fossils. The next topic involves the earliest records of life and a review of the Archean fossil record (Sect. 3.4). Aside from pushing back in deep time the history of life on Earth, these fossil discoveries and the controversies they engendered were crucial in shaping both the methods and the theoretical bases for the study of microbial fossils. As a part of this topic, we summarize a few of the now-classic debates which animated (or are still animating) the scientific community and provided much of the impetus for the development of a powerful set of criteria for microbial fossil recognition. Another topic covers the rise of early eukaryotes as reflected by the microbial fossil record, with a discussion of the criteria used to recognize them and a survey of the earliest types (Sect. 3.5). Next, we review the role of microbially mediated processes in the various fossilization pathways of other organisms—microbial-associated mineralization, plant, animal, and trace fossil preservation (Sect. 3.6)—and the fossil record of symbioses that involve microbial participants

(Sect. 3.7). The chapter ends with a discussion of future directions of investigation in the study of microbial fossils and of the role of paleomicrobiology in the study of life.

Throughout the chapter, we focus mainly on the record of body fossils, with some detours into geochemistry and sedimentology for discussions of biogenicity, microbially induced structures, and fossilization processes. The survey of the prokaryote and eukaryotic fossil record is limited to early occurrences—Archean for the former (4.0–2.5 Ga = billion years) and Paleoproterozoic and Mesoproterozoic (2.5–1.0 Ga) for the latter. However, the discussions of the roles of microbes in fossilization and of the fossil record of symbioses draw on examples from throughout the geologic time scale.

3.2 Microbial Fossil Preservation

Traces of microbial life occur as (1) body fossils, which can be preserved in several modes, (2) structures (micro- and macroscopic) generated by microbial presence and activities, and (3) chemical compounds present in the rock record as a result of microbial metabolism (chemical biosignatures) (Fig. 3.1). This chapter deals mostly with body fossils and, to a somewhat lesser extent, with microbially induced structures. While chemical biosignatures can offer very useful insights into early life on Earth and investigations of biogenicity of candidate microfossils (Brasier and Wacey 2012), in this chapter, the impressive body of work produced by geochemists [e.g., Knoll et al. (2012) and references therein] is touched upon only lightly.

3.2.1 Body Fossils

The modes of preservation of microbial body fossils parallel those described for plant fossils (e.g. Schopf 1975; Stewart and Rothwell 1993) and include *permineralization* (also known as petrifaction), *coalified compression*, *authigenic* or *duripartic preservation*, and *cellular replacement* with minerals. In permineralization, minerals (usually calcium carbonate, silica, iron sulfide) precipitate from solutions inside and around cells, so the organisms end up incorporated in a mineral matrix and preserved three dimensionally, sometimes in exquisite detail. The quality of cellular preservation depends on the extent of decomposition of the organisms preceding the permineralization phase. Many early prokaryotes are preserved as permineralizations. In filamentous types, such as cyanobacteria, permineralized specimens often preserve mainly the external cellular envelopes (sheaths), whereas cells and their contents are altered to various degrees or not preserved at all (e.g., *Eoschizothrix*; Seong-Joo and Golubic 1998) (Fig. 3.1a, b). This is consistent with the results of chemical, structural (Helm et al. 2000), and

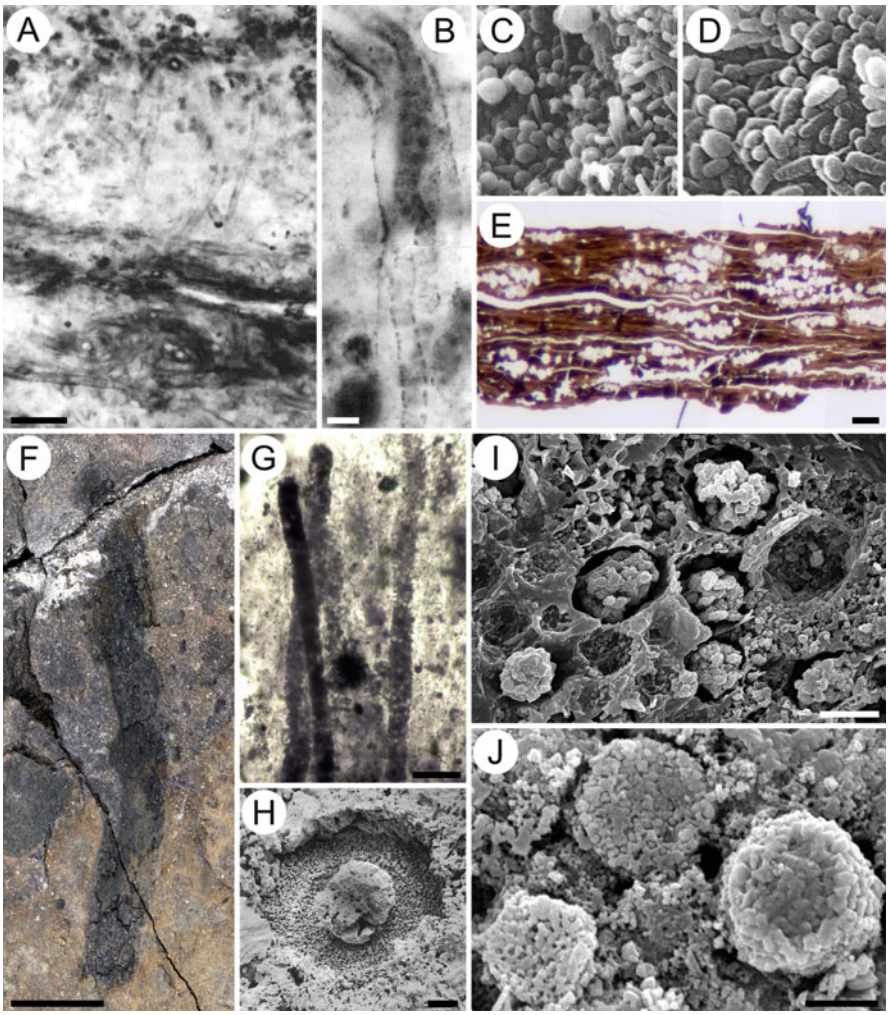

Fig. 3.1 Modes of microbial fossil preservation. (**a**) Permineralization, mats of cyanobacterial filaments (*Eoschizothrix*) preserved in silicified stromatolites of the Mesoproterozoic Gaoyuzhuang Formation, China. (**b**) Permineralization, multiple filaments of *Eoschizothrix* in a common extracellular polysaccharide sheath; Gaoyuzhuang Formation. (**c**) Cellular replacement, phosphatized fossil bacteria preserved in the eye of a fish from Tertiary oil shales in Germany. (**d**) Cellular replacement, calcified fossil bacteria preserved in the eye of a fish from tertiary oil shales in Germany. (**e**) Coalified compression and cellular replacement; cross section through a cyanobacterial colony (*Prattella*) showing brown coalified material representing extracellular polysaccharide sheath material and molds left by dissolution of mineral replaced (pyritized cells), Early Silurian Massanutten Sandstone, Virginia, USA. (**f**) Coalified compression, the coaly material formed by fossilization of *Prattella* extracellular polysaccharide sheath material, Massanutten Sandstone. (**g**) Cellular replacement, fragment of *Prattella* colony where the coalified extracellular polysaccharide matrix was cleared using oxidizing agents to expose filaments consisting of pyrite-replaced cells, Massanutten Sandstone. (**h**) Authigenic preservation, cross section of a possible cyanobacterial filament preserved in carbonate deposits, with the extracellular

experimental taphonomic (Bartley 1996) studies, which have stressed the higher resistance to degradation of extracellular polymeric substances (i.e., sheath and slime) in contrast that of the cell contents.

Coalified compressions are formed when the layers of sediment that incorporate the organisms are subjected to lithostatic pressure during rock forming processes (diagenesis). The pressure and temperature associated with burial in the Earth's crust induce changes in the geometry and chemistry of cells along a gradient of coalification of the carbonaceous material. For unicellular microfossils, a high degree of coalification can lead to complete obliteration of diagnostic features, to the point of rendering them unrecognizable as biogenic objects. However, lesser degrees of coalification can preserve diagnostic features even down to the ultrastructure level, as in the case of some early unicellular eukaryotes (Javaux et al. 2001, 2004) (Figs. 3.9e, f, 3.10e, 3.11b), while also increasing the preservation potential of fossils by rendering their organic compounds more chemically inert. Sometimes, microbial colonies can form compressions, as in the case of cyanobacterial colonies whose copious extracellular sheath material is coalified (Tomescu et al. 2006, 2008) (Fig. 3.1e, f).

Authigenic preservation refers to removal of the organic material previously enclosed in rock (by oxidation, decomposition) and its replacement with secondary material (precipitated minerals or sediment) that forms casts, whereas duripartic preservation involves the precipitation of minerals due to metabolic processes of the organisms that are fossilized. Duripartic mineral precipitation can occur in the cell walls, in the extracellular sheaths of colonies, or around the organisms, forming molds that can preserve cell-level structural details. Various minerals are known to form on microbial cell surfaces as a consequence of interactions between the microbial metabolism and the chemistry of its environment (reviewed by Southam and Donald 1999). Many fossil cyanobacteria are preserved as calcium carbonate (micrite) rinds that coated the organisms (e.g., *Girvanella*; Golubic and Knoll 1993) (Fig. 3.1h), which corresponds to a combination of authigenic and duripartic preservation. Cellular replacement is a cell-to-cell process in which diagenetic minerals precipitate inside individual cells, replacing their content. Different by its discrete nature from both authigenic and duripartic preservation which involve wholesale processes, cellular replacement is nevertheless more akin to authigenic preservation. Pyrite is widespread in cellular replacement (e.g., Munnecke et al. 2001; Kremer and Kazmierczak 2005) (Fig. 3.1i, j), but the list of minerals

Fig. 3.1 (continued) sheath preserved as micrite and the filament lumen filled with sparry calcite. (**i**) *Prattella* SEM of framboidal pyrite aggregates replacing individual cyanobacterial cells of *Prattella* and occupying molds in the coalified extracellular polysaccharide matrix, Massanutten Sandstone. (**j**) Cellular replacement, coccoid cells of a cyanobacterial mat replaced by framboidal pyrite aggregates, Silurian, Poland. Scale bars: (**a**) 50 μm, (**b**) 10 μm, (**c**) the bacterial cells are 0.5–1.5 μm, (**d**) the bacterial cells are 0.5–1 μm, (**e**) 20 μm, (**f**) 1 cm, (**g**) 50 μm, (**h**) 10 μm, (**i**) 5 μm, (**j**) 5 μm. Credits—images used with permission from (**a**) John Wiley & Sons (Seong-Joo and Golubic 1998). (**c**), (**d**) Blackwell Science Ltd. (Liebig 2001). (**h**) Blackwell Science Ltd. (Golubic and Knoll 1993). (**j**) Society for Sedimentary Geology (Kremer and Kazmierczak 2005)

is broad and includes apatite, calcite, siderite, hematite, and silica (Liebig 2001; Noffke et al. 2013b) (Fig. 3.1c, d).

In some instances, modes of preservation are combined, as in the case of the cyanobacterium *Prattella* (Tomescu et al. 2006, 2009) in which the macroscopic colonies of multitrichomous filaments are enveloped in high amounts of extracellular slime which forms coalified compressions, but within these compressions individual cyanobacterial cells are preserved by cellular replacement with framboidal pyrite aggregates (Fig. 3.1e, f, g, i).

3.2.2 Microbially Induced Structures

Microbially induced structures are structures produced by interactions between microbes and the sediment or rock. The different types of microbially induced structures encompass a wide spectrum of morphologies and range in size from the submillimeter scale up several orders of magnitude; some can form associations and layers with sizes ranging up to the kilometer scale. Microbially induced structures are known in large numbers from Proterozoic and Phanerozoic rocks, but their Archean record is less extensive (Awramik and Grey 2005; Noffke et al. 2003, 2006, 2013a). Two broad categories of microbially induced structures can be distinguished: *microbialites* and *microborings*.

3.2.2.1 Microbialites

Microbialites (Burne and Moore 1987) are constructional organosedimentary structures formed as a result of interactions between microbial mats and sediment. Depending on whether their formation involves the precipitation of minerals or not, microbialites are further divided into *stromatolites* (Kalkowsky 1908) and *microbially induced sedimentary structures* (MISS), respectively (Noffke and Awramik 2013).

Microbially Induced Sedimentary Structures

Because they do not involve mineral precipitation, MISS do not form thick or tall buildups like the stromatolites; instead, they have a more flattened, two-dimensional form. Microbial mats form at the interface between their substrate (usually the sediment surface) and water or air, and MISS formed as a result of interactions between the microbial mat and sediment (stabilizing, trapping) mark the transient location of such surfaces. Modern analogues of MISS found in tidal siliciclastic and terrestrial environments, which host a wide range of types with different morphologies (Noffke et al. 1996; Beraldi-Campesi and Garcia-Pichel

2011), allow us to understand the processes that lead to the formation of MISS encountered in the fossil record (Schieber et al. 2007).

The types of interactions between mats and sediment that lead to both MISS and stromatolite formation are binding and biostabilization, baffling and trapping, and growth (Noffke and Awramik 2013). Binding of microbial populations by cooperative secretion of extracellular polymeric substances leads to formation of a microbial mat. Once established, the mat alters the structure and physical properties of the sediment, stabilizing it (biostabilization) and, thus, reducing the effects of erosion (e.g., Fang et al. 2014). Sudden changes of fluid dynamic patterns at the interface between the sediment and water (or air) that increase the risk of bacterial mat erosion trigger increased or renewed biostabilizing activity in the microbial mat. Baffling and trapping occur when microbial mats baffle the water current around them, causing suspended particles to sediment and become trapped in the mat. Growth is the lateral and vertical expansion of the microbial mat by production of more extracellular polymeric substances or more cells, and sediment may become trapped within the mat while growth and associated binding are taking place.

MISS are ultimately formed when the surfaces hosting microbial mats are buried in sediment and lithified; then, the finer-grained layer trapped and bound by the microbial mat serves to separate two sedimentary beds and assist the preservation of any surface structure (Noffke 2009; Noffke and Awramik 2013). Thus, in the sedimentary record, MISS are recovered as structures on bedding planes, associated with recognizable microscale sedimentary patterns immediately beneath the bedding plane (laminae of organic matter concentration, grain size sorting, heavy mineral concentrations, etc., microtextures—Noffke 2009) (Figs. 3.2a–c, 3.3a, 3.11f). The wide morphological variety of MISS is the result of different sedimentary environments, substrates (sediment), types of interaction, and taphonomic processes. Because these interactions and processes have not changed significantly over 3.5 billion years, the morphologies of MISS in the fossil record are directly comparable with microbial mat-induced sedimentary structures documented in modern environments (Noffke et al. 2013b). Although identified as such relatively recently, MISS have received a lot of attention as traces of early life and a considerable body of literature on their genesis, recognition, classification, and geologic record has accumulated (e.g., Noffke 2009, 2010; Noffke and Awramik 2013; Noffke et al. 2013b).

Stromatolites

We use the term stromatolites here to designate any sedimentary structure formed as a result of microbial mats baffling, biostabilizing, and trapping sediment, in association with mineral precipitation. In other words, stromatolites can be regarded as MISS cemented by mineral precipitation. On the centimeter-to-meter scale, these structures exhibit varied morphologies, including wavy laminations, domes, and branched or unbranched columns (Awramik and Grey 2005) (Figs. 3.3b–d, 3.6b, 3.7 h, 3.8f, g), some of which have received specific names—

e.g., dendrolites and thrombolites (Aitken 1967; Kennard and James 1986; Shapiro 2000). However, here we group all these different morphologies under the umbrella term stromatolite as they all share a laminated organization (the precipitated mineral is often calcium carbonate) and origin involving the activity of microbial mats (Shapiro 2000; Awramik and Grey 2005). Reitner et al. (2011) provide a comprehensive review of stromatolite research.

The most widely accepted mechanism for stromatolite formation involves sediments that are trapped and bound within microbial mats by the same basic mechanisms that form MISS and carbonate or some other type of mineral precipitation that cements the layer thus formed (Noffke and Awramik 2013). Over time, the microbial mat grows above the cemented portion forming a new layer which is, in turn, cemented, leading to upward growth of the stromatolite. The repetition of recolonization of the upper stromatolite surface by the microbial mat and subsequent cementation with precipitated minerals produces the characteristic laminated structure of stromatolites. Laboratory studies suggest that the extracellular polymeric substances produced by the microbial mats play an important role in carbonate precipitation (Altermann et al. 2006; Dupraz et al. 2009) and that heterotrophic members of microbial mat communities may initiate mineral precipitation (Noffke and Awramik 2013). If the precipitating minerals permineralize the microbial cells that form the mats, body fossils can be associated with the stromatolites. Although such occurrences tend to be rare (Wacey 2009), they have been documented both in the fossil record (e.g., Schopf and Blacic 1971; Schopf and Sovietov 1976; Knoll and Golubic 1979) and in modern stromatolites (Kremer et al. 2012a).

Structures described from shallow, hypersaline marine environments, such as Shark Bay in Western Australia (e.g., Awramik and Riding 1988), are often presented as good modern analogues for ancient stromatolites (Fig. 3.2f). This is because these structures are formed by microbial mats that trap and bind sediment, producing morphologies similar to those of stromatolites from the geologic record (Awramik and Grey 2005; Awramik 2006). However, most modern structures proposed as stromatolites are primarily formed by binding or trapping of sediments, without significant precipitation, whereas mineral (usually carbonate) precipitation is a prominent feature of ancient stromatolites (Kazmierczak and Kempe 2006; Noffke and Awramik 2013). To date, the only modern stromatolite analogues formed by both microbial mat activity and carbonate precipitation are those described from caldera lakes in Tonga (south Pacific) by Kazmierczak and Kempe (2006) and Kremer et al. (2012a) (Fig. 3.2d, e). Kazmierczak and Kempe (2006) propose that the highly alkaline chemistry of the caldera lakes is similar to the chemistry of Precambrian seas that hosted the wealth of stromatolites documented in the geologic record and that the rarity of this particular type of conditions in modern marine environments should account for the infrequency of modern carbonate-precipitating stromatolites and the presence of only comparable but nonprecipitating structures in modern benthic environments.

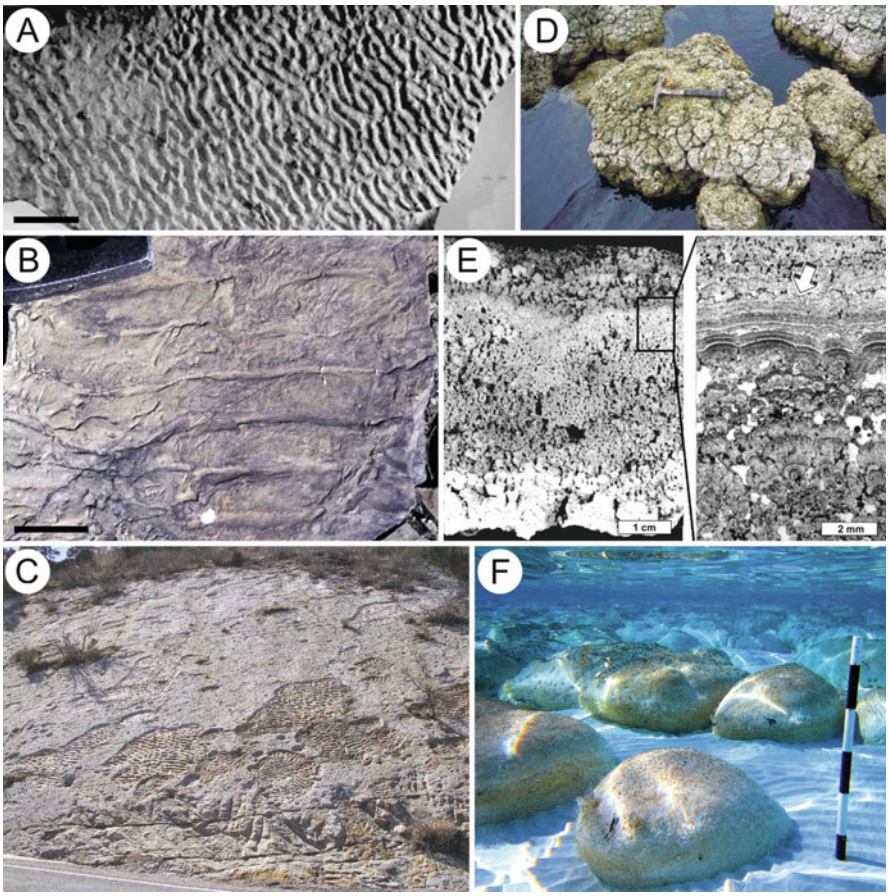

Fig. 3.2 Microbially induced structures. (**a**) Wrinkle structures representing buried microbial mats, Archean Mozaan Group, Pongola Supergroup, South Africa. (**b**) Wrinkle structures representing in situ preserved, thin microbial mats, Neoproterozoic Nama Group, Namibia. (**c**) Landscape-scale preservation of MISS on a hill side; tidal flat morphology resulting from partial erosion of a mat-stabilized sedimentary surface—the raised flat-topped areas are ancient microbial mats and the ripple marked depressions represent areas where the mats were eroded, Cretaceous Dakota Sandstone, Colorado, USA. (**d**) Stromatolites from caldera lakes on Niuafo'ou Island (Tonga Archipelago, south Pacific), recently recognized as the closest modern analogues of Precambrian Stromatolites. (**e**) Vertical sections through Niuafo'ou Island stromatolites showing the variety of internal structures. (**f**) Stromatolites such as these, from Shark Bay (Western Australia), were recognized early as modern analogues of Precambrian stromatolites. Scale bars: (**a**) 2 cm, (**b**) 5 cm, (**d**) hammer for scale 28 cm, (**f**) measuring pole painted in 10 cm intervals. Credits—images used with permission from (**a**) Geological Society of America (Noffke et al. 2003). (**b**) Elsevier Science Publishers (Noffke 2009). (**c**) Society for Sedimentary Geology (Noffke and Chafetz 2012). (**d**) and (**e**) Springer-Verlag (Kazmierczak and Kempe 2006). (**f**) Geological Society of America (Noffke and Awramik 2013)

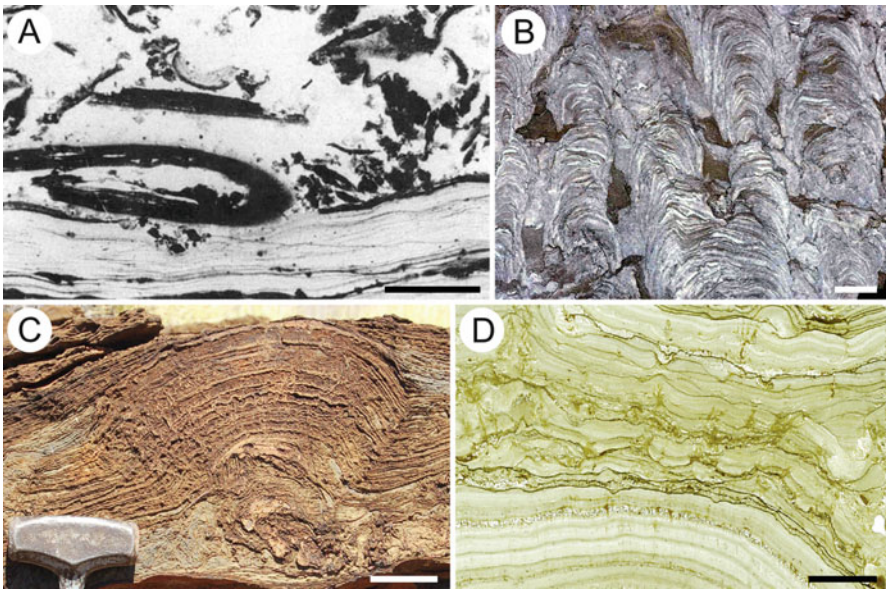

Fig. 3.3 Microbially induced structures. (**a**) Fine carbonaceous laminations with one layer folded over itself and overlain by a deposit of microbial mat-like fragments, Archean Kromberg Formation, Onverwacht Group, South Africa. (**b**) Vertical section through stromatolite deposit, Neoproterozoic Shisanlitai Formation, China. (**c**) Stromatolite in the Archean Tumbiana Formation, Fortescue Group, Western Australia. (**d**) Complex lamination at several scales in a thin section through Tumbiana Formation stromatolite. Scale bars: (**a**) 500 μm, (**b**) 2 cm, (**c**) 5 cm, (**d**) 5 mm. Credits—images used with permission from (**a**) Elsevier Science Publishers (Walsh 1992). (**b**) Geological Society of America (Noffke and Awramik 2013). (**c**) Elsevier Science Publishers (Lepot et al. 2009b). (**d**) Springer Science + Business Media B.V. (Wacey 2009)

3.2.2.2 Microborings

Microborings are microscopic, tubular, usually branched cavities that record the activity of euendolithic microbes. Although the differences are sometimes blurred, only some of the rock-inhabiting (endolithic) microbes, the euendoliths, actively bore into rock, whereas others occupy preexisting fissures and pore spaces of the rock (chasmoendoliths and cryptoendoliths, respectively) (Golubic et al. 1981; McLoughlin et al. 2007). In the rock record, microborings are found in both sedimentary (Campbell 1982; McLoughlin et al. 2007) (Fig. 3.8h) and volcanic rocks (Furnes et al. 2004, 2007; McLoughlin et al. 2012) (Figs. 3.4d–f, 3.7d, g, 3.8i). Living analogues have also been discovered in a wide range of environments, including near-surface sedimentary rocks (Knoll et al. 1986) and volcanic glass (Thorseth et al. 1991; Fisk et al. 1998).

Modern euendoliths employ several metabolic strategies, including photoautotrophy in near-surface environments and chemolithoautotrophy in deeper endolithic environments (McLoughlin et al. 2007). In carbonate rocks, endoliths

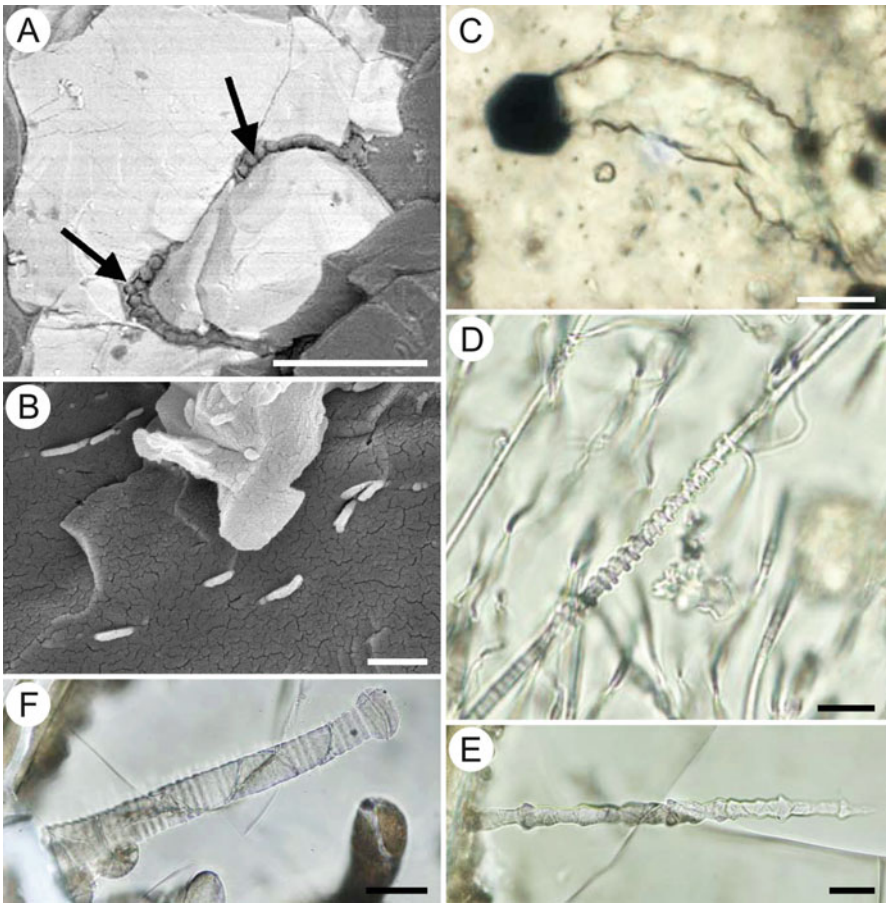

Fig. 3.4 (**a**) Chains of non-syngenetic endolithic fossilized coccoidal cells (*arrows*) penetrating a crack around a magnetite grain in Archean rocks of the Isua Greenstone Belt, Greenland. (**b**) Indigenous and syngenetic heterotrophic bacteria preserved in fossil extracellular polysaccharide sheaths of a cyanobacterial colony (*Prattella*); the bacterial cells are exposed in fresh breaks of the carbonaceous material (as seen here in SEM) which demonstrate that they did not penetrate through fissures at a later time; the bacterial cells also exhibit plastic deformation characteristic of soft, organic bodies (toward *bottom right*), corroborating hypotheses of biogenicity, Early Silurian Massanutten Sandstone, Virginia, USA. (**c**) Ambient inclusion trail with terminal pyrite grain and jagged tube edges, Archean Apex chert, Warrawoona Group, Western Australia. (**d**), (**e**), and (**f**) Microbial bioerosion structures (microborings) in volcanic glass of the Troodos ophiolite (Cretaceous, Cyprus), (**d**) *Tubulohyalichnus spiralis*, (**e**) *Tubulohyalichnus annularis* with unevenly spaced annulations, (**f**) *Tubulohyalichnus annularis* with uniformly spaced annulations and a terminal swelling. Scale bars: (**a**) 50 μm, (**b**) 1 μm, (**c**) 10 μm, (**d**) 10 μm, (**e**) 20 μm, (**f**) 20 μm. Credits—images used with permission from (**a**) Elsevier Science Publishers (Westall and Folk 2003). (**c**) Geological Society of London (Wacey et al. 2008). (**d**), (**e**), and (**f**) Geological Society of London (McLoughlin et al. 2009

have been shown to dissolve the host rock by producing organic acids or bioalkalization (McLoughlin et al. 2007) and exant euendoliths that live within volcanic glass or other siliceous rocks dissolve the host rock using similar pH-altering mechanisms (Callot et al. 1987; Thorseth et al. 1995; Staudigel et al. 1998, 2008; Büdel et al. 2004).

3.3 Recognizing Microbial Fossils

As their biogenicity receives support from both chemical and morphological lines of evidence, microbially induced structures represent more reliable indicators of prehistoric life than exclusively chemical biosignatures. Nevertheless, the most robust line of evidence in documenting the presence of microbial life, especially in the search for the earliest records of it in the Archean, is represented by body fossils (Ueno et al. 2001a). Yet when objects are recognized as candidate microbial fossils in the rock record, their identification as actual fossilized microbes (biogenicity) can be hampered by a series of factors (Buick 1990; Schopf and Walter 1983). The small size of microbes renders them easily degradable during diagenesis and, hence, unrecognizable. A wide variety of non-biogenic objects are known that mimic biogenic morphologies (mineral dendrites, crystallites, spheroids, filaments; Schopf and Walter 1983; Westall 1999; Brasier et al. 2006). Because of their simple morphology, fossil microbes are difficult to tell apart, unequivocally, from abiogenic microbial-looking objects, and we are missing a lot of the data needed to predict what kinds of such abiogenic objects may have been produced by diagenesis in the host rocks (Buick 1990). Furthermore, it has been argued that early microbial life may have looked and lived differently than modern microbes (Buick 1990), but exactly because we are looking for the earliest forms of life, we have no reference base, so we don't know what types of fossil to expect (Schopf and Walter 1983); for example, Archean microbes may not be directly comparable to modern counterparts whose morphologies and metabolisms may have been shaped by adaptation to living in a world filled with complex eukaryotes which were absent in the Archean (Brasier and Wacey 2012). Because of all these reasons, the literature on microfossils includes various terms conveying different degrees of certainty about the biogenicity (or absence thereof) of fossil-like objects: dubiofossils (fossil-like objects of uncertain origin; Hofmann 1972), pseudofossils (fossil-like objects undoubtedly produced by abiogenic processes; Hofmann 1972), bacteriomorphs (abiotic structures morphologically similar to bacteria; Westall 1999), biomorphs (abiogenic structures that mimic biological structures; Lepot et al. 2009a).

3.3.1 Recognizing Microbial Body Fossils

The need to recognize bona fide microbial fossils and distinguish them from abiogenic fossil-like objects on empirical bases was fueled by discoveries of putative microbial fossils in Precambrian rocks. Questions on the biogenicity of such fossils coming from progressively older rocks have been approached from two epistemologically opposite directions. One of these relies on inductive lines of reasoning focusing on demonstration of biogenicity by application of a set of criteria, whereas the other emphasizes falsification of non-biogenicity in a suite of contexts that range from geologic to metabolic. The former approach (*traditional approach* hereafter) was perfected in time by trial and error, whereas the latter (*contextual approach* hereafter) is a more recent development that stems from work on some of the oldest putative traces of life for which the simple application of the traditional set of criteria does not produce sufficient resolution and unequivocal conclusions (Brasier et al. 2006; Brasier and Wacey 2012). However, in theory, if they are applied rigorously and given enough relevant data, the two approaches to demonstrating biogenicity should ultimately lead to similar conclusions.

3.3.1.1 The Traditional Approach

The now-classic set of criteria for biogenicity used in the traditional approach was distilled over many years (e.g., Cloud 1973; Cloud and Hagen 1965; Knoll and Barghoorn 1977; Cloud and Morrison 1979; Schopf and Walter 1983; Buick 1990; Walsh 1992; Golubic and Knoll 1993; Horodyski and Knauth 1994; Morris et al. 1999; Schopf 1999; Southam and Donald 1999; Westall 1999; Schopf et al. 2010) and broadened based on the accumulation of knowledge brought about by successive discoveries of putative fossil microbiota. Each new discovery presented scientists with its own type of putative fossils, set of geologic conditions leading to fossilization (taphonomy), and modes of preservation. Each claim for the oldest record of fossils in a given category at a given moment was thoroughly scrutinized by the community (Brasier and Wacey 2012) which resulted in rejection or acceptance of the new record—see, for example, Barghoorn and Tyler's (1965) reevaluation of the initial inferences of Tyler and Barghoorn (1954) or Knoll and Barghoorn's (1975) rejection of the presence of eukaryotes in the 800 Ma (million years) Bitter Springs Formation (Australia); numerous other examples are summarized by Schopf and Walter (1983), and some are discussed below for the Akilia, Isua, Apex Chert, and Martian meteorite ALH84001 controversies and debates. Of these grew an increasingly more comprehensive, objective, and stringent set of criteria which is in use today (with some differences between authors). In general, application of these criteria involves addressing two fundamental types of questions: (1) Is the putative fossil indigenous to, and formed at the same time with, the host rock (*indigenousness* and *syngenicity*), as opposed to a modern contaminant or material introduced in the rock at a later time after rock formation? (2) Is the nature

of the putative fossil demonstrably biological (*biogenicity*) (Table 3.1)? Only if it passes these two tests is a candidate fossil confirmed as a bona fide microbial body fossil.

Indigenousness

To demonstrate indigenousness of the putative fossils, one has to demonstrate that they are embedded in the prehistoric rock matrix. Contamination by modern biota within the rock can arise by percolation through cracks and microfissures or during sampling, but it can also be comprised of modern endolithic organisms inhabiting pores and fissures beneath the rock surface (e.g., recent endoliths inhabiting the cracks and fissures of the 3.7 Ga rocks at Isua, Greenland, along with carbonaceous remains washed into cracks by rainwater; Westall and Folk 2003) (Fig. 3.4a). Because of these, many authors recommend use of fresh samples from beneath the weathering front of outcrops and use of petrographic thin sections to ascertain microscopically that the putative fossils do not occur on fissures (Schopf and Walter 1983; Buick 1990; Morris et al. 1999). Scanning electron microscopy can also provide evidence for indigenousness when fresh breaks in the rock are analyzed and they reveal breaking of the putative fossils in the same plane, which also indicates syngenicity (Fig. 3.4b); alternatively, putative fossils found exclusively on surfaces with dissolution features are suspect of representing contamination (Morris et al. 1999). If the microfossils are extracted by dissolution of the rock, special care must be taken to avoid any modern contaminants in the facilities and on equipment (Buick 1990) and to exclude from analysis the outermost layers of rock samples that may introduce contaminants acquired during sampling (Redecker et al. 2000).

Syngenicity

Demonstrating the syngenicity (also referred to as *syngeneity*) of candidate fossils involves proving that they were placed in the rock matrix upon its formation and not later (Schopf and Walter 1983; Buick 1990). For this, the age of the rock and the processes which led to its formation need to be well understood. Fossils need to be fully enclosed in the host rock as identifiable in petrographic thin sections, and when broken, they should fracture in a manner consistent with the way the groundmass of the host rock breaks around them (Morris et al. 1999). If the candidate fossils form only very localized assemblages or are consistently associated with discontinuities in the rock structures, their syngenicity is questionable as they may have been transported and emplaced along veins or other secondary diagenetic structures. Additionally, one expects to see overall consistency between the chemistry of syngenetic fossils and host rock, therefore presence in the candidate fossils of elements or compounds that are absent in the groundmass of the host rock supports non-syngenicity (Morris et al. 1999). In one example, Javaux

Table 3.1 Criteria for recognition of bona fide microbial fossils; based primarily on Schopf and Walter (1983), Buick (1990), Morris et al. (1999), Westall (1999), Brasier and Wacey (2012)

Traditional approach		Contextual approach	
Age	• Age and stratigraphy of rocks is resolved	Geologic context: ancient and viable for life and fossil preservation	• Age of rocks is resolved • Candidate fossils are indigenous to the host rock • Lithology and stratigraphy denote an environment that could have harbored life • Petrology reflects diagenetic history favorable to preservation of traces of life • Petrography indicates emplacement of candidate fossils contemporaneous with formation of rock unit
Indigenousness	• Candidate fossils are indigenous to the host rock		
Syngenicity	• Petrography indicates emplacement of candidate fossils in host rock at the time of its deposition • Occurrence at several locations in rock • Chemistry consistent with that of host rock		
Biogenicity	Direct: morphology and chemistry of candidate fossils • Morphology is consistent with that of living and fossil organisms (cellular organization) • Range of morphological variation within the population of candidate fossils is consistent with that seen in living and fossil organisms (non-uniformity) • Chemistry roughly matching that of host rock; carbonaceous or formed by biologically mediated mineral precipitation or mineral replacement • Dissimilar from potentially coexisting abiological organic objects	Morphological context: candidate fossils fit within the morphospace of cellular organization	• Morphology is consistent with cellular organization • Range of morphological variation within the population of candidate fossils is consistent with that seen in living organisms • Distinct from abiogenic mimics expected within the same kind of setting • All plausible explanations for abiogenic origin of like morphologies can be falsified
		Behavioral context: candidate fossils associate in patterns consistent with biological behavior	• Associated with microbially induced structures (e.g. biofilms, cements) • Associated with structures of the same kind in clusters or mats • Position within rock denotes biologically mediated substrate preferences
	Indirect: patterns of association, geologic, chemical, and evolutionary context • Abundance of occurrence • Associated in a multi-component assemblage of such objects (non-monospecific assemblage) • Geologic context is consistent with an environment that could have harbored life and conditions favorable to fossil preservation • Chemistry of candidate fossils/host rock consistent with that of microbial metabolic processes • Age and level of organization consistent with overall context of the evolution of life	Metabolic context: chemistry of candidate fossils and surrounding rock is consistent with living organisms and their metabolic products	• Cell walls, when present, have chemical composition consistent with a metabolic pathway • Host rock around candidate fossils bears chemical signatures of metabolic extracellular effusions and their effects on the mineral environment • Host rock bears chemical signatures of interlinked metabolic pathways (and their spatial zonation) characteristic of functioning ecosystems

et al. (2010) demonstrated syngenicity of 3.2 Ga microfossils from the Moodies Group (South Africa) (Fig. 3.10a) by showing that the organic matter comprising the microfossils had undergone the same degree of metamorphism as dispersed organic matter in the host rock, based on Raman spectrometry. Recently, Olcott Marshall et al. (2014) demonstrated that the carbonaceous material in the 3.46 Ga Apex Chert (Warrawoona Group, Australia) represents four generations of material with different thermal alteration histories and associated with different episodes of matrix formation, indicating that at least some of the four generations (if not all) are not syngenetic.

Biogenicity

The biogenicity of candidate fossils is demonstrated both by direct assessment of the objects themselves—morphology and chemistry—and indirectly, based on their broader taphonomic, geologic, chemical, and evolutionary-biostratigraphic context. The shapes and sizes of candidate fossils have to be consistent with those of known fossil and living organisms (Schopf and Walter 1983). Morphologies indicative of biogenicity include cells exhibiting phases of division (Knoll and Barghoorn 1977) (Fig. 3.7c, f) or plastic deformation characteristic of soft, organic bodies (Tomescu et al. 2008) (Fig. 3.4b). Morphological requirements for confirmation of biogenicity include sizes within the range of known microbes ($>0.01\ \mu m^3$) and hollow objects (coated in carbonaceous material), i.e., walls or sheaths of cells or cell colonies (filaments) with or without internal divisions (Buick 1990).

Ideally, the candidate fossils show cellular elaboration, but this criterion is the source of much debate (Buick 1990) as abiogenic objects can mimic some features of cellular organization. Several authors recommend special caution in the interpretation of spheroids comparable to coccoid prokaryotes, even when these exhibit morphologies comparable to dividing cells, as such morphologies can be formed by abiogenic processes (Westall 1999; Brasier and Wacey 2012). In such cases, independent lines of evidence are required to corroborate biogenicity. Furthermore, even more complex filamentous morphologies comparable to Precambrian microfossils can be generated abiotically, as shown by Garcia-Ruiz et al.'s (2003) experiments on precipitates formed by metallic salts in silica gels; however, the structures thus formed are not hollow. Abiogenic structures mimicking microbial filaments are also formed when local dissolution of the rock matrix allows for displacement of crystals representing mineral inclusions which leave trails (Knoll and Barghoorn 1974) (Fig. 3.4c); when carbonaceous inclusions from the rock are also included in the trails, these can be easily mistaken for microbial filaments (Lepot et al. 2009a). Only careful study of the microstructure and distribution of carbonaceous matter, along with the fact that the "filaments" have mineral crystals at their ends, reveals the abiogenic nature of such biomorphs (Brasier et al. 2002; Lepot et al. 2009a).

The chemistry of candidate fossils can help in assessment of their biogenicity, which is supported by the presence of cell walls or internal structures consisting of kerogen (geologically transformed organic matter; see Sect. 3.6.2.1) and by chemical compositions that roughly match that of the rock groundmass but show elevated

carbon content (Buick 1990; Morris et al. 1999). Stable carbon isotope ratios ($\delta^{13}C$) of carbonaceous material in candidate fossils have been used extensively in discussions of biogenicity (Westall 1999), and ^{13}C-depleted values are thought to indicate biological fractionation of carbon and, thus, biogenicity (e.g., Ueno et al. 2001b). However, a survey of the modern biota reveals that biogenic $\delta^{13}C$ values can vary at least as broadly as −41‰ to −3‰ PDB (Pee Dee Belemnite, a standard used for reporting carbon isotopic compositions and based on the Cretaceous marine fossil cephalopod *Belemnitella americana*), overlapping toward the top of this range with inorganic carbon (Buick 2001; Schidlowski 2000; Fletcher et al. 2004). Therefore, caution should be applied in drawing generalizations based on $\delta^{13}C$ values (Buick 2001), which should at best be used to support biogenicity only in conjunction with other independent sources of evidence.

The requirement for presence of organic carbon compounds (kerogen) excludes most traces of microbial life comprised exclusively of inorganic material, such as some microbially induced structures for which biogenicity criteria are discussed below. A particular case of inorganic structures of biogenic origin are the magnetosomes, ferromagnetic magnetite particles that are biomineralization products of magnetotactic bacteria. Magnetosomes are produced inside the bacterial cells, and when the latter are degraded, their magnetosomes form chains that mark the location of former filaments, but very similar magnetite grains can also have a fully abiogenic origin. The equivocal nature of such magnetite grains fuelled a significant part of the Martian meteorite ALH84001 debate (McKay et al. 1996; Thomas-Keprta et al. 2001; Golden et al. 2004; see below Sect. 3.4.4). More recently, Gehring et al. (2011) were able to identify dispersed magnetite particles in Holocene lake sediments as magnetosomes using two-frequency ferromagnetic resonance spectroscopy, thus opening the way to detection of this group of bacteria based on acellular but biogenic body fossils.

Whether organic carbon is present or not, another set of morphological criteria address biogenicity in terms of assemblage-level features. Candidate fossils co-occurring with more clearly discernable microfossils (e.g., spheroids co-occurring with rod-shaped fossils or a fossilized biofilm) are more likely to have a biogenic origin (Westall 1999). While some morphological variation is to be expected in assemblages of bona fide microbial fossils, the fossils have to be consistent in morphology and size throughout the assemblages (Figs. 3.7c, f and 3.8a, b, d), and significant disparities in the size of morphologically similar objects within an assemblage indicate abiogenic origin (Buick 1990; Westall 1999). Also at the scale of the entire candidate fossil assemblage, occurrence in abundance throughout the rock volume (a criterion for indigenousness and syngenicity as well) and the presence of multiple morphological types, thus non-monospecific assemblages (Fig. 3.7a), support biogenicity (Schopf and Walter 1983).

In a broader perspective, beyond the realm of morphology, the geology of the host rock has to reflect both genesis in an environment favorable to the presence of life and a subsequent geologic history conducive to fossil preservation (Schopf and Walter 1983; Buick 1990). Microbial body fossils are not thought to preserve in metamorphic rocks formed beyond low-grade metamorphism conditions. Microbe-like objects found in medium- to high-grade metamorphic rocks or in igneous rocks

are either abiogenic, or if they are bona fide fossils, they represent nonindigenous microbes (contaminants) or non-syngenetic microbial fossils. The chemistry of the host rock can also be used to support inferences of biogenicity of candidate fossils when it roughly matches that of the putative fossils, and it is characterized by significant levels of elements and minerals formed by the direct or indirect activities of microbes (e.g., pyrite produced by sulfate-reducing bacteria or magnetite, as discussed above) (Morris et al. 1999; Westall 1999). Finally, the level of biological complexity and organization of candidate fossils has to be consistent with the age of the host rock and the overall context of the known history of life on Earth (Schopf and Walter 1983). In this context, candidate fossils that appear out of context are likely to be abiogenic, nonindigenous, or non-syngenetic.

3.3.1.2 The Contextual Approach

The search for the oldest traces of life adds another set of challenges (as discussed by Brasier et al. 2006) to those encountered in documenting the microbial fossil record in younger rocks. First, whereas Proterozoic (<2500 Ma old) rocks have yielded a rich microfossil record, older rocks (especially pre-Neoarchean; >2800 Ma old) have produced very rare candidate fossils that the traditional approach to biogenicity can resolve unequivocally. Second, the environments of early Earth were very different from those we are familiar with or that we can even imagine today, and the potential life forms they hosted were very likely more similar to those of modern environments we are just exploring today (e.g., deep intraterrestrial endoliths, hyperthermophiles, anaerobes) than to anything else. Third, there is currently increasing recognition that a variety of abiogenic self-organizing structures generated by natural processes can mimic the morphological complexity of bona fide traces of life.

In most cases, the situations generated by these constraints reside beyond the sphere of resolution of the traditional inductive approach to biogenicity. Furthermore, the initial recognition of putative microfossils is based on intuition and experience; however, intuition and experience are double-edged swords, as they can easily lead one down the path of simply seeking evidence in support of a preferred interpretation, without consideration of alternative explanations. Such considerations, along with the challenges of identifying traces of life deeper and deeper in the rock record, have led some workers (e.g., Brasier et al. 2002, 2006) to reject the traditional approach and adopt a falsificationist approach wherein microbial structures are not accepted as biogenic until the alternative null hypothesis of abiogenicity is falsified. This approach emphasizes the integrative use of a comprehensive set of methods and an outlook based on asking open-ended questions about types of processes (biogenic and abiogenic) and geologic settings, and whether they could have produced the candidate fossil structures, rather than on comparisons with known fossil or modern organisms and structures (Brasier et al. 2006). In other words, instead of proving the biogenicity of structures, this approach strives to demonstrate that they cannot be abiogenic. For this, questions

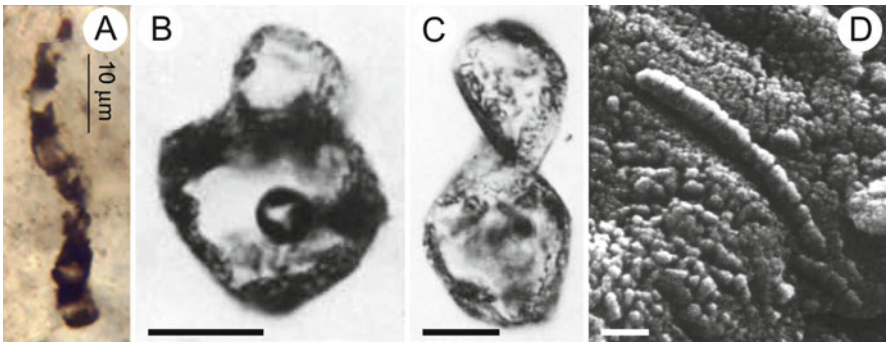

Fig. 3.5 Debates and controversies. (**a**) Putative microbial filament (*Primaevifilum amoenum*) from the Archean Apex Chert (Warrawoona Group, Western Australia). (**b**) and (**c**) Limonite-stained inclusions or cavities in Archean rocks of the Isua Greenstone Belt (Greenland), initially interpreted as microbial fossils (*Isuasphaera isua*). (**d**) Structures from the ALH 84001 Martian meteorite initially interpreted as bacterial magnetosomes. *Scale bars*: (**a**), (**b**), and (**c**) 10 µm; (**d**) 10 nm. Credits—images used with permission from (**a**) Elsevier Science Publishers (Schopf et al. 2007). (**b**) and (**c**) Springer-Verlag (Pflug 1978b). (**d**) Wikimedia Commons; file: ALH84001_structures.jpg; author: NASA

are asked to assess the level of support for biogenicity in a hierarchy of contexts: (1) geologic, (2) morphological, (3) behavioral-taphonomic, and (4) metabolic (Table 3.1).

The method of the contextual approach has been formalized by Brasier et al. (2006), Wacey (2009), and Brasier and Wacey (2012). Not surprisingly, some of the criteria applied in the contextual approach necessarily overlap with those of the traditional approach. However, due to the degree of generality of questions asked in applying it, the applicability of this approach extends beyond body fossils, to microbially induced structures. The approach has been used to reject the biogenicity of putative prokaryote fossils of the 3.46 Ga old Apex Chert in Australia (Brasier et al. 2002) (Fig. 3.5a) and to demonstrate the biogenicity of prokaryote fossils in the 3.4 Ga old Strelley Pool Formation in Australia (Wacey et al. 2011a) (Fig. 3.8a, b) and in an extensive critical analysis of all claims for early Archean life (Wacey 2009). Below we summarize the elements of the contextual approach as set forth by Brasier and Wacey (2012)—see also Table 3.1.

1. In a *geologic context*, questions are aimed at establishing the age of the rock hosting the candidate fossils, as well as the indigenousness and syngenicity of the latter, much in the same way that these are addressed traditionally. Furthermore, regional stratigraphy and petrology are mapped and sampled at the kilometer -to-meter scale in order to gain an understanding of whether the past local environments reflected by the rock record could have harbored life and whether the rock sequence reflects a diagenetic and post-diagenetic history favorable to fossil preservation. Detailed mapping of petrography and geochemistry at the cm-to-nm scale are then used to document spatial and temporal

relationships between the candidate fossils and their emplacement in the rock, on the one hand, and the host rock and its history, on the other hand. These allow for more in-depth assessment of the suitability of the host rocks for fossil preservation and for reconstruction of a detailed time line of the events of putative fossil formation and rock genesis, which allows for assessment of indigenousness and syngenicity. Inability to document in detail all of these aspects of the geologic context leaves the door open for alternative untestable (because unknown) hypotheses of nonindigenousness, non-syngenicity, or non-biogenicity.

2. The *morphological context* provides information important in assessing the biogenicity of candidate fossils regarded as members of a population of similar objects. The level of support for biogenicity is tested by documenting the morphospace occupied by the population (ranges of morphological and size variation) and asking whether it fits within the morphospace of cellular organization in terms of both shape and size and range of variation. For example, ranges that are too broad may indicate abiogenic structures whose variability is not constrained by genetics or habitat. Importantly, biogenicity is assessed at the same time in terms of the potentiality for the documented morphospace to be occupied by abiogenic objects expected within the geological context under consideration—for this the morphology of candidate fossils has to be considered in concert with their chemistry. All plausible explanations for abiogenic origin of objects with morphologies similar to that of the candidate fossils have to be falsified to demonstrate biogenicity. In this context, Brasier and Wacey (2012) emphasize the need for greater emphasis on improved mathematical modeling of morphospace occupation by different populations of objects, in order to produce more powerful tests for distinguishing biological populations from amalgamations of abiogenic structures (e.g., Boal and Ng 2010).
3. Because living organisms have behaviors which may be reflected in the taphonomy of their fossils, support for biogenicity has to be tested in a *behavioral-taphonomic context*. Patterns of association documented within assemblages of candidate fossils are assessed for the presence of features characteristic of biological behaviors. These include populations of candidate fossils assembled in clusters or mats reflecting colonial associations (Figs. 3.6a, 3.7a, b, 3.8d), or populations associated with microbially induced structures and textures (biofilm-like textures, biogenic or organomineral cements), as well as assemblages of candidate fossils positioned in response to substrate preferences (Fig. 3.8b). Just like with the morphological context, care must be taken to falsify abiogenic explanations for these types of association patterns: abiotic mineral growth can also form clusters, sometimes at the contact between contrasting lithologies which may be interpreted as a substrate surface colonized by a microbial mat; and inferences of biogenicity need to be corroborated by chemical data.
4. The metabolism of living organisms influences their environment and this may be reflected in the chemistry of candidate fossils and their host rock, which offers a *metabolic context* for testing hypotheses of biogenicity. Candidate fossils that comprise a carbonaceous fraction are tested for ^{12}C-enriched stable carbon

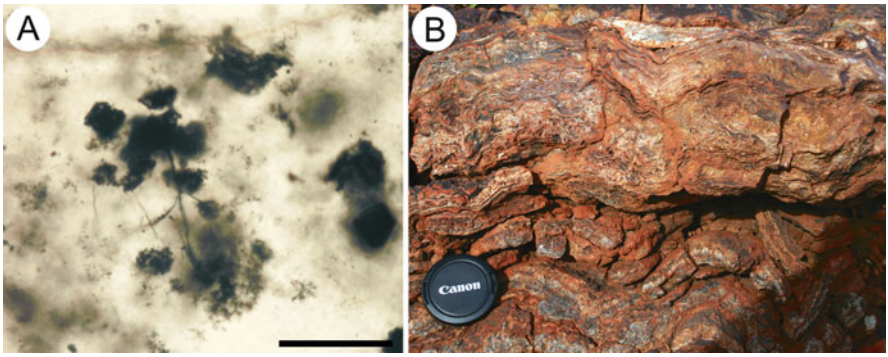

Fig. 3.6 Archean Dresser Formation (Warrawoona Group, Western Australia). (**a**) Putative filamentous microfossils; some exhibit helical geometries, others are interwoven, branched, or radiate from kerogen clots. (**b**) Putative stromatolite. Scale bars: (**a**) 50 μm, (**b**) lens cap diameter ca. 6 cm. Credits—images used with permission from (**a**) and (**b**) Springer Science + Business Media B.V. (Wacey 2009)

isotope ratios characteristic of biogenic carbonaceous material (kerogen). An enrichment in chemical elements comprising major building blocks of living matter (hydrogen, oxygen, nitrogen, sulfur, phosphorus) relative to the host rock matrix is also to be expected in biogenic objects. Due to the small size of microfossils, their chemistry is compared to that of surrounding mineral grains. Additionally, bona fide body fossils will be associated with chemical signatures generated by their metabolic extracellular effusions in the host rock (discussed in some detail below—see Sect. 3.6.2 Authigenic mineralization). In such cases, if microbial communities are preserved in situ, the host rock can record the chemical signatures of interlinked metabolic pathways (e.g., carbon fixation and carbon respiration; Brasier and Wacey 2012) and their spatial zonation characteristic of functioning microbial ecosystems.

3.3.2 Recognizing Microbially Induced Structures

The recognition of diverse structures in the geologic record as traces of microbial life follows the same paradigms as that of microbial body fossils. Some authors apply sets of criteria in a traditional inductive approach, while others favor a context-based falsificationist approach, and the criteria used vary somewhat among authors. The methods used for assessing the criteria also vary somewhat for different types of microbially induced structures (MISS, stromatolites, microborings) because of differences in the types of microorganisms that generated the structures and their mode of formation. However, the fundamental requirements for recognizing diverse structures in the geologic record as traces of microbial life are the same as for microbial body fossils. Biogenic-like morphologies are what initially recommends them as candidate microbially induced structures, and the

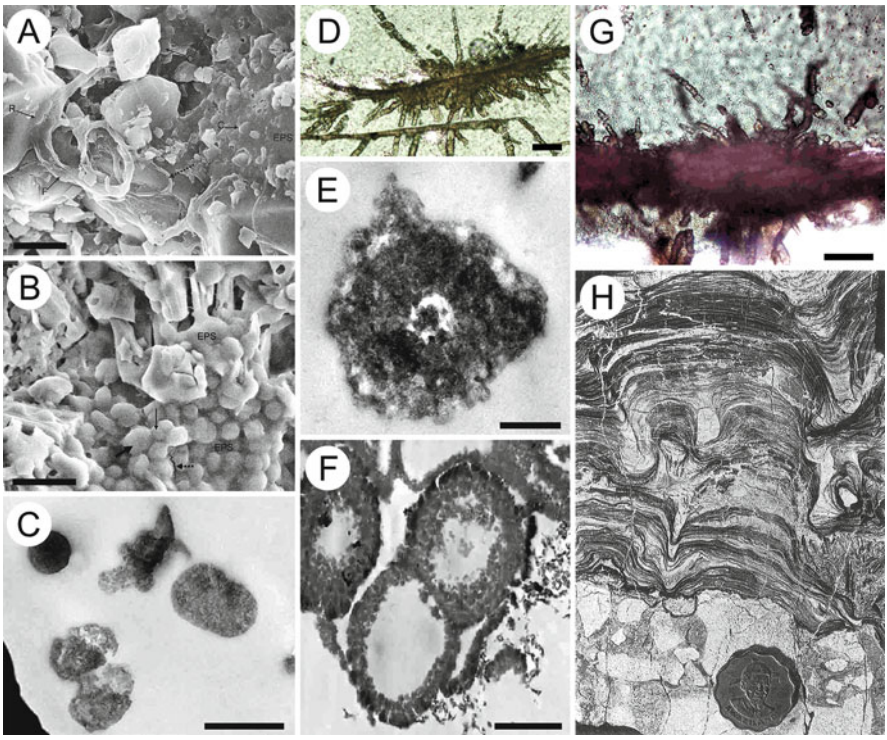

Fig. 3.7 (**a**) and (**b**) Microfossils from the Archean Kitty's Gap Chert (Warrawoona Group, Western Australia), filamentous, rod-shaped, and coccoid microorganisms. (**c**)–(**g**) Microbial fossils of the Archean Hooggenoeg Formation (Onverwacht Group, South Africa), (**c**) cell-like bodies showing possible stages of division, (**d**) candidate microborings—titanite (*brown*) in volcanic glass (*green*), (**e**) granular-textured body showing porosity and central cavity, (**f**) aggregate of cell-like bodies showing central cavities, (**g**) candidate microborings. (**h**) Stromatolites of the Archean Onverwacht Group. Scale bars: (**a**) and (**b**) 2 μm, (**c**) 0.5 μm, (**d**) 50 μm, (**e**) 0.2 μm, (**f**) scale 2 μm, (**g**) scale 50 μm, (**h**) coin ca. 20 mm diameter. Credits—images used with permission from (**a**) and (**b**) Geological Society of America (Westall et al. 2006). (**c**), (**e**), and (**f**) Elsevier Science Publishers (Glikson et al. 2008). (**d**) Geological Society of America (McLoughlin et al. 2012). (**g**) Elsevier Science Publishers (Furnes et al. 2007). (**h**) Blackwell Science Ltd. (Golubic and Knoll 1993)

geologic context needs to reflect conditions suitable for life and syngenicity (except for microborings which can be emplaced subsequent to the formation of their host rock) (Schopf and Walter 1983; Buick 1990; McLoughlin et al. 2007). Aside from morphology, geochemical analyses are called upon in the assessment of biogenicity, to test for evidence for metabolic activity (Brasier et al. 2006; McLoughlin et al. 2007; Brasier and Wacey 2012). Furthermore, in a contextual approach (as outlined above), the null hypothesis of abiotic origin must be rejected for any candidate microbially induced structure (Brasier et al. 2006; Brasier and

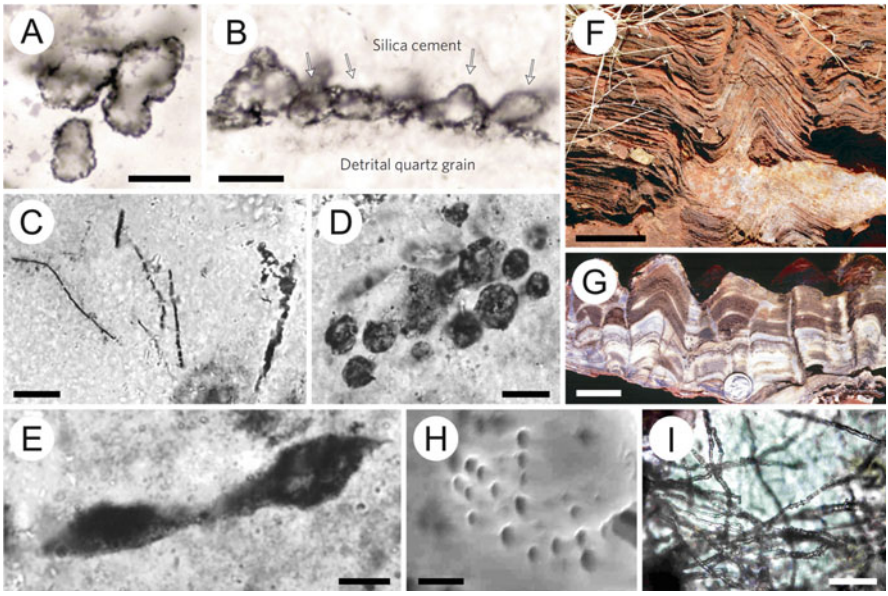

Fig. 3.8 Microbial fossils of the Archean Kelly Group (Western Australia); (**a**)–(**h**) Strelley Pool Formation, (**i**) Euro Basalt. (**a**) Cluster of cells, some showing cell wall folding and invagination. (**b**) Cells attached to quartz grain exhibiting preferred alignment parallel to the surface of the quartz grain. (**c**) Carbonaceous threads of rodlike objects representing putative microbial filaments. (**d**) Colony of loosely clustered hollow spheroidal microfossils. (**e**) Pair of linearly arranged lenticular carbonaceous microfossils. (**f**) and (**g**) Stromatolites. (**h**) Microbial etch pits (microborings) in pyrite. (**i**) Segmented microborings in volcanic glass. *Scale bars*: (**a**) and (**b**) 20 μm, (**c**) 20 μm, (**d**) 20 μm, (**e**) 10 μm, (**f**) 4 cm, (**g**) 3 cm, (**h**) 3 μm, (**i**) 25 μm. Credits—images used with permission from (**a**) and (**b**) Nature Publishing Group (Wacey et al. 2011a). (**c**), (**d**), and (**e**) Elsevier Science Publishers (Sugitani et al. 2013). (**f**) and (**g**) Springer Science + Business Media B.V. (Wacey 2009). (**h**) Elsevier Science Publishers (Wacey et al. 2011b). (**i**) Elsevier Science Publishers (Furnes et al. 2007)

Wacey 2012). Several authors have proposed different recognition criteria and ways in which these may be satisfied for specific types of structures.

3.3.2.1 Microbialites

Most microbialites lack microfossils and determining their biogenicity requires attention to the geologic context, overall morphology, microstructure, and chemistry. Modern analogues of stromatolites are very rare (Kazmierczak and Kempe 2006) (Fig. 3.2d, f) and little is known about their formation from direct observations. As a result, definitions of stromatolites and the criteria used to recognize them as biogenic structures are widely different between authors and are still debated. In contrast to stromatolites, which have been recognized and studied for at least a century (Awramik and Grey 2005), the study of microbially induced sedimentary

structures as fossil traces of life, and especially in the search for the earliest traces of life, is a relatively recent development. In part because of its recent rise, but also due to the wealth of modern sedimentary environments that host microbial mats providing as many modern analogues, the study of MISS is firmly grounded in an empirical comparative approach that was pioneered by Noffke and Krumbein (Noffke et al. 1996; Noffke et al. 2001).

Microbially Induced Sedimentary Structures

Noffke (2009) provided the most recent treatment of the lines of evidence used for recognizing MISS, summarizing them in a set of six criteria of biogenicity which we discuss below. These criteria are based on numerous studies of both modern and fossil microbial mats and MISS, but emphasize MISS formed by photoautotrophic mat-building microbes in aqueous environments.

1. *Broader geologic context*: MISS occur in sedimentary rocks that have experienced, at most, low-grade metamorphism (lower greenschist facies). Higher-grade metamorphism is unfavorable not only to the preservation of body fossils but also to MISS preservation—the often complicated diagenesis of metamorphic rocks can render syngenicity difficult to assess, metamorphic textures and structures can overprint the sedimentary structures, and, overall, biosignatures are altered and difficult (or impossible) to recognize.
2. *Sequence stratigraphy*: MISS are associated with regression-transgression turning points (the term transgression indicates a relative rise in sea level, while regression indicates a relative drop in sea level). More specifically, it is the transgressive phases that succeed those turning points that witness expansion of tidal flat and shallow shelf areas favorable to microbial mat formation along the passive continental margins, due to sea level rise.
3. *Depositional environment*: MISS occur in rocks formed in environments favorable to the establishment and preservation of microbial mats. Although modern photoautrophic mat-building microbes are often found in environments characterized by fine-grained sand substrates and low current velocities (10–25 cm/s), it is conceivable that chemoautotrophic microbes could build mats beyond the photic zone and on substrates suitable to their metabolic needs.
4. *Hydraulic regime*: the types of MISS and their spatial and stratigraphic distribution are consistent with the hydraulic regime implied by sedimentology, as specific types of modern MISS have been shown to characterize environments with different hydraulic regimes (e.g., shallow shelf, lagoon, different tidal zones).
5. *Morphology*: constrained by the same biology throughout the ages, microbial mats have maintained the same functional morphology traits, therefore geometries and dimensions of fossil MISS match those of modern MISS.
6. *Microtexture*: microscopic textures and structures related to, caused by, or representing microbial mats are found associated with the macroscopic MISS.

These include (often poorly) fossilized or mineral-replaced microbial filaments, wavy laminae concentrating organic matter and associated with sharp microstratigraphic geochemical gradients (Noffke et al. 2013b), finer-grained clasts or heavy minerals, upward-fining microsequences, and minute pores left by gases accumulating under the microbial mat.

Stromatolites

The realization, early in the history of stromatolite studies, that some laminated precipitation structures represent microbially induced structures led to a period of somewhat undiscerning application of the label of biogenicity to any finely laminated structure in the rock record, which resulted in a plethora of reports of stromatolites (and therefore microbial fossils) from rocks of all ages [e.g., the 3.4 Ga Buck Reef Chert of South Africa, listed as a stromatolite by Schopf (2006) but not treated as one by Tice and Lowe (2004)]. The subsequent realization that not all laminated structures are biogenic (e.g., Lowe 1994) led to disagreement over what defines a stromatolite (Hofmann et al. 1999; Awramik and Grey 2005). Because of that, distilling a set of criteria of biogenicity for stromatolites is much more difficult than for MISS (e.g., Riding 2011). Whereas some authors define stromatolites as laminated structures that are formed by microbial activities and mineral precipitation (Awramik and Margulis 1974; Buick et al. 1981), others use the term stromatolite for laminated, lithified sedimentary structures, regardless of the involvement of microbes in their formation (e.g., Semikhatov et al. 1979; Antcliffe and McLoughlin 2009). Consequently, the disagreement also extends over whether such laminated structures could represent good evidence for ancient life, and a number of different sets of criteria for stromatolite biogenicity have been proposed.

Buick et al. (1981) assembled probably the most stringent set of criteria that focuses on morphological lines of evidence:

1. The candidate structures (termed stromatoloids; Buick et al. 1981) occur in sedimentary or metamorphosed sedimentary rocks;
2. The structures are synsedimentary with the host rock; because most stromatolites are built by photosynthetic microbial communities that tend to be thicker in positions receiving the most light and therefore raised with respect to the rest of the substrate;
3. Most structures in a stromatolite have a convex-upward morphology (e.g., Figs. 3.2d–f, 3.3b–d, 3.6b, 3.7h, 3.8f, g) and
4. Individual laminae are thicker over the upward-facing convex surfaces (e.g., Figs. 3.3b, c, 3.7h, 2.8g);
5. Laminations are wavy and wrinkled or have several orders of curvature (e.g., Figs. 3.2e, 3.3c, d, 3.7 h) because bedding irregularities are amplified by the phototropic tendencies of the microbial communities listed above;
6. Microbial body or trace fossils are present in the structures;

7. Changes in the microfossil assemblages are associated with changes in the morphology of sedimentary structures, indicating a relationship between the microbial communities and the formation of the structure; and
8. Microfossils are preserved in situ and in positions that indicate accretion activities—binding, trapping, or precipitation.

It is worth noting that, based on strict morphological criteria and including requirements that microfossils be present and proven to contribute to sedimentary accretion, this set of criteria diagnoses as abiogenic most structures accepted as stromatolites by other systems of evaluation.

In his criteria for stromatolite biogenicity, Walter (1983) was concerned with syngenicity—orientation of laminated structures with respect to bedding planes indicating formation at the same time with adjacent layers and occurrence in rocks where the laminated structures can only be explained as primary sedimentary features—and biogenicity as reflected in morphology, microbial origin, and chemistry. Hofmann et al. (1999) used careful studies of morphology, sedimentology, and local microstratigraphic relationships in their assessment of the biogenicity of 3.45 Ga conical laminated structures from the Warrawoona Group (Australia). Their approach was aimed at rejecting hypotheses of abiogenic origin and their arguments were later regarded as a set of criteria for biogenicity (Awramik and Grey 2005). Hofmann et al. (1999) rejected regional deformational processes as a potential explanation, based on the geographically broad extent of the structures, combined with their narrowly constrained stratigraphic and lithologic circumstances. They also used the geometry and relative position of laminae to reject sideways compression (folding), downright directed slumping, and strictly chemical precipitation as explanations for different morphological aspects of the structures, supporting their formation by upward accretion. Furthermore, these authors used the steep angles of the structures to reject simple sedimentation as a formation mechanism, supporting the presence biological binding. Finally, Hofmann et al. (1999) invoked the wide acceptance of other independent lines of evidence (at the time; some of these were later contested), such as body fossils and chemical biosignatures, for the presence of life in coeval rocks, as making biogenic causes even more plausible.

The contextual approach (see above; Brasier et al. 2002; Brasier and Wacey 2012) is applicable, with some changes, to MISS and stromatolites (Wacey 2009). The fact that stromatolite-like morphologies have been proven to form by abiogenic processes (Grotzinger and Rothman 1996; McLoughlin et al. 2008) implies that morphology alone is not enough to determine biogenicity and that microstructural and geochemical analyses are necessary to reject the null hypothesis of abiogenic formation for any given stromatolite. It is interesting to note that Awramik and Grey (2005) have expressed doubt about whether any abiogenically formed structures can convincingly resemble stromatolites. On a more general level, these authors criticized the contextual approach for setting lofty standards for paleontology. They point out that alternative modes of genesis are thoroughly considered by workers adopting a traditional inductive approach to stromatolite biogenicity, even if the associated

deliberations are not included in the final publication. Instead of what they call the binary character of the contextual approach, Awramik and Grey (2005) advocate an approach that emphasizes morphology (without excluding other types of data) aimed at finding evidence for the contribution of biogenic processes to the formation of candidate structures and placement of that evidence on a scale of credibility (unequivocal-compelling-presumptive-permissive-suggestive evidence).

Most of the disputes on stromatolite biogenicity and the criteria to assess it are certainly rooted in the absence of microbial body fossils from many candidate stromatolites (Hofmann et al. 1999). Addressing this topic, Kremer et al. (2012a) studied calcification and silicification processes in cyanobacterial mats that form the best modern analogues of fossil stromatolites, in Tonga (south Pacific; Kazmierczak and Kempe 2006) (Fig. 3.2d, e). They showed that morphological preservation of cyanobacteria by primary mineralization depends on two main factors: the type of mineral phase and the time of mineralization. Variations in the two factors produce a wide spectrum of modes of morphological preservation which encompass several stages of degradation that were documented for both filamentous and coccoidal cyanobacteria. These observations led Kremer et al. (2012a) to suggest that Archean life may have been more abundant than previously thought based on meager findings, but difficult to recognize because of the alteration of original microbial body fossils or sedimentary structures due to recrystallization and mineral replacement.

3.3.2.2 Microborings

In contrast to stromatolites, microborings have abundant modern counterparts. However, the abundance and ubiquity of modern microborings (included by some authors in the broader category of *bioalteration textures*; Furnes et al. 2007) is only starting to become appreciated and studied. At a general level, the criteria used to establish that microborings are ancient and biogenic are the same as those applied to other microbially induced structures and to body fossils. However, due to their relatively simple morphology and unique mode of formation of microborings, the specific application of these criteria is somewhat different than for other fossil biosignatures. In their treatment of microborings, McLoughlin et al. (2007) and Furnes et al. (2007) propose an approach that includes evaluation in three contexts—geologic, morphological, and geochemical-metabolic—aimed at determining the age of structures and at falsifying an abiogenic origin.

1. *Age*: since microbes producing microborings are at work today just as they were in the Proterozoic, it is imperative that microborings reported from ancient rocks and presumably of ancient age be demonstrated to have originated early during diagenesis of the host rocks. Age is established based on the relationships of the microboring with surrounding features of the rock. Early diagenetic microborings will crosscut early stage fractures in the host rock and will be crosscut by later (younger) metamorphic mineral growths (McLoughlin

et al. 2007). Furthermore, ancient microborings will show the same level of metamorphosis as their host rock (Furnes et al. 2007), and in the case of microborings in volcanic rock filled with titanite (Fig. 3.7d, g), the absolute age of the titanite can be directly determined by U-Pb dating (e.g., the microborings of the 3.35 Ga Euro Basalt, Pilbara Craton, Australia; Banerjee et al. 2007) (Fig. 3.8i).

2. *Geologic context*: the regional and local scale context of the microborings has to be consistent with the presence of life. This is becoming an increasingly less stringent requirement as modern and fossil biogenic microborings are being discovered in (unforeseen) settings that broaden our ideas about the range of environments where we can expect to find traces of life (e.g., subseafloor oceanic crust; Furnes et al. 2001; McLoughlin et al. 2012). The geologic setting of microborings is expected to be consistent with behavioral aspects of microbial biology—microborings should demonstrate substrate preferences in the host rock for metabolically useful compounds, or if their origin is cyanobacterial, the stratigraphy and sedimentology of the host rock should be consistent with a shallow, photic depositional environment (McLoughlin et al. 2007).
3. *Morphological context*: the morphology of microborings has to be consistent with biogenic origin. Since microborings have a relatively simple morphology, consisting only of branched tubes, it is difficult to establish a set of morphological criteria that applies to all microborings and excludes all abiogenic mimics. Nevertheless, a list of features that would lend support to a biogenic origin of such tubes would include μm-scale size and branching or changes in direction as they encounter other such structures (Furnes et al. 2007). These features, considered singly, cannot provide compelling evidence for biogenicity, and morphology alone can rarely be used to determine the biogenicity of putative microborings, without supporting geochemical evidence (McLoughlin et al. 2007).
4. *Geochemical-metabolic context*: geochemical evidence provides the strongest support for the biogenicity of most microborings. Euendoliths producing microborings are chemolithoautotrophic prokaryotes, so microborings preferentially occupying areas of the host rock rich in compounds that are metabolically important for bacteria, such as metal inclusions, provide evidence for biological processing (Brasier et al. 2006). Finer scale geochemical evidence from both the microtubes and their filling can provide even stronger support for biogenicity. For example, depletion of Mg, Ca, Fe, Na in the rock matrix around putative microborings indicates metabolic processing by euendoliths (Alt and Mata 2000). Fine (<1 μm thick) linings of C, N, and P in both recent and prehistoric microtubes have been interpreted as cellular remains (Giovannoni et al. 1996; Furnes and Muehlenbachs 2003), so similar linings of biologically important elements may be used as evidence for a biogenic origin of putative microborings. Additionally, analyses of in situ carbon within the microborings can also provide insights into their potential biogenicity (Furnes et al. 2004; McLoughlin et al. 2012).

5. *Null hypothesis of abiogenicity*: in most cases, the alternative explanation of micron-sized tubular structures resides in *ambient inclusion trails* (AIT) (Lepot et al. 2009a); therefore it is essential that putative microborings are shown to not belong in this category of structures. Although the exact conditions that lead to formation of AIT are not well understood (McLoughlin et al. 2007), they have been suggested to form by the movement of a crystal (e.g., pyrite, garnet) through the crystalline silica matrix of the rock. The movement is thought to be the result of pressure-solution processes and potentially driven by the thermal decomposition of organics into gases (Tyler and Barghoorn 1963; Knoll and Barghoorn 1974; Wacey et al. 2008; Lepot et al. 2009a).

While relatively few morphological characters can be used in support of the biogenicity of putative microborings [although see McLoughlin et al.'s (2009) formal taxonomy of microborings as trace fossils (Fig. 3.4d–f)], many more features can be used to identify tubular structures as AIT of abiogenic origin. McLoughlin et al. (2007) provided a list of characters present in AIT that can be used to distinguish them from bona fide microborings: (1) presence of a mineral grain at the end of the tube (Fig. 3.4c); (2) longitudinal striations caused by the facets of the mineral grain as it was driven through the rock; (3) angular cross-sectional geometry and twisted paths, particularly toward the end of the tubes (due to the increasing resistance of the host rock); and (4) a tendency to crosscut other tubes or branch, with sudden changes in diameter at branching points—branches with different diameters are caused when the mineral grain forming the AIT splits and the resulting fragments continue to form one AIT each.

Despite the abiogenic mode of AIT formation, an interesting aspect of these structures that can be relevant to early microbial life is the nature of the organic material that drives the movement of the trail-forming crystals. Wacey et al.'s (2008) study of the 3.4 Ga Strelley Pool sandstone (Australia) provides a good example of biogenicity assessment for tubular trace fossils and AIT recognition using the criteria outlined above. Furthermore, using nanoSIMS (secondary ion mass spectrometry) analyses, these authors were able to confirm the role of decomposing organic matter in AIT formation (proposed by Knoll and Barghoorn 1974) and to demonstrate features consistent with biogenic origin for the organic material associated with the trails.

3.4 Earth's Oldest Fossils and the Archean Fossil Record

3.4.1 An Archean-Proterozoic Disparity

Archean evidence for life includes all types of fossils discussed thus far: microbial body fossils (microfossils), microbially induced structures (stromatolites, MISS), and chemical biosignatures. This section focuses primarily on microfossils, with microbially induced structures addressed only in the summary of the oldest

evidence for life (Sect. 3.4.5). A sweeping glance at the Precambrian microfossil record reveals a marked change in the quality and number of fossils from the Proterozoic to the Archean (Schopf et al. 2010). The Proterozoic rock record hosts numerous localities with well-preserved, unequivocal microfossils (Sergeev 2009). The high diversity of microfossil types and morphologies seen among these localities suggests that prokaryotic life arose and started diversifying much earlier, in the Archean (Altermann and Schopf 1995; Sergeev 2009). However, despite decades of research aimed at finding signals of life in the Archean, microfossils from this time period are comparatively rare and often highly controversial (Schopf and Walter 1983; Altermann and Schopf 1995; Wacey 2009). A historical focus on the Proterozoic by researchers may have been at the origin of this disparity in the early stages of the discipline. Nevertheless, continued studies are now indicating that this discrepancy in the quality and abundance of microfossils between the Archean and the Proterozoic is predominantly an artifact of the geologic record and not the result of lack of study or differences in the early biosphere (Schopf and Walter 1983; Schopf et al. 2010; Wacey 2012). This can be attributed to a series of factors that include (1) relatively low levels of cratonic sedimentation (i.e., on continental landmasses) during the Archean; (2) comparatively intense metamorphism and deformation of Archean sedimentary rocks, which are predominantly found today in metamorphic greenstone belts (Schopf and Walter 1983; Buick 1990) that consist of metamorphosed basalt with minor sedimentary rock interlayers; and (3) the fact that the silica forming most Archean cherts that preserve candidate fossils precipitated from relatively hot, acidic, and concentrated hydrothermal fluids, whereas Proterozoic cherts formed from cooler, more neutral, and dilute surficial fluids (Buick 1990). Such processes degrade the remains of organisms and biological compounds, complicating efforts to identify them in Archean rocks. Thus, although Archean rocks can be found in many areas, those that are well exposed, have undergone relatively little metamorphism, are of clear sedimentary origin, and have yielded bona fide body fossils thus far are found in only two places on Earth: the Kaapvaal Craton in South Africa and the Pilbara Craton of Western Australia (Wacey 2009; Hickman and Van Kranendonk 2012), which may have been part of the same landmass in the Archean (Zegers et al. 1998) and possibly in close vicinity to each other. It is from these two regions that nearly all Archean microfossils known to date originate, including the very earliest evidence of life.

3.4.2 Brief History of Discovery

The first bona fide Precambrian microfossils were reported in 1907 from ca. 1 Ga old Torridonian sedimentary phosphates in Scotland (Peach et al. 1907; Wacey 2009), but it was not until Tyler and Barghoorn (1954) first published descriptions of microfossils from the Gunflint iron formation (Canada) that sustained work went into documenting microbial diversity in the Precambrian (Schopf and Walter 1983). Dated to 1.9 Ga, the Gunflint iron formation microfossils provided the first solid

evidence of Proterozoic life older than 1 billion years. Much older microfossils were reported from Archean rocks of South Africa during the 1960s and from Australia as early as the late 1970s (Knoll and Barghoorn 1977; Dunlop et al. 1978; Awramik et al. 1983). However, nearly all of these claims were questioned or contested in some capacity (Nisbet 1980; Schopf and Packer 1987; Buick 1984). It was not until microfossils from the 3.46 Ga Apex Basalt (Australia) (Fig. 3.5a) were described that an assemblage of early Archean (Paleoarchean) microfossils was widely accepted as evidence of early Archean life (Schopf and Packer 1987; Schopf 1993). For over a decade, these fossils were embraced as the best and earliest evidence for life on Earth (Brasier et al. 2004). In 2002 Brasier et al. presented evidence refuting all the lines of evidence on which the biogenicity claims for the Apex microfossils were based, sparking a debate that continues to the present day (e.g., Schopf and Kudryavtsev 2012; Pinti et al. 2013). Despite their later contentiousness, the initial wide acceptance of these fossils established an enduring paradigm that shapes our conception of the timing of the emergence of life. This idea of an early Archean origin for life has been dubbed the "Early Eden Hypothesis" (Brasier et al. 2004). Regardless of the biogenicity of the Apex microfossils, a look at the Archean microfossil record known to date reveals numerous lines of evidence which, even in the absence of a smoking gun, point strongly toward the emergence of life around 3.5 billion years ago (see below).

3.4.3 Salient Patterns in the Archean Fossil Record

Several major patterns emerge from a review of the Archean record of life. In terms of the host rock, Archean microfossils occur in sedimentary rocks, most commonly cherts and sandstones, formed in marine environments and metamorphosed to greenschist facies. Most of these fossils are found in cherts (Table 3.2) and a small proportion originate from sandstones such as those from the Strelley Pool Formation in Australia and Moodies Group in South Africa (Noffke et al. 2006; Wacey 2009). Despite their rarity in the Archean microfossil record, sandstones record valuable data that are difficult to extract from other types of rock, including successive depositional and diagenetic stages or microbially induced structures (e.g., Noffke et al. 2006, 2013a; Wacey et al. 2011b). Sandstones may also provide some protection to the fossil structures from mechanical stress and strain during metamorphism (Wacey 2009). Although early studies focused on rocks originating from environments thought to be most conducive to early life at the time, such as shallow marine environments, more recent work has focused on searching for biosignatures in what were previously considered unlikely contexts, such as in hydrothermal deposits and pillow basalts (Rasmussen 2000; Furnes et al. 2004; Duck et al. 2007; Furnes et al. 2007; Wacey 2009; McLoughlin et al. 2012).

Geographically, as previously mentioned, Archean microfossils occur exclusively in rocks of the Kaapvaal Craton in South Africa and in the Pilbara Craton of Western Australia. However, within each of these regions, fossil localities have

Table 3.2 Archean microfossil record, with an emphasis on rock units older than 3 Ga and microbial body fossils, *MISS* microbially induced sedimentary structures

Age (Ma)	Rock unit	Location	Fossil evidence	References
3480	Dresser Formation (Warrawoona Group, Pilbara Supergroup)	Australia	Microfossils[a]—filaments spiral, tubular branched and unbranched, some septate; spheroids MISS ?Stromatolites	Buick et al. (1981), Ueno et al. (2001a, b), Awramik and Grey (2005), Van Kranendonk (2006), Schopf (2006), Wacey (2009), Noffke et al. (2013a)
?3470[b]	?Mount Ada Basalt (Warrawoona Group, Pilbara Supergroup)	Australia	Microfossils—tubular sheaths; filaments unbranched, some septate	Awramik et al. (1983)
3466	Kitty's Gap Chert in Panorama Formation (Warrawoona Group, Pilbara Supergroup)	Australia	Microfossils—colonies of primarily coccoid cells, some chain-like; some filaments and rare rod-shaped cells	Westall et al. (2006)
3465	Apex Chert in Apex Basalt (Warrawoona Group, Pilbara Supergroup)	Australia	Microfossils[c]—filaments unbranched septate	Schopf and Packer (1987), Schopf (1993, 2006)
3450	Hooggenoeg Formation (Onverwacht Group, Swaziland Supergroup)	South Africa	Microfossils—narrow filaments; clusters of spherical, subspherical structures, cell walls; rod-shaped cells Microborings in pillow lavas	Walsh (1992), Walsh and Westall (2003), Westall et al. (2001, 2006), Furnes et al. (2004), Glikson et al. (2008), Wacey (2009), Fliegel et al. (2010), McLoughlin et al. (2012)
3426–3350	Strelley Pool Formation (Kelly Group, Pilbara Supergroup)	Australia	Microfossils—threadlike and hollow tubular filaments, filmlike structures, hollow spheroids, lenticular microfossils (ellipsoids) Stromatolites Microborings	Hofmann et al. (1999), Brasier et al. (2006), Allwood et al. (2007), Wacey et al. (2006, 2011a, b), Sugitani et al. (2010, 2013)

(continued)

Table 3.2 (continued)

Age (Ma)	Rock unit	Location	Fossil evidence	References
3416–3334	Kromberg Formation (Onverwacht Group, Swaziland Supergroup)	South Africa	Microfossils—spheroids, ellipsoids, rod-shaped cells, spindle-shaped microfossils Microborings in pillow lavas	Walsh (1992), Furnes et al. (2007), Wacey (2009)
3416	Buck Reef Chert (Onverwacht Group, Swaziland Supergroup)	South Africa	Microfossils—occasional filaments in laminations MISS	Tice and Lowe (2004), Wacey (2009)
3350	Euro Basalt (Kelly Group, Pilbara Supergroup)	Australia	Microborings	Banerjee et al (2007), Wacey (2009)
3260	Swartkoppie Formation (Onverwacht Group, Swaziland Supergroup)	South Africa	Microfossils—coccoid cells	Schopf (2006)
3245	Sheba Formation (Fig Tree Group, Swaziland Supergroup)	South Africa	Microfossils—coccoid cells	Schopf (2006)
3240–3235	Kangaroo Caves Formation (Sulphur Springs Group, Pilbara Supergroup)	Australia	Microfossils—unbranched filaments and bundles of tubes, spheroids (small, 50–100 nm diameter)	Rasmussen (2000), Duck et al. (2007), Wacey (2009)
3200	Dixon Island Formation (West Pilbara Superterrane)	Australia	Microfossils—filaments, spheroids, microbial mat remnants	Kiyokawa et al. (2006), Schopf et al. (2006), Wacey (2009)
3200	Moodies Group (Swaziland Supergroup)	South Africa	Microfossils—spheroids MISS	Noffke et al. (2006), Wacey (2009), Javaux et al. (2010)
3000	Cleaverville Formation (Gorge Creek Group, De Grey Supergroup)	Australia	Possible microfossils—spheroids	Wacey (2009)
3190–2970	Farrell Quartzite (Gorge Creek Group, De Grey Supergroup)	Australia	Microfossils—threadlike, filmlike, spheroidal, lenticular, or spindle-like	Sugitani et al. (2007), Wacey (2009)
2750	Hardey Formation (Fortescue Group, Mount Bruce Supergroup)	Australia	MISS	Rasmussen et al. (2009)

(continued)

Table 3.2 (continued)

Age (Ma)	Rock unit	Location	Fossil evidence	References
2723	Tumbiana Formation (Fortescue Group, Mount Bruce Supergroup)	Australia	Microfossils—filaments Lacustrine stromatolites	Schopf and Walter (1983), Buick (1992), Schopf (2006), Lepot et al. (2008), Awramik and Buchheim (2009)
2600	Monte Cristo Formation (Chuniespoort Group, Transvaal Supergroup)	South Africa	Microfossils—filamentous, coccoid, rod shaped	Schopf (2006)
2560	Lime Acres Member, Ghaap Plateau Dolomite (Campbell Group, Transvaal Supergroup)	South Africa	Microfossils—coccoid, ellipsoid, filamentous, tubular sheaths	Altermann and Schopf (1995), Schopf (2006)
2516	Tsineng Member, Gamohaan Formation (Ghaap Group, Transvaal Supergroup)	South Africa	Microfossils—tubular sheaths	Klein et al. (1987), Schopf (2006)

[a]The biogenicity of microfossils in the Dresser Formation is equivocal (see Wacey 2009)
[b]Precise locality unknown (Schopf 2006; Wacey 2009; Brasier and Wacey 2012; see Sect. 3.4.4)
[c]The biogenicity of microfossils in the Apex Chert is debated (see Sect. 3.4.4.1)

been described from several stratigraphic levels and widely spread locations. These are summarized in Table 3.2 which contains a list of reported occurrences; it is worth noting that the biogenicity of some of the microfossils included in the table is debated. A few of these controversial occurrences are outlined later in this section, but in-depth assessments of the biogenicity of most of the reported Archean fossil assemblages have been provided by Wacey (2009).

Microfossils from the Kaapvaal Craton are found in the Swaziland and Transvaal Supergroups. The oldest of these fossils originate from the Swaziland Supergroup, which ranges from 3550 to 3220 Ma in age and can be divided into three stratigraphic intervals: the lowermost Onverwacht Group (~3550–3300 Ma), the Fig Tree Group (~3260–3225 Ma), and the Moodies Group (3220 Ma) (Van Kranendonk et al. 2007). Spheroidal or coccoid microfossils have been reported from each of these groups. Additional diversity of morphological types is known from the Onverwacht Group, where filamentous, "sausage"-shaped, and spindle-shaped microfossils have also been documented (Walsh 1992; Westall et al. 2001, 2006; Glikson et al. 2008; Wacey 2009). Younger microfossils are known from the Transvaal Supergroup and include filamentous, coccoid, rod-shaped, and ellipsoid forms (Altermann and Schopf 1995; Schopf 2006).

The microfossil-bearing units of the Pilbara Craton in Western Australia include the Pilbara Supergroup (3530–3170 Ma) in the East Pilbara Terrane and the overlying De Grey Supergroup (~3020–2930 Ma) (Van Kranendonk et al. 2007; Wacey 2009). The Pilbara Supergroup consists of volcano-sedimentary greenstone belts and is subdivided into four groups: the Warrawoona Group (~3520–3427 Ma), the Kelly Group (~3350–3315 Ma), the Sulphur Springs Group (~3270–3230 Ma), and the Soansville Group (~3230–3170 Ma). Microfossils are also known from the Dixon Island Formation (3200 Ma, Kiyokawa et al. 2006) in the West Pilbara Subterrane and the Tumbiana Formation (2723 Ma, Schopf 2006). Morphological types reported from the Pilbara Craton are similar to those of South Africa and include branched and unbranched filaments, septate filaments, tubular sheaths, coccoid or spheroidal forms, rod-shaped, ellipsoid, and lenticular or spindle-shaped microfossils (reviewed by Schopf 2006; Wacey 2009; and Wacey 2012).

Aside from microfossils, other types of evidence of life have been identified in these Archean cratons. Compelling examples include microbially induced structures that have been reported from the Moodies and Onverwacht Groups in South Africa, as well as the 3.48 Ga Dresser Formation (Warrawoona Group), and the 3.35 Ga Euro Basalt and ~3.42–3.35 Ga Strelley Pool Formation (Kelly Group) in Australia. In rocks of the Moodies Group, MISS are considered promising biosignatures and include wrinkle structures, desiccation cracks, and roll-up structures in sandstone (Noffke et al. 2006; Wacey 2009). Microborings in the rims of pillow lavas, consisting of mineralized tubular structures, from the Onverwacht Group and the Euro Basalt, are thought to have formed by the corrosion of the volcanic glass by endolithic microbes and are similar to those found in modern oceanic crust (Furnes et al. 2004; Banerjee et al. 2007; Wacey 2009; McLoughlin et al. 2012). The diverse MISS reported from the Dresser Formation (~3480 Ma) include sedimentary structures that are interpreted as originating from microbial mats in an ancient coastal sabkha (Noffke et al. 2013a). Microborings have also been described in pyrite grains of the Strelley Pool sandstone (Wacey 2009; Wacey et al. 2011b).

The later part of the Archean may have witnessed the advent of oxygenic photosynthesis with the evolution of cyanobacteria. Atmospheric oxygen concentrations rose to relatively stable, moderate to high levels (the "Great Oxidation Event") in the early Paleoproterozoic, ca. 2.4–2.3 Ga ago (Bekker et al. 2004). It is generally though that this was due to the evolution of cyanobacteria, which is placed somewhere toward the end Archean, ca. 2.8–2.7 Ga ago, based on several lines of evidence (Buick 2012; Konhauser and Riding 2012):

1. Presence of biomarkers associated with cyanobacteria (2α-methylhopanes) in the 2.72–2.6 Ga Fortescue and Hamersley Groups (Australia) (Brocks et al. 1999; Brocks et al. 2003a, b)
2. The stromatolites of the 2.7 Ga Tumbiana Formation (Fortescue Group, Australia) wherein fabrics indicating construction by microbes and the absence of iron- and sulfur-rich sediments indicate oxygenic photosynthesis (Buick 1992, 2012)

3. Assemblages of filamentous microfossils described from the 2.6 to 2.5 Ga peritidal carbonates of the Campbell Group (Transvaal Supergroup, South Africa), which include forms similar to modern oscillatoriacean cyanobacteria, such as *Lyngbya* and *Phormidium* (Altermann and Schopf 1995).

However, it is worth noting that the cyanobacterial affinities of the Campbell Group microfossils are not unequivocal (Knoll 2012) and the oldest unambiguous cyanobacteria to date are mid-Paleoproterozoic and comprise colonial forms described from the ca. 2 Ga Belcher Supergroup (Canada) by Hofmann (1976) and Golubic and Hofmann (1976).

Interestingly, the Tumbiana Formation stromatolites represent the oldest such structures formed in a freshwater lacustrine system, as indicated by the type of evaporite mineral association present, which includes carbonate and halite, with no sulfate present (Buick 1992; Awramik and Buchheim 2009). Another Fortescue Group unit, the 2.75 Ga Hardey Formation, hosts an occurrence of laminated microstructures of probably biogenic origin, which have been interpreted as the products of photosynthetic and methanotrophic prokaryotes forming microbial biofilms in cavities of lake-bottom sediments (Rasmussen et al. 2009).

3.4.4 Reevaluating Archean Fossil Datapoints

Establishing the biogenicity of early microfossils is a complex process requiring multiple lines of evidence. As the criteria used for identifying bona fide Archean microfossils keep being updated in the wake of successive debates over questionable fossils, many older discoveries may require reevaluation. As discussed in depth in a previous section, microfossils that are widely accepted as biogenic meet criteria for biogenicity that consider the geologic context, morphology, patterns of association and taphonomy, as well as the geochemistry of the fossils. Historically, geochemical analyses were not widely used in studying Archean microfossils and many methods of analysis were recently developed or employed in this field—Knoll (2012) provides a good summary of chemistry and microscopy techniques of more recent use in studies of Precambrian microfossils.

A technique that is not so new to the field anymore, laser Raman spectroscopy, has already seen ebbs and tides of usage (Pflug and Jaeschke-Boyer 1979; Ueno et al. 2001a; Schopf et al. 2002; Pasteris and Wopenka 2003; Brasier et al. 2002, 2004; Marshall et al. 2010). Raman spectroscopy has been used primarily for fine-scale mineralogy and is also a reliable method for determining the crystallinity of reduced carbon, a good proxy for the metamorphic and diagenetic history of carbonaceous material (Marshall et al. 2010; Knoll 2012; Ohtomo et al. 2014). Fourier transform infrared (FTIR) spectroscopy has been used in combination with Raman spectroscopy at microscale to determine the molecular composition and structure of Proterozoic eukaryotes and putative eukaryotes (Marshall et al. 2005). Secondary ion mass spectrometry (SIMS) can be used to determine elemental and

isotopic compositions and map them on samples at high resolution (House et al. 2000; De Gregorio et al. 2009). The molecular composition of microfossils has been assessed using laser pyrolysis gas chromatography—mass spectrometry (Arouri et al. 2000). Furthermore, several types of electron microscopy (transmission electron microscopy [TEM], scanning-transmission electron microscopy [STEM], and high-resolution transmission electron microscopy [HRTEM]) have been employed to examine the morphology and nanostructure of carbon (Ohtomo et al. 2014) and microfossils (Javaux et al. 2004, 2010). Fossil imaging is also performed using confocal laser microscopy (Schopf et al. 2006; Lepot et al. 2008). Synchrotron-based scanning-transmission X-ray microscopy (STXM) has been used in combination with X-ray absorption near-edge structure spectroscopy (XANES) for imaging, as well as elemental and molecular mapping (Boyce et al. 2002; De Gregorio et al. 2009).

These techniques represent important sources of new information in the reevaluation of older discoveries. This is the case for some of the fossils listed in Table 3.2, including microfossils from the Kromberg Formation and some of the microfossils reported from the Hooggenoeg Formation (Onverwacht Group) (Wacey 2009), as well as those from the Tumbiana Formation (Buick 2001). Moreover, in order to identify the oldest evidence of life, the age of the rock and syngenicity of the microfossils must be firmly established, for which thorough understanding of the geologic context of the locality is key. When microfossils from the ~3470 Ma Mount Ada Basalt were reported in 1983, these were the oldest convincing microfossils known at the time (Awramik et al. 1983). However, the precise collection locality remains unknown and has never been resampled, which casts reasonable doubts on the age of these fossils, as they could originate from the much younger Fortescue Group (Schopf 2006; Wacey 2009; Brasier and Wacey 2012).

3.4.4.1 The Apex Chert Debate

Microfossils from cherts in the Apex Basalt (Warrawoona Group, Australia) (Fig. 3.5a) were first reported by Schopf and Packer (1987) and later described by Schopf (1993). Eleven taxa of filamentous prokaryotes were circumscribed based on various aspects of their morphology. They were interpreted as bona fide Archean microfossils based on their frequent presence in the rocks, the early Archean age of the fossiliferous cherts, the occurrence of the fossils within clasts of the brecciated chert and absence from the surrounding matrix, and their morphological complexity and similarity to younger prokaryotes (Schopf 1993). Data from Laser-Raman analysis was later presented in support of biogenicity (Schopf et al. 2002), showing that the microfossils contained kerogen (geologically transformed organic matter). The Apex fossils were widely accepted as the oldest and best-preserved microbial fossils (Marshall et al. 2011) until Brasier et al. (2002) disputed their biogenicity, sparking a debate that has made them the most controversial Archean microfossils.

Arguments against the biogenicity of the Apex microfossils focus on the microfossils themselves and the carbonaceous material associated with them. Evidence inconsistent with biogenicity and suggesting the microfossils are instead artifacts includes (1) the fact that many of the microfossils branch extensively or are connected to crystals (like in ambient inclusion trails) when examined in multiple focal planes (Brasier et al. 2002), (2) the discovery of similar structures throughout the unit and in younger crosscutting features (Brasier et al. 2002; Marshall et al. 2011), and (3) a study demonstrating that comparable microfossil-like structures are actually quartz and hematite-filled fractures (Marshall et al. 2011). Extensive debate has centered on the nature of the carbonaceous material detected by Schopf et al. (2002). Also using Raman spectroscopy, Brasier and colleagues (2002) contended the carbonaceous material was abiogenic graphite and not kerogen. Subsequently, others have pointed out that Raman spectroscopy cannot be used to determine the origin of carbonaceous material or to distinguish different types of biogenic carbon (Pasteris and Wopenka 2003; Brasier et al. 2004; Marshall et al. 2010). An independent study using a suite of different methods (transmission electron microscopy, synchrotron-based scanning-transmission X-ray microscopy, and secondary ion mass spectrometry) concluded that biogenic origin is more likely, without entirely ruling out abiogenic origin (De Gregorio et al. 2009). However, a recent study using high-resolution transmission electron microscopy found four different populations of carbonaceous material in the Apex Chert. This indicates that the carbonaceous material was deposited at four separate times, most likely by postdepositional hydrothermal fluid flow, and that the carbonaceous material is not syngenetic with the original rock (Olcott Marshall et al. 2014). As the debate on the Apex Chert is currently ongoing without an end in sight (Wacey 2012), the search for traces of the earliest life should turn to other assemblages in the meanwhile.

3.4.4.2 The Isua and Akilia Debates

The oldest supracrustal rocks on Earth are located in rocks of the 3.81–3.7 Ga Isua Supracrustal Belt and 3.83 Ga Akilia Island of West Greenland (Lepland et al. 2002; Pons et al. 2011; Wacey 2009). The age and sedimentary origin of these rocks make them potential sources of the oldest biosignatures. However, intensive deformation and metamorphism of these units have presented substantial challenges in determining the validity of putative biomarkers and even the sedimentary nature of the protoliths (source rocks).

At Akilia, the discovery of ^{13}C-depleted graphite associated with apatite was interpreted as evidence of life earlier than 3.83 Ga (Mojzsis et al. 1996). This interpretation was later challenged, and a recent study has suggested an abiotic origin for the carbon, from fluid deposition during metamorphism (Lepland et al. 2011). Nonetheless, in light of debates over the sedimentary nature of the protolith, any claims of biogenic graphite from Akilia should be treated cautiously (Wacey 2009). The small outcrop containing the graphite in question was initially

interpreted as originating from sedimentary iron formations (McGregor and Mason 1977; Mojzsis et al. 1996; Papineau et al. 2010). However, a separate team revisited the outcrop and concluded that the protolith was igneous and not sedimentary, casting significant doubts on the biological origin of the graphite (Fedo and Whitehouse 2002). Yet another study presented evidence in support of a sedimentary origin (Dauphas et al. 2004) and the debate is ongoing, while the nature of the protolith remains unclear (Wacey 2009; Papineau et al. 2010).

The sedimentary origins of rocks in the Isua Supracrustal Belt are, in contrast, unequivocal (Van Zuilen et al. 2003). As the oldest confirmed sedimentary rocks on Earth, studies seeking biological signals within these strata have been ongoing since Moorbath and colleagues discovered the age of these rocks in 1973 (Moorbath et al. 1973; Appel et al. 2003). Putative microfossils, consisting of small, black spherical objects in quartz grains, were later discovered and named *Isuasphaera isua* (Pflug 1978a, b) (Fig. 3.5b, c). Their biogenicity, however, was subsequently contested and the structures reinterpreted as limonite-stained fluid inclusions or cavities (Bridgewater et al. 1981; Roedder 1981). Upon reexamination of the locality, an independent group concluded that the extreme stretching and deformation of the host rocks could not have preserved syndepositional spherical objects (Appel et al. 2003).

The presence of graphite in Isua rocks has been reported by a number of studies and has been proposed as evidence for biological activity (Schidlowski 1988; Mojzsis et al. 1996; Rosing 1999). Such claims are debated and a number of considerations have been raised regarding these graphite inclusions. Some authors have proposed the thermal decomposition of ferrous carbonate (siderite) as an abiotic mechanism for graphite formation at Isua (Van Zuilen et al. 2003). Others point out that many of the carbonate rocks at Isua, which contain some of the graphite in question, are not sedimentary in origin, and therefore graphite originating from such samples should be treated with caution (Lepland et al. 2002). Further, some of the carbon in the Isua rocks was found to originate from recent endolithic organisms infiltrating cracks and fissures in the rock. This indicates that studies using bulk-sampling methods may have detected carbon from these nonindigenous sources (Westall and Folk 2003). Although the evidence discussed above is inconsistent with an ancient biological origin for the Isua graphite, none of these studies have been able to firmly reject biogenicity.

In the latest twist, Ohtomo et al. (2014) analyzed graphite from black-gray schists at Isua and concluded that it represented traces of early life. Using Raman spectroscopy and geochemical analyses, the team determined that the schists formed from clastic marine sediments and that the carbonaceous material was present in the rock prior to prograde metamorphism. They further ruled out thermal degradation of ferrous carbonate as an abiotic formation mechanism, as proposed by others (i.e., Van Zuilen et al. 2003), and electron microscopy revealed structural characteristics consistent with biogenic graphite (Ohtomo et al. 2014). These results provide the most compelling evidence to date for the presence of life ca. 3.7 billion years ago. However, the contentious nature of biomarkers from Isua, the recent publication date of this study, and the brief life span of unchallenged claims in the

field of early biosignature research caution against immediate adoption of these findings which await scientific consensus and independent corroboration.

3.4.4.3 The Alan Hills 84001 Martian Meteorite Controversy

Although only indirectly relevant to questions about early life on Earth, the Alan Hills—ALH84001 Martian meteorite controversy is included here because of its relevance to issues of biogenicity and their implications for astrobiology. In 1996, McKay et al. argued for the presence of traces of Martian life in meteorite ALH 84001. The evidence they presented in support of their claim came from several types of data: (1) polycyclic aromatic hydrocarbons interpreted as diagenetic products of microorganisms and considered to be indigenous to the meteorite, (2) chemistry and mineral composition and structures suggestive of (microbial) biogenic products or biologic behavior, (3) magnetite particles similar to magnetofossils (magnetosomes) left by magnetotactic bacteria (Fig. 3.5d), and (4) submicron bacteriomorphs similar to nanobacteria (Folk 1993) and bacterial fossils.

McKay et al.'s (1996) claim that these ALH 84001 features represented evidence of ancient Martian life was met with a great deal of skepticism (Bradley et al. 1997 and others). Multiple research groups have verified the presence of polycyclic aromatic hydrocarbons in ALH84001 (Clemett et al. 1998; Steele et al. 2012). However, mechanisms for abiotic formation of polycyclic aromatic hydrocarbons have been documented (Zolotov and Shock 2000; McCollum 2003; Treiman 2003a). Additionally, Steele et al. (2012) demonstrated that abiotically formed organic compounds are present on multiple Martian meteorites (including ALH84001) and that these compounds were not contaminants from Earth. These findings are inconsistent with the original claims of biogenic polycyclic aromatic hydrocarbons in ALH84001. The claim that the mineral composition—magnetite, iron sulfide, and siderite—is indicative of life and its byproducts has also been scrutinized. This suite of minerals is well known in low-temperature, aqueous systems (Anders 1996; Golden et al. 2000) and has not been shown to be exclusively indicative of biologic behavior (Treiman 2003b).

There is disagreement over how similar the magnetite grains in ALH84001 are to the magnetosomes of Earth bacteria (such as the marine magnetotactic vibrio *Magnetovibrio blakemorei* strain MV-1) (Clemett et al. 2002; Treiman 2003b). While some authors point to close similarity (Thomas-Keprta et al. 2001), others have documented differences in morphology between magnetosomes of MV-1 and other bacterial strains, and the magnetite crystals in ALH84001 (Buseck et al. 2001; Golden et al. 2004). Golden et al. (2004) demonstrated that the morphology of ALH84001 magnetite crystals is replicated abiogenically and that the most common crystal morphology for biogenic magnetite is different from that in both ALH84001 and abiogenic magnetite, concluding that rather than representing a compelling biosignature, the morphology of the ALH84001 magnetite crystals is consistent with an abiogenic origin. Finally, the submicron bacteriomorphs from

ALH84001 are largely discounted as biogenic structures (Treiman 2003b) based on the fact that at < 100 nm they are just below the size of the smallest free-living prokaryotes (Gorbushina and Krumbein 2000) and that a number of abiotic mechanisms have been proposed for the formation of such structures, including mineral precipitation from solution (Bradley et al. 1998; Kirkland et al. 1999; Vecht and Ireland 2000; Grasby 2003).

Overall it is the inability to reject the null hypothesis of abiotic formation (Brasier and Wacey 2012) that does not allow the features described in ALH84001 to be considered biogenic (Treiman 2003b). Since the polycyclic aromatic hydrocarbons have been shown to be abiotic (Steele et al. 2012), the mineral composition of the carbonate globules is not a definitive indicator of biological activity, and both the magnetite grains and nano-bacteriomorphs shaped could have formed abiotically, it is unlikely that ALH84001 contains biogenic material. However, it will be interesting to see the results of the application of Gehring et al.'s (2011) method of distinguishing between bacterial magnetosomes and abiogenic magnetite to the ALH84001 magnetite grains.

3.4.5 Oldest Traces of Life

In the context of the findings summarized above, it is clear that there is a large body of evidence suggesting that life has existed since the Paleoarchean (3600–3200 Ma), despite the questionable or equivocal status of some of these fossils (Knoll 2012). Although not all stromatolite and other microbially induced structure occurrences are included in Table 3.2, it is worth noting that the stratigraphic extent of stromatolites, MISS, and microborings mirrors closely that of microfossils (e.g., Hofmann 2000; Awramik and Grey 2005; Brasier et al. 2006; Fliegel et al. 2010). While the oldest reported putative microfossils originate from the ~3480 Ma Dresser Formation (Australia) (Fig. 3.6a), their biogenicity remains equivocal. The most convincing of these microfossils are carbonaceous filaments reported by Ueno et al. (2001a, b), but their biogenic interpretation based on morphology and stable carbon isotopes awaits further verification (Wacey 2009). Microbial presence in the Dresser Formation is also supported by putative stromatolites (Buick et al. 1981; Awramik and Grey 2005; Van Kranendonk 2006; Wacey 2009) (Fig. 3.6b). Irrespective of the verdict on the microfossils and stromatolites, unequivocal MISS described by Noffke et al. (2013a) in the Dresser Formation demonstrate presence of microbial life very close to 3.5 Ga ago. The Dresser Formation MISS formed in shallow-water, low-energy evaporitic coastal environments (Buick and Dunlop 1990; Noffke et al. 2013a).

Convincing microfossils, only slightly younger than the Dresser Formation fossils, are known from the ~3466 Ma Kitty's Gap Chert (Warrawoona Group) (Westall et al. 2006) (Fig. 3.7a, b); the ~3450 Ma Hooggenoeg Formation (Onverwacht Group), particularly those reported by Glikson et al. (2008) (Fig. 3.7c, e, f); and the ~3426–3350 Strelley Pool Formation (Kelly Group)

(Wacey et al. 2011a; Sugitani et al. 2013) (Fig. 3.8a–e). Dresser Formation microfossils notwithstanding, the Kitty's Gap Chert, and Hooggenoeg Formation host the oldest unequivocal microbial body fossils known to date. Although slightly younger, the Strelley Pool Formation microfossils provide very good evidence for life corroborated by independent studies, with good geochemical evidence supporting their biogenicity, and the presence of other types of fossils within the formation, including microborings and stromatolites (Hofmann et al. 1999; Brasier et al. 2006; Allwood et al. 2007; Wacey et al. 2006, 2011a, b; Sugitani et al. 2013) (Fig. 3.8f–h). Aside from the Strelley Pool Formation microborings, which are hosted in sedimentary rocks and the oldest known to date in the fossil record, the oldest microborings in volcanic glass have been reported from 3.34 Ga in the Hooggenoeg Formation (Furnes et al. 2004; Fliegel et al. 2010; McLoughlin et al. 2012) (Fig. 3.7d, g) and from the 3.42–3.31 Ga Euro Basalt of the Kelly Group (Banerjee et al. 2007) (Fig. 3.8i).

3.5 Microbial Eukaryotes: Recognition and Early Fossil Record

Irrespective of the detailed circumstances of their evolution, as proposed by several competing hypotheses, eukaryotes arose from prokaryotic stock (Knoll and Bambach 2000; Lang and Burger 2012). Whereas in the case of the earliest prokaryotes proof of biogenicity is one of the biggest hurdles, in early eukaryotes their very eukaryotic affinities are challenging to ascertain. Because of their prokaryotic origins, it is to be expected that early eukaryotes were unicellular organisms and that they will be difficult to distinguish from prokaryotes. Indeed, the earliest bona fide eukaryotes and even older putative eukaryotes are unicellular dispersed microfossils (Javaux et al. 2010; Knoll 2014). From the perspective of the paleontologist, most early eukaryotes fall in the category of acritarchs (e.g., Figs. 3.9a–d, 3.10a–d, g, 3.11a, c), an artificial group of organic-walled unicellular microfossils of large size (50 μm or more) and uncertain biological affinities which comprise the most abundant and widely distributed record of Proterozoic protists (Knoll et al. 2006; Buick 2010).

3.5.1 Recognizing Early Eukaryotes

Known from dispersed unicellular microfossils in Proterozoic rocks (and possibly going as far back in time as the Archean; Javaux et al. 2010; Knoll et al. 2006; Knoll 2014), early eukaryotes have to pass the same tests of indigenousness and syngenicity as their prokaryotic counterparts (e.g., Bengtson et al. 2009; Javaux et al. 2010), in addition to satisfying eukaryote-specific criteria. Putative eukaryotes

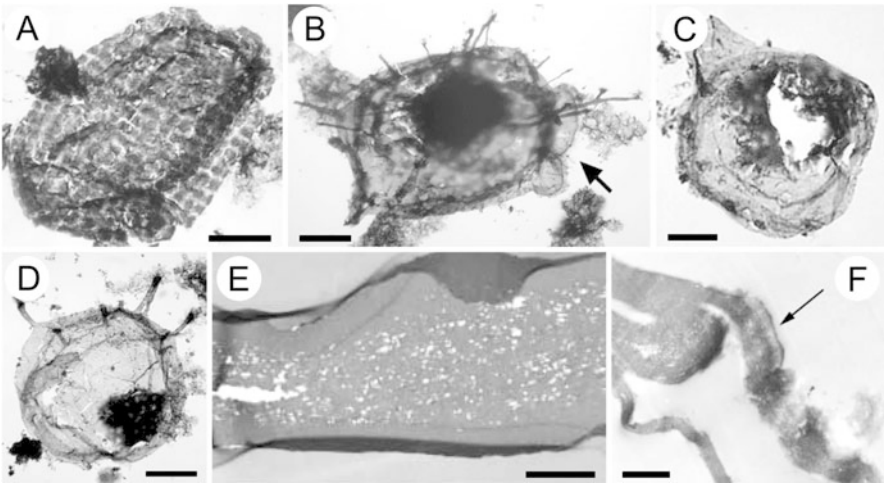

Fig. 3.9 Recognizing early unicellular eukaryotes—acritarchs. (**a**) *Satka favosa*, showing surface ornamentation (cell wall consisting of interlocking panels), Mesoproterozoic Roper Group, Australia. (**b**) *Tappania plana*, showing asymmetrically distributed long processes (some of which are branched) protruding from the cell wall and bulbous protrusions (arrow) potentially indicative of vegetative reproduction by "budding," Roper Group. (**c**) *Tappania plana*, showing possible excystment structure at the apex of a necklike extension (at *top left*), Roper group. (**d**) *Tappania plana*, showing asymmetrically distributed long cell surface processes, Roper Group. (**e**) *Leiosphaeridia jacutica*, showing complex cell wall structure: two electron-dense, homogeneous layers that sandwich a thick central layer with electron-dense, porous texture, Roper Group. (**f**) *Leiosphaeridia crassa*, showing complex cell wall organization consisting of as many as four structurally distinct layers preserved at places (*arrow*), Roper Group. Scale bars: (**a**) 40 μm, (**b**) 35 μm, (**c**) 20 μm, (**d**) 35 μm, (**e**) 1 μm, (**f**) 1.6 μm. Credits—images used with permission from (**a**), (**b**), and (**d**) Nature Publishing Group (Javaux et al. 2001). (**c**), (**e**), and (**f**) Blackwell Publishing Ltd. (Javaux et al. 2004)

have generally been recognized based on the fact that they display complexity unknown in prokaryotes (Schopf and Klein 1992; Javaux 2007). This is expressed in the interrelated abilities to synthesize complex polymers and produce complex structures (e.g., Javaux et al. 2004; Javaux 2007). The production of complex polymers is reflected in the recalcitrant nature of cell walls or their ability to withstand acid maceration, a feature often considered important in distinguishing taxonomic affinities at the domain level (e.g., Javaux et al. 2004; Knoll et al. 2006; Javaux 2007). In turn, recalcitrant cell walls preserve complex cell surface structures. Aside from these, large size (> ca. 50 μm) is often treated as indicative of eukaryotic affinities (e.g., Schopf and Klein 1992). However, size is not diagnostic by itself, as large bacteria and cyanobacterial sheaths are known (e.g., Waterbury and Stanier 1978; Schulz et al. 1999), as well as eukaryotes smaller than 1 μm in diameter (e.g., Courties et al. 1994).

The hallmark of complex cell structure, cellular organelles, has yet to be unequivocally substantiated in the early fossil record. Early reports of acritarchs

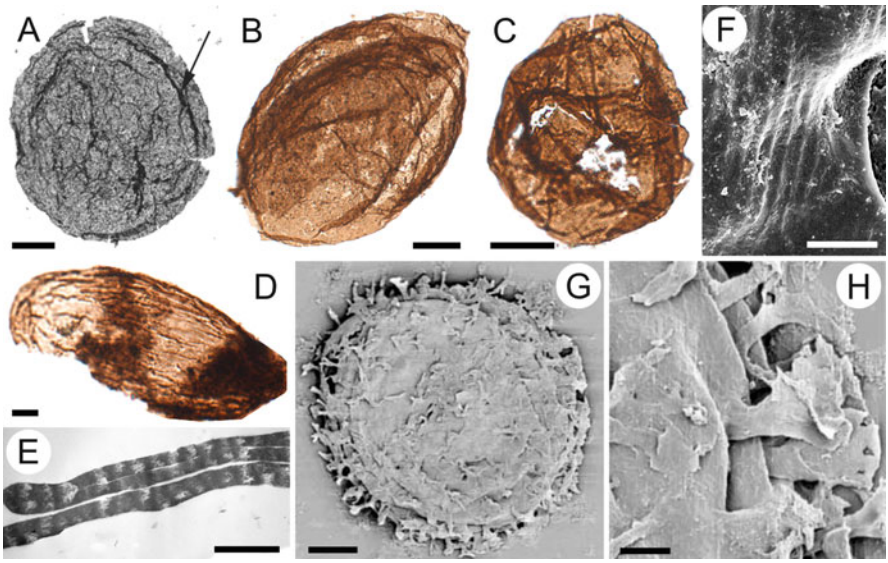

Fig. 3.10 Earliest eukaryotic fossils–acritarchs. (**a**) Microfossil representing a putative eukaryote, showing surface covered with very fine granules and concentric folds, Archean Moodies Group, South Africa. (**b**) Ellipsoidal acritarch with a medial split possibly indicating excystment. Paleoproterozoic Changzhougou Formation, China. (**c**) Acritarch with multilayered wall structure observed as sequential differences in contrast and brightness visible in successive planes of focus, Changzhougou Formation. (**d**) Ellipsoidal acritarch displaying cell wall ornamentation (longitudinal striations), Changzhougou Formation. (**e**) Section through acritarch wall showing ultrastructure that consists of alternating electron-dense and electron-tenuous bands spaced at 0.2–0.3 μm, Paleoproterozoic Changlinggou Formation, China. (**f**) Striated ornamentation of inner surface of acritarch wall, consisting of ridges spaced at 0.2–0.3 μm, Changlinggou Formation. (**g**) *Shuiyousphaeridium macroreticulatum*, acritarch showing flaring furcating cell wall processes; not very conspicuous, a reticulated pattern also characterizes the cell wall of this acritarch, Mesoproterozoic Ruyang Group, China. (**h**) Detail of (**g**). Scale bars: (**a**) 50 μm, (**b**) 20 μm, (**c**) and (**d**) 20 μm, (**e**) 1 μm, (**f**) 1 μm, (**g**) 50 μm, (**h**) 10 μm. Credits—images used with permission from (**a**) Nature Publishing Group (Javaux et al. 2010). (**b**), (**c**), and (**d**) Elsevier Science Publishers (Lamb et al. 2009). (**e**) and (**f**) Elsevier Science Publishers (Peng et al. 2009). (**g**) and (**f**) Blackwell Publishing Ltd. (Javaux et al. 2004)

with internal organelle-like structures have originated from the 800 Ma Bitter Springs Formation (Australia) (Schopf 1968; Oehler 1976, 1977). Initially interpreted as organelles, pyrenoids or pyrenoid-like bodies, their nature was questioned both at the time of publication (e.g., Knoll and Barghoorn 1975) and recently (Pang et al. 2013). Experimental results indicate that some of the "cells" preserved in the Bitter Springs Formation represent prokaryotic mucilaginous sheaths containing collapsed and condensed cell contents (reported as "pyrenoids") (Pang et al. 2013). Nevertheless, based on the same set of experiments, Pang et al. (2013) concluded that the internally preserved structures of some microfossils in an older rock unit, the 1.60–1.25 Ga Ruyang Group (China), represent in vivo

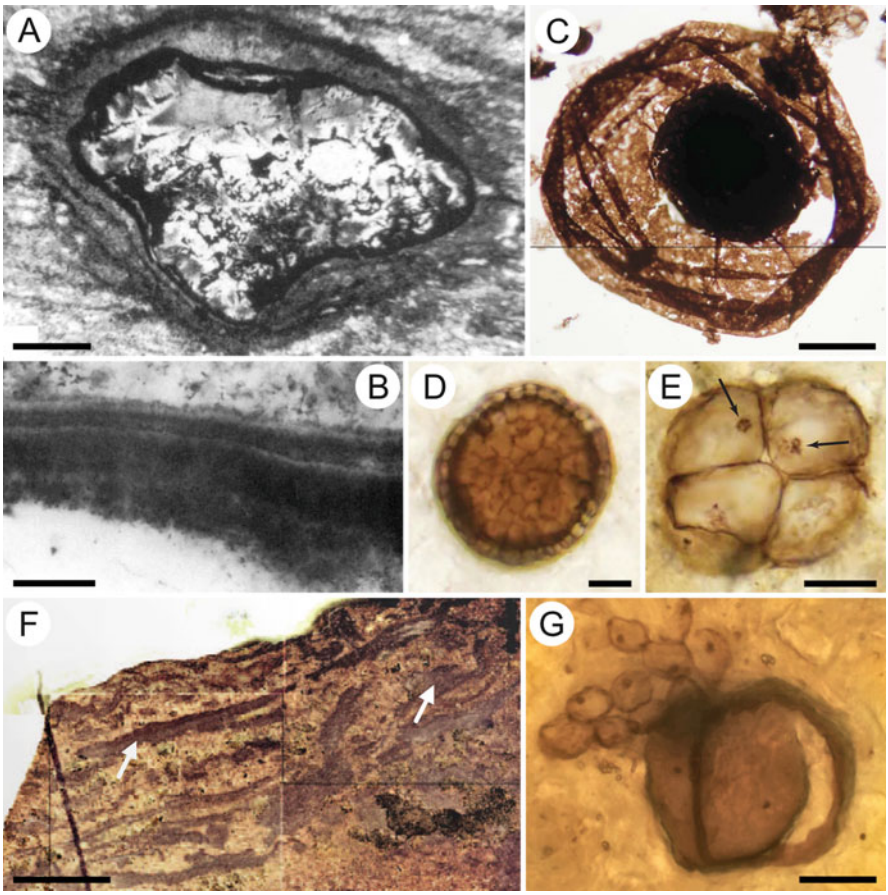

Fig. 3.11 Early eukaryotic fossils. (**a**) *Crassicorium pendjariensis* acritarch within chert nodule, showing internal exfoliation of wall lamellae, Mesoproterozoic Bangemall Group, Australia. (**b**) *Crassicorium pendjariensis*—detail of multilayered wall structure, Bangemall Group. (**c**) Large acritarch with a dense central body (at *center*), basal Neoproterozoic Diabaig Formation, Torridon Group, Scotland. (**d**) Spherical ball of cells enclosed within a complex wall (thin section from phosphatic nodule), Diabaig Formation. (**e**) Cell cluster exhibiting mutually appressed cells with internal "spots" (*arrowed*) (thin section from phosphatic nodule), Diabaig Formation. (**f**) Siltstone containing microbially induced sedimentary structures (roll-up structures, dark-toned, at arrows); this sample also yielded microfossils, composite image, Mesoproterozoic Dripping Spring Quartzite, Apache Group, Arizona. (**g**) Complex microfossil in phosphatic nodule, showing the emergence of an adjoined cluster of at least ten light-walled ellipsoidal coccoids from a single point of a larger, dark-walled coccoid structure, basal Neoproterozoic Cailleach Head Formation, Torridon Group, Scotland. Scale bars: (**a**) 200 μm, (**b**) 20 μm, (**c**) 25 μm, (**d**) 5 μm, (**e**) 10 μm, (**f**) 1 cm, (**g**) 10 μm. Credits—images used with permission from (**a**) and (**b**). The Paleontological Society (Buick and Knoll 1999). (**c**), (**d**), and (**e**) Nature Publishing Group (Strother et al. 2011). (**f**) Society for Sedimentary Geology (Beraldi-Campesi et al. 2014). (**g**) Elsevier Science Publishers (Battison and Brasier 2012)

protoplasm condensation corresponding to an encystment stage common in some algae, thus supporting their eukaryotic affinities.

3.5.1.1 Morphological Criteria

Dispersed unicellular microfossils are most compellingly recognized as eukaryotes based on morphological criteria (Javaux et al. 2003) although geochemical data on biomarkers have also been used, sometimes exclusively (e.g., Brocks et al. 1999), in support of eukaryote presence. In terms of morphology, three categories of features are considered diagnostic of eukaryotic nature, especially when co-occurring, in studies of microfossils (Javaux et al. 2003): complex cell surface features, excystment structures, and complex wall organization.

1. *Complex cell surface features*: these include ornamentation (Figs. 3.9a and 3.10a, d, f) and processes protruding from the cell surface (Figs. 3.9b, d and 3.10 g, h). The use of complex surface features to recognize eukaryotic cells stems from Cavalier-Smith's (2002) reasoning that production of such surface features would require that the cell possesses an endomembrane system and cytoskeleton, which are fundamental components of the eukaryotic cell. Javaux et al. (2004) point out that while prokaryotic organisms can synthesize both cell wall ornament and preservable structures, wall ornamentation rarely occurs on the size scale observed in Precambrian candidate eukaryotes and is seldom found on preservable structures.

   Regular polygonal patterns occurring at the micron scale are seen on the surfaces of Proterozoic eukaryotic microfossils (Javaux et al. 2003, 2004). Although many prokaryotes possess oblique, square, or hexagonal crystalline arrays on their surfaces, these shapes occur at the nanometer scale. Furthermore, their easy removability by chemicals in culture studies suggests that they are unlikely to preserve or to survive the acid maceration processes used to extract dispersed carbonaceous microfossils from the rock (Javaux et al. 2003). Other examples of surface ornamentation include striations and lineations (Fig. 3.10d), chagrinate (covered with very fine granules) surfaces (Fig. 3.10a), cruciform structures, or internal (inner wall surface) striations (Fig. 3.10f) (Javaux et al. 2001, 2004; Butterfield 2009). Sometimes, larger bulbous protrusions suggestive of vegetative reproduction through budding are present, as in *Tappania plana* (Javaux et al. 2001, 2004) (Fig. 3.9b).

   Cell surface processes documented in early eukaryotes have varied morphologies, from spiny or thin and unbranched to bulbous or branched (Javaux et al. 2003). Some can be long (e.g., up to 60 μm in *Tappania plana* of the 1.50–1.45 Ga Roper Group, Australia; Javaux et al. 2001) (Fig. 3.9b, d), while others are septate, branched (Fig. 3.9b and 3.10 g, h), and anastomosing (e.g., the putative basal fungus "*Tappania*" from the 850 to 750 Ma Wynniatt Formation, Canada; Butterfield 2009). Processes with irregular length, exhibiting heteromorphism within one cell or asymmetric distribution on the cell surface (Javaux

et al. 2001; Knoll et al. 2006) (Fig. 3.9b, d), can only be accounted for by active growth and remodeling of the cell which requires a dynamic cytoskeletal architecture and regulatory networks that characterize eukaryotes (Javaux et al. 2001, 2004).

2. *Excystment structures*: these are openings in the walls of microfossils that are thought to be produced by liberation of internal vegetative cells from the wall of a resting stage, another eukaryotic feature (Fig. 3.9c and 3.10b). Commonly recognized in Phanerozoic microfossils, excystment structures are much more equivocal in Precambrian fossils (Javaux et al. 2003). For instance, in the Roper Group fossils, at least two taxa show possible excystment structures. Because these structures are perforations or splits that run some length of the cell wall, they are not regularly occurring (there are few occurrences in the population), and the microfossils generally lack evidence of vegetative cells having been present, interpretation as degradational ruptures or breaks in the microfossil cell wall seems equally likely. More complex structures, such as those seen in *Tappania plana* which possesses a slit at the apex of a necklike extension (Javaux et al. 2003) (Fig. 3.9c), are more credible as eukaryotic excystment structures.
3. *Complex cell wall organization*: the structural complexity of eukaryotic cell walls can be preserved in microfossils and distinguished from acetolysis-resistant structures formed by bacteria (Javaux et al. 2003). Thus, ultrastructural features (Figs. 3.9e, f, 3.10e, and 3.11b) can provide evidence for eukaryotic affinities, even in microfossils in which morphology is not diagnostic (Javaux et al. 2004). These authors undertook a careful TEM study of cell wall ultrastructure demonstrating that while some eukaryotes (recognized based on morphological characters observed in light microscopy and SEM) share nondiagnostic wall ultrastructures consisting of single, homogeneous, electron-dense layers of variable thickness, in others cell wall organization is more complex (Fig. 3.9e, f). In the latter microfossils, some of which do not display other features indicative of eukaryotic affinities, cell walls exhibit at least four distinct types of structures characterized by multiple layers of different density and organization (e.g., dense, porous, laminar, fibrous) (Javaux et al. 2004) (Fig. 3.9f).

   Discussing the multilayered structure of *Leiosphaeridia crassa* from the Roper Group, Javaux et al. (2004) point out that such structures occur in the acetolysis-resistant walls of many green algae. Several authors have discussed similarities between the cell wall structure of different early eukaryotes and those of extant chlorococcalean green algae (Arouri et al. 1999), prasinophyte green algae (Loeblich 1970), or volvocalean green algae (Moczydlowska and Willman 2009). Javaux et al. (2004) also discuss the possibility that acetolysis-resistant walls structurally similar to those described in the early putative eukaryotes are produced by prokaryotic organisms; this seems not to be the case, as few bacteria make spores with comparable size, surface ornamentation, and preservation potential. For example, myxobacteria (which are mostly terrestrial) produce spore-enclosing structures (sporangioles) up to 50 μm in diameter, but these have smooth walls and unknown chemical composition and are

not known to preserve in sediments. Actinobacteria have spores up to 3 μm in diameter that can be ornamented, but their surface ornaments are very small, proteinaceous, and are unlikely to survive fossilization processes. In contrast, the extracellular polysaccharide sheaths that envelop coccoidal cyanobacterial colonies can exceed 100 μm in size and are commonly fossilized (Bartley 1996); however, these envelopes are smooth walled, and their ultrastructure consists of fibrous layers distinct from those of eukaryotes (Javaux et al. 2004).

3.5.1.2 Geochemistry: Hydrocarbon Biomarkers

Steranes are molecular fossils representing the geologically stable derivatives of sterols, which are eukaryote-specific compounds (Summons and Lincoln 2012). As a result, steranes in the rock record have been used as biomarkers for eukaryote presence. The oldest claims for eukaryotes are based exclusively on the presence of steranes, unaccompanied by body fossils, in Archean rocks dated at 2.72–2.60 Ma in Australia (Fortescue and Hamersley Groups; Brocks et al. 1999; Brocks et al. 2003a, b) and at 2.67–2.46 Ga in South Africa (Transvaal Supergroup; Waldbauer et al. 2009). However, when not backed by microfossil evidence, the use of hydrocarbon biomarkers as evidence for eukaryotes is contentious for several reasons (Buick 2010; Knoll 2014). One of the reasons is that sterol biosynthesis requires molecular oxygen, which was not present in the Archean, except maybe for rare, very localized "oxygen oases" produced by photosynthetic cyanobacteria in microbial mats (Knoll 2014). Another reason is that although very rare, some prokaryotic organisms are known to synthesize sterols; this reason is relatively easy to dismiss as known prokaryotic sterols are simple and, thus, could not have generated the complex steranes that have been reported from Archean rocks (Knoll 2014). The most contentious issues are those of indigenousness and syngenicity, because hydrocarbons are known to migrate through rock over significant distances and thicknesses from their layers of origin (geological contaminants) or can be introduced in drill core samples by the drilling process (modern contaminants) (Knoll 2014). Indeed, based on very different carbon isotope ratios measured in different organic fractions of the same rocks, Rasmussen et al. (2008) showed that the biomarkers reported by Brocks et al. (1999) are not indigenous. To date, the oldest unequivocally dated steranes come from >2.2 Ga fluid inclusions trapped by metamorphic processes in closed systems, and therefore contamination-proof, in the Matinenda Formation (Canada; Dutkiewicz et al. 2006; George et al. 2008).

3.5.2 Oldest Evidence for Eukaryotes

As pointed out by Knoll (2014), when it comes to the oldest evidence for eukaryotes, there is no clear-cut age limit—rather, the geological record presents us with evidence that falls along a sliding scale of certainty that ranges from bona fide,

confidently interpreted fossils down to around 1.8–2.0 Ga ago to increasingly more equivocal fossils or chemical biosignatures in older rocks. At least ten rock units around the world have yielded Paleoproterozoic and Mesoproterozoic acritarchs of eukaryotic affinities to date (Table 3.3); the morphological diversity of acritarchs in most of these units has been carefully summarized by Knoll et al. (2006). Some of these units also host putative multicellular eukaryotes.

3.5.2.1 Acritarchs

The oldest acritarchs interpreted with reasonable confidence as eukaryotes have been reported from the late Paleoproterozoic Changzhougou Formation and the overlying Changlinggou Formation (Chang Cheng Group, China; Lamb et al. 2009; Peng et al. 2009) dated between 1.80 and 1.65 Ga (Table 3.3) (Fig. 3.10b–f). They include several distinct forms with complex cell wall structure (Fig. 3.10c, e), wall ornamentation (Fig. 3.10d, f), or putative excystment structures (Fig. 3.10b), indicating that eukaryotes had already started diversifying before the end of the Paleoproterozoic (Lamb et al. 2009). The ca. 1.65 Ga Mallapunyah Formation (Australia) has also yielded acritarchs with ornamented cell walls interpreted as eukaryotes (Javaux et al. 2004). In the Mesoproterozoic, several rock units dated between 1.6 and 1.1 Ga host diverse eukaryotic acritarch assemblages—the Ruyang Group in China (Xiao et al. 1997; Yin 1997; Javaux et al. 2004) (Fig. 3.10g, h), the Sarda and Avadh Formations in India (Knoll et al. 2006), and the Bangemall Group in Australia (Buick and Knoll 1999) (Fig. 3.11a, b). Detailed studies of both the morphology and the distribution of eukaryotic acritarchs in the Roper Group of Australia (Fig. 3.9a–f) have revealed high morphological diversity and suggest niche partition among early eukaryotes 1.50–1.45 Ga ago, at the beginning of the Mesoproterozoic (Javaux et al. 2001, 2003, 2004). Another early Mesoproterozoic unit containing diverse acritarchs is the Chamberlain Shale of Montana (1.47–1.42 Ga; Horodyski 1980). Considerable eukaryotic acritarch diversity has been reported from the middle and late Mesoproterozoic Thule Supergroup (1.3–1.2 Ga; Greenland), which includes several fossiliferous subunits (Samuelsson et al. 1999), and the Lakhanda Group (1.1–1.0 Ga; Siberia; Knoll et al. 2006).

The oldest evidence for eukaryotic life on land may be preserved in the ca. 1.2 Ga Dripping Spring Quartzite (Apache Group, Arizona; Beraldi-Campesi et al. 2014) (Fig. 3.11f). Here, diverse and abundant MISS preserved on paleosurfaces that display desiccation features and bear strong morphological resemblance to modern terrestrial biocrusts co-occur with eukaryote- and prokaryote-like microfossils in river floodplain deposits. These have been interpreted as evidence that microbial communities, including eukaryotic components, were already adapted to live in dry habitats and formed biological soil crust-like communities long before the advent of land plants (Beraldi-Campesi et al. 2014). Previously, the ca. 1 Ga Torridon Group in Scotland was considered to provide the oldest evidence for eukaryotic life on continents represented by

Table 3.3 Mesoproterozoic and older eukaryotic fossil record

Age (Ga)	Rock unit	Location	Eukaryotic fossils	References
~2.1	Negaunee Iron Formation	USA (Michigan)	*Grypania* macrofossils	Han and Runnegar (1992)
1.80–1.65	Changzhougou and Chuanlinggou Formation	China	Acritarchs, multicellular filaments	Yan and Liu (1993), Knoll et al. (2006), Lamb et al. (2009), Peng et al. (2009)
1.7–1.6	Lower Vindhyan Supergroup	India	*Grypania*-like macrofossils, multicellular filaments	Han and Runnegar (1992), Bengtson et al. (2009)
~1.65	Mallapunyah Formation	Australia	Acritarchs	Javaux et al. (2004); Knoll et al. (2006)
1.60–1.25	Ruyang Group	China	Acritarchs	Xiao et al. (1997), Yin (1997), Knoll et al. (2006)
1.6–1.0	Sarda and Avadh Formation	India	Acritarchs	Knoll et al. (2006)
1.6–1.0	Bangemall Group	Australia	Acritarchs and *Horodyskia* macrofossils	Grey and Williams (1990), Buick and Knoll (1999), Grey et al. (2010), Knoll et al. (2006)
1.50–1.45	Roper Group	Australia	Acritarchs	Javaux et al. (2001, 2003, 2004)
1.47–1.42	Chamberlain Shale	USA (Montana)	Acritarchs	Horodyski (1980), Knoll et al. (2006)
~1.4	Gaoyuzhuang Formation	China	*Grypania* macrofossils	Walter et al. (1990)
1.4–1.3	Greyson Shale/ Appekunny Argillite	USA (Montana)	*Grypania* and *Horodyskia* macrofossils	Walter et al. (1976, 1990), Horodyski (1982)
1.3–1.2	Thule Supergroup	Greenland	Acritarchs	Samuelsson et al. (1999)
~1.2	Hunting Formation	Canada (Somerset Island)	*Bangiomorpha* and two other putative multicellular eukaryotes	Butterfield (2000, 2001)
~1.2	Dripping Spring Quartzite	USA (Arizona)	Putative eukaryote microfossils	Beraldi-Campesi et al. (2014)
1.1–1.0	Lakhanda Group	Russia (Siberia)	Acritarchs and diverse macrofossils	Knoll et al. (2006)
~1.0	Torridon Group	Scotland	Acritarchs (lacustrine environment)	Strother et al. (2011), Battison and Brasier (2012)

diverse acritarchs described from lacustrine deposits (Strother et al. 2011; Battison and Brasier 2012) (Fig. 3.11c–e, g).

3.5.2.2 Macrofossils

Enigmatic macrofossils reported from the Paleoproterozoic and Mesoproterozoic may also represent eukaryotic organisms. The most common of these are *Grypania* and *Horodyskia*. Their regular morphology and macroscopic size suggest a eukaryotic origin (Knoll 2014). *Grypania* occurs as strap-shaped compressions of originally cylindrical organisms that form coils up to 24 mm across (Walter et al. 1976, 1990) and has been interpreted as a sessile algal eukaryote that was most likely multinucleate (coenocytic or multicellular) (Han and Runnegar 1992). *Horodyskia* fossils consist of 1–4 mm spheroidal (or sometimes conical, ovoid or rectangular) bodies connected by thin threads to form uniseriate structures (Yochelson and Fedonkin 2000). Eukaryotic affinity of *Horodyskia* is considered probable, but not beyond debate (Knoll et al. 2006). The oldest *Grypania* are known from mid-Paleoproterozoic rocks older than the earliest eukaryotic acritarchs (2.1 Ga; Negaunee Iron Formation, Michigan; Han and Runnegar 1992). The genus is also known from several younger rock units which include the ca. 1.4 Ga Gaoyuzhuang Formation in China (Walter et al. 1990), the 1.4–1.3 Ga Greyson Shale (Appekunny Argillite) of Montana (Walter et al. 1976, 1990; Horodyski 1982), and possibly from the 1.7–1.6 Ga lower Vindhyan Supergroup in India (Rohtas Formation, where it has been described as *Katnia*; Tandon and Kumar 1977; Han and Runnegar 1992). The oldest *Horodyskia* fossils have been reported from the Mesoproterozoic Bangemall Group in Australia (Grey and Williams 1990) but the genus is also known from the Greyson Shale of Montana (Horodyski 1982).

Tubular objects 100–180 μm in diameter with walls replaced by apatite are preserved in the lower Vindhyan Supergroup of India (Tirohan Dolomite; Bengtson et al. 2009). These fossils date from around the Paleoproterozoic-Mesoproterozoic boundary (1.7–1.6 Ga) and display regular annulation (shallow transverse grooves) on the outer surface corresponding to internal septa. Bengtson et al. (2009) interpret these fossils as filamentous algae (multicellular eukaryotes). Similar tubular or filamentous fossils are described by Yan and Liu (1993) from the late Paleoproterozoic in the 1.8–1.65 Ga Chang Cheng Group (China) and by Butterfield (2001) from the mid-Mesoproterozoic in the 1.2 Ga Hunting Formation (Somerset Island, arctic Canada). These fossils are associated with two other multicellular types: flat, layered units with internal differentiation and a stratified cellular structure (compared to phylloid algae; Butterfield 2001) and *Bangiomorpha*, the first unequivocal occurrence of complex multicellularity in the fossil record, the oldest reported occurrence of sexual reproduction, and the oldest record for an extant phylum (Rhodophyta, the red algae) and an extant family (Bangiaceae) (Butterfield 2000). Finally, in the late Mesoproterozoic, the Lakhanda Group hosts, along with diverse acritarchs, larger eukaryotic fossils compared to xanthophyte algae,

fungi, and metazoans (Knoll et al. 2006; Hermann and Podkovyrov 2006; German and Podkovyrov 2009).

3.5.2.3 Eukaryotes in the Archean?

Some microfossils older than the Chang Cheng Group biota have been discussed as potential eukaryotes. The most prominent case is that of the spheroidal microfossils described as *Eosphaera* by Barghoorn and Tyler (1965) from a diverse biota in the Gunflint Iron Formation of Ontario (ca. 1.88 Ga; Schneider et al. 2002). *Eosphaera* fossils are small (up to 15 μm) and comprised of two concentric spherical envelopes enclosing up to 15 small spheroidal tubercles in the circular space between the two envelopes. Although *Eosphaera* has been compared to volvocalean green algae (Kazmierczak 1979), currently most authors agree that the Gunflint microfossil assemblage is entirely prokaryotic (e.g., Awramik and Barghoorn 1977) and that *Eosphaera* does not preserve sufficient detail in support of eukaryotic affinities (Knoll 1992). However, other lines of evidence indicate that eukaryotic life might have originated before the late Paleoproterozoic and even as early as the Archean (older than 2.5 Ga).

The shales of the Francevillian B Formation of Gabon, dated at 2.1 Ga, have yielded pyritized macrofossils consisting of elongated to isodiametric flattened specimens up to 12 cm in size, with a thicker central area and thinner radially patterned, undulate, and lobed margins (El Albani et al. 2010). The morphology of the fossils has been interpreted as reflecting growth that requires cell-to-cell signaling and coordinated growth responses indicative of well-integrated colonial organization or multicellular life in the early Paleoproterozoic, an interpretation bolstered by the detection of steranes in the same layers (El Albani et al. 2010).

Both the Gabonese macrofossils and *Grypania*—if the latter indeed represents a multicellular (or multinucleate) eukaryote—with its oldest occurrence at 2.1 Ga (Han and Runnegar 1992), predate the oldest unicellular eukaryotes (acritarchs) of the Chang Cheng Group (Lamb et al. 2009; Peng et al. 2009) by at least 300 million years. Assuming that unicellular eukaryotes evolved before multicellular forms, this implies that the prototypical unicellular eukaryote evolved prior to 2.1 Ga and we should expect to find eukaryotic acritarchs older than that age. Javaux et al. (2010) have reported organic-walled microfossils from shallow-marine deposits in the 3.2 Ga Moodies Group of South Africa. These microfossils are older than the oldest claims for sterane biomarkers (2.7–2.5 Ga; Brocks et al. 1999; Waldbauer et al. 2009). They are the oldest and largest Archean organic-walled microfossils reported to date (Javaux et al. 2010) and co-occur with microbially induced sedimentary structures (Noffke et al. 2006). The fossils display features consistent with eukaryotic affinities, such as good organic preservation, which is indicative of cell walls containing recalcitrant polymers and large sizes (ca. 30–300 μm) (Fig. 3.10a). These microfossils could, in principle, be eukaryotic, but their lack of cell surface ornamentation and their simple cell wall structure also make them easily comparable to the extracellular envelopes of some bacteria, thus

precluding unequivocal interpretation as eukaryotes (Knoll 2014). It will be interesting to see if geochemical studies of the Moodies Group (not published to date) ascertain the presence of sterane biomarkers.

3.5.3 *Salient Patterns in the Early Eukaryotic Fossil Record*

The oldest bona fide unicellular eukaryotes are known from 1.80 to 1.65 Ga (mid-Paleoproterozoic) rocks, but the fossil record provides strong evidence that organisms capable of producing macroscopic bodies by growth processes that required coordinated responses, whether in a coenocyte or an aggregation of cells, had evolved by 2.1 Ga. This mode of development is not known in prokaryotes but is consistent with coenocytic or multicellular organization in eukaryotes, in which multicellularity has been achieved independently and to different extents in different clades (Niklas and Newman 2013; Niklas et al. 2013). Since complex intracellular organization evolved in eukaryotes well before the appearance of metazoans (Knoll et al. 2006), the earliest unicellular eukaryotes should be sought after in rocks older than 2.1 Ga (early Paleoproterozoic and Archean), ideally using approaches that combine morphological and ultrastructural characterization with geochemical studies.

Precambrian eukaryotes have been reported predominantly from rocks deposited in marine environments, and only starting with the ca. 1.2 Ga Dripping Spring Quartzite (Beraldi-Campesi et al. 2014) do we see eukaryotes on continents. Considering the living environments of the early marine acritarchs, Knoll et al. (2006) echo the views of Butterfied (2005a, b) that not all acritarchs represent reproductive cysts of planktonic algae—some must be the remains of benthic heterotrophic organisms. Javaux et al. (2001) documented, in their study of the Roper Group acritarchs, an onshore-offshore pattern in fossil distribution between depositional environments ranging from marginal marine to basinal. Overall, their data show seaward decrease in abundance and decline in diversity, as well as changing dominance among different species. These are interpreted as reflecting the effects of natural selection by physical habitat variables on species distributions by ca. 1.5 Ga, contributing to the rise of biological diversity (Javaux et al. 2001).

Late Proterozoic and Mesoproterozoic rocks contain abundant eukaryotic fossils, but morphological diversity (disparity; Wills 2001) of these fossil assemblages maintains low to moderate levels (summarized by Knoll et al. 2006). Among these, microfossils of large size and with complex wall structure and surface ornamentation are frequent in rocks up to ca. 1.6 Ga, but in older rocks, the cell surface ornamentation and ultrastructure are less distinctive, leading some to posit some residual uncertainty concerning taxonomic assignments at the domain level (Knoll 2014). A significant leap in the level of eukaryote disparity becomes apparent around 800 Ma, marking the end of the long interval between the evolution of the first eukaryotes and their taxonomic radiation in the second half of the Neoproterozoic (Knoll et al. 2006).

The morphologies of Proterozoic eukaryotes are varied, from simple unornamented cells, morphologically complex ornamented unicells, to three-dimensionally complex multicellular organisms displaying cellular differentiation, but for many of these fossils, phylogenetic placement is difficult because the dearth and generality of characters preserved do not support unequivocal taxonomic affinities (Knoll et al. 2006). For example, Knoll et al. (2006) point out that filamentous fossils document the early evolution of a molecular capacity for simple multicellularity which was subsequently exploited by multiple clades. Branching of structures, thought to require a more sophisticated intracellular organization (Knoll et al. 2006), cell-to-cell signaling, and polarity of cell development and division, is first seen in the bifurcating processes of unicellular *Tappania* of the Roper Group (Javaux et al. 2001) and in ca. 1 Ga filamentous fossils (Knoll et al. 2006). By 1.2 Ga, multicellularity and polarity of cell divisions had led to the evolution of complex body plans—e.g., *Bangiomorpha* (Butterfield 2000).

3.6 Roles of Microbes in Taphonomic Pathways

Another dimension of the microbial contribution to the fossil record has to do with the role of microbes in processes leading to fossilization (fossil preservation). Taphonomy, a field of paleontological investigation pioneered by Ivan Efremov (1940), is concerned with elucidating decay, disarticulation, transport, and burial pathways that result in fossilization—or not. Taphonomic studies document biostratinomy (physical and chemical changes incurred after death) and diagenesis (physical and chemical changes incurred after burial). Most investigations of taphonomy are biased toward those fossilization pathways leading to Konservat-Lagerstätten, deposits in which fossilized organisms exhibit exceptional preservation (Schiffbauer and Laflamme 2012). Sometimes these even include the preservation of soft tissues which may have resulted from carcass burial in an anoxic environment. Microbes play substantial roles in the formation of most Konservat-Lagerstätten, where they act as agents of degradation, as well as, ironically, preservation. Much of what is known about the roles of microbes in taphonomic pathways derives from studies of Konservat-Lagerstätten.

Another important body of evidence contributing to understanding of microbial roles in taphonomic pathways results from experimental investigations of taphonomy in living organisms and modern environments; these experiments are sometimes referred to as "actualistic" (not to be confused with the philosophic position, although the association is enlightening). By comparing the outcomes of actualistic experiments with observations from the fossil record, paleontologists have gained a strong appreciation for the necessity and ubiquity of microbial contributions to exceptional preservation. First and foremost, microbes facilitate authigenic mineralization, which is a special type of "cast and mold" formation, acting as nucleation sites and by altering local geochemical gradients. Microbes can also entirely replicate soft tissue by consuming original tissue and replacing it with extracellular

polymeric substances (EPS). Finally, microbial mats can form "death masks" over specimens, which inhibit decay and disarticulation in addition to promoting mineralization, as well as stabilizing sediment interfaces, which has important implications for studies of fossil trackways. It is important to note that many of the roles that microbes play in taphonomic pathways occur concurrently (e.g., Darroch et al. 2012; Cosmidis et al. 2013; Iniesto et al. 2013). As such, although we have broken the following discussion into several major categories of microbe-mineral-fossil interactions, it should be understood that these are artificial and intergrading.

3.6.1 Cautionary Tales

As microbial contribution to exceptional preservation is most often implicated in preservation of ephemeral structures and soft tissue, it is useful to briefly review what is presently known about the organic structures that can, and (thus far) cannot, be found in the fossil record. This is particularly germane as many of the debates surrounding these structures invoke or include fossil or living bacteria. For instance, a putative dinosaurian heart has been refuted as such, but the cemented sediment does bear evidence of microbiogenic texture (Cleland et al 2011). Structures preserved within the body cavities of three early Cretaceous birds from the Jehol biota have been interpreted as ovarian follicles (Zheng et al. 2013), but this is unlikely, as gonads are among the first visceral organs to suffer autolytic and bacterial decay (Mayr and Manegold 2013). Finally, the sensational report of nonmineralized soft tissue in a tyrannosaurid (Schweitzer et al. 2005) was later reinterpreted as evidence that many fossil specimens are colonized by microbes after fossilization and exhumation (Kaye et al. 2008), in addition to during biostratinomy. Schweitzer et al. (2005) originally reported transparent hollow tubules obtained from acid digestion of dinosaur bone. The tubules were interpreted as blood vessels and contained spherical microstructures that were interpreted as nuclei from endothelial cells (Schweitzer et al. 2005). In their actualistic reinvestigation, Kaye et al. (2008) acid-digested a variety of fossil bones and recovered structures very similar to those observed by Schweitzer et al. (2005). SEM-EDX analyses indicated that the microspheres were likely to have originally been framboidal pyrite, diagenetically altered to iron oxides (Kaye et al. 2008), consistent with an earlier hypothesis put forth by Martill and Unwin (1997). Fourier transform infrared (FTIR) spectroscopy indicated that as opposed to reflecting diagenetically altered collagen, the material was comparable to modern biofilms; their lack of antiquity was confirmed by carbon dating. Kaye et al. (2008) suggested that recent biofilms had lined voids in fossil bones, thus producing the hollow structures morphologically similar to blood vessels and osteocytes.

Unlike the aforementioned putative soft tissues, some reports of original biopolymers in dinosaurian tissue are more compelling, having been assessed with FTIR spectroscopy. These include collagen peptides (San Antonio et al. 2011) and amide groups (Manning et al. 2009) reported from Cretaceous bones and in

embryonic Jurassic bone, which presently constitutes the oldest evidence of in situ preservation of complex organics in vertebrate remains (Reis et al. 2013). Other biopolymers known to be highly resistant with good fossilization potential include chitin, cellulose, sporopollenin (Briggs 1999; Wolfe et al. 2012), and the compounds found in melanosomes (Liu and Simon 2003; Wilson et al. 2007; Vinther et al. 2008, 2010), the latter of which have been previously interpreted as fossilized bacteria (Wuttke 1983a). Not only can melanosomes be used to reconstruct color patterning (Li et al. 2010a; Knight et al. 2011), their presence is tightly correlated with the preservation potential of integument (Zhang et al. 2010). Maganins, which are peptides found in dermal secretions of some amphibians, also contribute to preservation of integument (McNamara et al. 2009). Maganins can permeate and lyse microbial cell membranes, and because they persist post mortem, they inhibit microbial decay to the extent that *Rana* skin remains intact more than 50 days, during which time all contents of the body cavity entirely decay (Wuttke 1983b).

Finally, reports of nuclei in the fossil record (e.g., Baxter 1950; Millay and Eggert 1974; Brack-Hanes and Vaughn 1978; Martill 1990; Schweitzer et al. 2007) have been problematic. Actualistic experiments have demonstrated pseudonucleic structures (Westall et al. 1995), but intracellular mineralization of legitimate nuclei remains elusive, with a sole exception to date—the recently published nuclei and chromosomes preserved in the root cells of a Jurassic (ca. 187 Ma) *Osmunda* fern rhizome from Scania (Sweden; Bomfleur et al. 2014). In the Miocene Clarkia flora, where plant fossils are preserved as compressions and ultrastructural TEM investigations have substantiated reports of nuclei, they are preserved at much lower abundance than chloroplasts or mitochondria (Niklas 1983), which typically autosenesce before nuclear disorganization occurs (Woolhouse 1984). This seeming discrepancy may result from partitioning of protoplast into nucleate and enucleate microprotoplasts via osmotic shock (Niklas et al. 1985). By isolating plastids from nuclei, nuclear-controlled autosenescence (Yoshida 1962) could have been circumvented (Niklas 1983). While this model would account for some reports of fossil nuclei in the absence of plastids, it is possible that other reports of fossil nuclei in plants represent condensed cellular contents (Niklas 1983). For instance, osmotic stress can cause protoplast shrinkage away from the cell walls within 10 min (Munns 2002). The shrunken protoplast, which may be as little as 1/3 or less of the cell volume, remains centrally positioned by attachment of plasma membrane strands (Fig. 5, Munns 2002). Plasma shrinkage has also been invoked (Pang et al. 2013) in refuting putative nuclei in Ediacaran Doushantuo Formation (ca. 555 Ma, China) specimens, which have become the focus of taxonomic disputes (e.g., Huldtgren et al. 2011). Because nuclei are composed of water, proteins, and nucleic acids, they are easily degraded in comparison to lipids (Eglinton et al. 1991); in animal fossils at least, all lipid bilayers could be expected to fossilize, and the lack of mitochondria in the Doushantuo specimens suggests the nucleus-like bodies are not what they seem (Pang et al. 2013).

3.6.2 *Authigenic Mineralization*

Authigenic minerals are defined simply as those minerals which are formed in situ and, contra Schopf et al. (2011), are not implicitly biogenic, although many biologically mediated pathways induce the precipitation of iron, carbonate, phosphate, sulfur, silicate, and clay minerals (e.g., Konhauser 1998; Bazylinski and Frankel 2003; Briggs 2003a, b; Martin et al. 2004; Peckmann and Goedert 2005; Konhauser et al. 2011; Darroch et al. 2012). Carbonaceous polymers alone may be sufficient to precipitate many minerals (McNamara et al. 2009; Schopf et al. 2011; Roberts et al. 2013)—this process has been termed *organomineralization* (Trichet and Defarge 1995) and is considered abiogenic, although the polymers may be derived from living tissue. *Biomineralization*, on the other hand, encompasses both active and passive precipitations of minerals and is defined as occurring in the presence of living cells (Trichet and Defarge 1995).

Active biomineralization occurs when the precipitation of minerals is under direct control of the cell (biologically controlled biomineralization; Konhauser and Riding 2012), as in the case of magnetite crystals formed within magnetotactic, microaerophilic bacteria (Bazylinski 1996). Passively induced precipitation (biologically induced biomineralization; Konhauser and Riding 2012) can occur through metabolic processes that alter local chemistry permitting stoichiometric precipitation (Lovley and Phillips 1986; Lovley et al. 1987; Roh et al. 2003; Straub et al. 2004) and may also occur through mineral nucleation on EPS or microbial surfaces (e.g., Ferris et al. 1987; Thompson and Ferris 1990; Fortin et al. 1997; Léveillé et al. 2000; Van Lith et al. 2003). EPS are chemically complex bacterial exudates that contain mucus, sugars, extracellular DNAs, and proteins (Wingender et al. 2012) and are anionic, resulting in metal ion sorption (Beveridge 1989). Bacterial cells are also characterized by the electric double layer immediately external to the cell walls, which results from proton shuffling to establish a proton motive force, forming a highly localized electrochemical gradient (Poortinga et al. 2002).

3.6.2.1 Organomineralization

Biomineralization has been generally recognized as a key factor in exceptional preservation (Briggs et al. 1993; Briggs and Kear 1993; Briggs and Wilby 1996; Martin et al. 2004; Darroch et al. 2012), but it is important to emphasize that fossilization may readily result from organomineralization as well. For instance, sulfurization, a common diagenetic phenomenon (Sinninghe Damsté and de Leeuw 1990), can preserve soft tissue as sulfur-rich organic residue (McNamara et al. 2009, 2010). Similarly, diagenetic (post-burial) processes often reduce recalcitrant biomolecules like chitin, cellulose, and lignin into geologically stable macromolecules, termed kerogen (Briggs 2003a, b); kerogen is composed of interlinked polycyclic aromatic hydrocarbons, and organomineralization could

proceed via hydrogen bonding between metal ions and peripheral hydrogen atoms (Schopf et al. 2011).

The precipitation of dolomite ($Ca(Mg)CO_3$) and disordered high-Mg carbonates can also occur via organomineralization (Roberts et al. 2013), and Klymiuk et al. (2013a) have suggested that some kerogenous plant fossils preserved in calcium carbonate concretions are at least partially mineralized with disordered high-Mg carbonates. The lack of an actualistic explanation for the precipitation, under ambient temperatures, of the geologically significant amounts of dolomite found in the rock record has often been referred to as "the dolomite problem," as it was only known to occur under a very narrow set of conditions, in rarely occurring environment—hypersaline sabkhas, in association with sulfate-reducing bacteria (Wright and Wacey 2004). Roberts et al. (2013) achieved abiotic nucleation of high-Mig carbonates on carboxylated polystyrene, and they suggest that Mg^{2+} ions are complexed and dewatered by surface-bound carboxyl groups. Because the model does not require metabolic activity, any type of organic matter—including microbial cell walls, which are rich in carboxyl groups—could serve as nucleation sites for dolomite precipitation (Roberts et al. 2013).

Fossils of 63 adult frogs, constituents of the late Miocene Libros biota of northeast Spain, provide evidence that tissue composition itself can control precipitation of authigenic phosphates (McNamara et al. 2009). In some of the specimens, the presence of distinctive microfabrics (Wilby and Briggs 1997; Briggs 2003a, b; Chin et al. 2003; Briggs et al. 2005) indicates that phosphate nucleated directly upon soft tissue without bacterial intermediates (McNamara et al. 2009). Bacterial contributions are often implicated in phosphatization, as calcium carbonate ($CaCO_3$) precipitation is thermodynamically favored over calcium phosphate ($CaPO_4$) at pH below 6.38 (Briggs 2003a, b), and bacterial decay leads to localized acidification. Phosphatization of the Libros frogs, however, was probably not significantly enhanced by diffusion of acidic microbial metabolites from internal biofilms, but was instead facilitated primarily by release of SO_4^{2-} during degradation of glycosaminoglycans (GAGs), which are abundant in extant adult *Rana* skin where they are chemically bound to collagen fibers (McNamara et al. 2009). Collagen contains abundant hydroxyl groups, to which Ca^{2+} readily adsorbs; calcium phosphate precipitates are extremely localized to dermal collagen fibers in the fossil frogs and absent elsewhere in the specimens (McNamara et al. 2009). The Libros frogs also serve as an opportunity to make an important distinction: mineral precipitation was *itself* not bacterially mediated, but the decay of collagen, which increases hydroxyproline and therefore the abundance of hydroxyl nucleation sites (Lawson and Czernuszka 1998), was almost certainly facilitated by bacterial collagenases (McNamara et al. 2009). The distinction as to whether mineralization is abiogenic or biogenically mediated is one that explicitly concerns *how the mineral is precipitated* and does not preclude subsidiary microbial interactions. Because decaying organic matter comprises heterogeneous microenvironments (Briggs and Wilby 1996), it is probable that most taphonomic pathways include both organomineralization and biomineralization.

3.6.2.2 Biomineralization

Burgess Shale-Type Preservation

Burgess Shale-type preservation is ubiquitous in Ediacaran and Cambrian deposits (Gabbott et al. 2004; Xiao et al. 2002; Zhu et al. 2008; Anderson et al. 2011; Cai et al. 2012). Factors thought to be crucial in the formation of Burgess Shale-type deposits include dysoxia (low oxygen content) or anoxia (Gaines et al. 2012; Cai et al. 2012), the lack of biogenic reworking of sediment (bioturbation) (Orr et al. 2003), and inhibition of autolysis. Many authors have hypothesized that early diagenetic mineralization is an intrinsic component of Burgess Shale-type taphonomic pathways. Butterfield (1995) suggested that authigenic clay minerals inhibit autolytic decay, whereas Orr et al. (1998) suggested that they adsorb to organic matter and create templates. Gabbott et al. (2004) considered pyritization more relevant for the Chengjiang biota, where it was precipitated on organic remains during bacterial sulfate and iron reduction. Finally, Petrovich (2001) has suggested that Fe^{2+} ions adsorbed to organic tissues, promoting nucleation of iron-rich clays. Still others (Gaines et al. 2008; Page et al. 2008; Butterfield et al. 2007) have maintained that clays are metamorphic in nature and play no role in early diagenesis.

Analyses of 53 fossils from 11 Burgess Shale-type deposits using scanning electron microscopy—energy-dispersive X-ray spectroscopy (SEM-EDX)—indicate that all share a principal taphonomic pathway (Gaines et al. 2008). According to Gaines et al. (2008), conservation of organic tissues (i.e., as kerogen), and not early diagenetic authigenic mineralization, is the primary mechanism responsible for preservation. Fossils from all sites display carbonaceous preservation, ranging from continuous robust through degraded films, but all are enriched with C and depleted of Al, Si, and O with respect to the surrounding matrix (Gaines et al. 2008). This principal pathway may be occasionally augmented by authigenic mineral replication of some tissues (Gaines et al. 2008), including pyrite precipitated in gut tracts of trilobites (Lin 2007), and calcium phosphate replication of some soft tissues (Butterfield 2002, 2007). More recent analyses, however, have examined unmetamorphosed fossils preserved in the Doushantuo Formation, which also exhibit Burgess Shale-type preservation (Anderson et al. 2011). All of the Doushantuo fossils examined are closely associated with clay and pyrite minerals, which appears to confirm the role of these two components in early diagenesis (Anderson et al. 2011).

The presence of authigenic clay minerals can be explained in several ways: reducing conditions at the sediment-water interface could be deflocculating aluminosilicate grains (Gaines et al. 2005); clay minerals could be attracted and adsorbed onto organic surfaces (Gabbott 1998), a process which is facilitated by sulfate reduction and reduced pH (Martin et al. 2004); clay minerals could be authigenically precipitated from pore waters, in which localized zones of reduced pH resulted in dissolution of metals from resident sediments (Gabbott et al. 2001);

or clay minerals could conceivably be bound to organic surfaces by bacterial biofilms (Konhauser et al. 1998; Toporski et al. 2002). By invoking reducing conditions and low pH, these models find at least a subsidiary role for sulfate-reducing bacteria, and actualistic studies of decay of lobster eggs indicate that quartz and clay mineral attachment to decaying tissue is enhanced in the presence of sulfate-reducing bacteria, precipitating in proximity to decaying tissue, while iron sulfides precipitate in surrounding sediments (Martin et al. 2004).

Phosphate Mineralization of Soft Tissue

In order to preserve details of soft tissue, mineralization must necessarily outpace decay (Allison 1988a); thus phosphatization, the replication of soft tissues by calcium phosphate (apatite, Ca_3PO_4), represents a biostratinomic or early diagenetic taphonomic pathway and a discrete temporal window for preservation. Phosphatization of soft tissues is relatively common in vertebrate fossils (Martill 1987, 1988, 1989, 1991; Martill and Unwin 1989; Kellner 1996a, b; Briggs et al. 1997; Frey et al. 2003), and, with only few exceptions (e.g., McNamara et al. 2009), it is generally conceded that bacteria have a vital role in soft tissue mineralization by Ca_3PO_4. Anaerobic decay generates steep geochemical gradients favoring Ca_3PO_4 precipitation over $CaCO_3$ (Briggs and Kear 1993, 1994; Hof and Briggs 1997; Sagemann et al. 1999; Briggs 2003a, b), and carbonate precipitation is inhibited at pH < 6.38 (Briggs 2003a, b) or when PO_4^{3-} concentrations are high (Sagemann et al. 1999). Chemical microenvironments in the vicinity of decaying carcasses geochemically differ from surrounding sediments in terms of ion concentration, pH, and Eh (oxidation potential) (Sagemann et al. 1999), and these differences become more extreme toward the interior of the carcass (Briggs and Wilby 1996). If PO_4^{3-} ions are sourced from the decaying tissue itself, mineral precipitation will be highly localized, whereas if PO_4^{3-} is derived from external sediments, or from microbial consortia engaged in active phosphate precipitation (Wilby et al. 1996; Cosmidis et al. 2013), phosphatization is likely to be extensive (Wilby and Briggs 1997).

Invertebrates tend to be less prone to widespread soft tissue phosphatization. In arthropods, muscle, hepatopancreas, gills, nerve ganglia (Briggs and Kear 1993, 1994; Hof and Briggs 1997; Sagemann et al. 1999), and midgut glands (Butterfield 2002) can be selectively mineralized. Actualistic experiments produce only partial phosphatization (Briggs and Kear 1994; Hof and Briggs 1997; Sagemann et al. 1999). For shrimp carcasses inoculated with sulfate-reducing bacteria and sulfide-oxidizing and fermenting bacteria, decay was most intense and phosphatization most extensive under anaerobic sulfate reduction (Sagemann et al. 1999). While this implies a prominent role for sulfate-reducing bacteria in invertebrate soft tissue phosphatization, Briggs et al. (2005) report organomineralization in a specimen of *Mesolimulus*, a horseshoe crab known from the Jurassic Solnhofen and Nusplingen biotas. Muscle fibers with distinct banding have been preserved by apatite precipitation directly onto fibers, although structures interpreted as cyanobacterial body fossils have also been observed (Briggs et al. 2005). The

preserved midgut of a trilobite (Lerosey-Aubril et al. 2012) was probably also organomineralized; the surrounding sediment is low in phosphate, and although microbial mats can concentrate phosphates (Wilby et al. 1996), none are present within the surrounding sediments. Instead, Lerosey-Aubril et al. (2012) suggest that epithelial cells of the midgut probably contained mineral calcium phosphate concretions, a form of mineral storage in preparation for ecdysis (molting).

Microbial activity can contribute phosphates to a microenvironment through active and passive mineralization. Calcium phosphate (apatite) is actively precipitated intra- and extracellularly by a number of bacteria, including *Bacterionema matruchotii*, *Chromohalobacter marismortui*, *Escherichia coli*, *Providencia rettgeri*, *Ramlibacter tataouinensis*, and *Serratia* sp. (reviewed in Cosmidis et al. 2013). Microbial metabolic activities alone may, however, be sufficient to generate amounts of free phosphate high enough to passively precipitate large quantities of laminar calcium phosphate (Arning et al. 2009). Lipid biomarkers associated with sulfate-reducing bacteria and abundance of the giant sulfur bacteria *Thiomargarita namibiensis* are correlated with PO_4^{3-} concentrations in modern phosphate-rich sediments (Schulz and Schulz 2005; Arning et al. 2008). Phosphatized fossils have not been assessed for biomarkers, but coccoid, spiral, and bacillus-like structures interpreted as bacterial body fossils are occasionally observed in zones of soft-tissue fossilization in vertebrates and invertebrates (Briggs et al. 1997; Toporski et al. 2002; Briggs et al. 2005; Skawina 2010; Pinheiro et al. 2012). While morphology cannot be used to circumscribe phylogenetic affinities of these putative fossil bacteria, actualistic experiments in freshwater decay of invertebrate tissue (Skawina 2010) reveal a succession of bacterial morphotypes that are generally correlative with the stage of decay: cocci predominate over bacilli when pH >7 (i.e., at the beginning and end of decay; Briggs and Kear 1994; Hof and Briggs 1997; Skawina 2010), whereas bacilli are more prevalent when pH is reduced <7. These observations thus provide a tentative link between bacillus-type structures and sulfate-reducing agents of anaerobic decay.

Iron Minerals and Pyritization

Although some iron oxides can be precipitated abiotically in steep geochemical gradients, like those resulting from collagen decay (Kremer et al. 2012b), precipitation of many iron oxides, iron carbonates, and iron sulfide (pyrite) is bacterially mediated (Ferris et al. 1987; Beveridge 1989; Ferris 1993; Konhauser 1998; Bazylinski and Frankel 2003; Châtellier et al. 2004; Konhauser et al. 2011). For instance, direct precipitation of iron oxides onto bacterial EPS releases a proton into the extracellular microenvironment; by acidifying their immediate surroundings, aerobic iron-oxidizing bacteria can enhance the proton motive force, thus increasing the energy-generating potential of a cell (Chan et al. 2004). Alternately, authigenic pyrite formation is frequently a result of bacterial metabolisms employing sulfate reduction. Sulfate-reducing bacteria utilize sulfate as a terminal electron acceptor under anaerobic conditions; H_2S results as a metabolic by-product

and reacts with dissolved iron, precipitating iron sulfide (Frankel and Bazylinski 2003). In some cases, the cellular membrane itself can serve as an anionic matrix, immobilizing Fe^{2+}, which then reacts with metabolic H_2S, autolithifying the bacterial cell in the process (Ferris et al. 1988). Despite the ubiquity of these processes in modern environments, there are relatively few reports of pyritized bacterial body fossils (Southam et al. 2001; Schieber and Riciputi 2005; Cosmidis et al. 2013; and possibly those reported by Tomescu et al. 2008).

Bacteriogenic pyrite is generally depleted in ^{34}S (Canfield and Thamdrup 1994), and when crystals do not nucleate directly upon cell surfaces, they are framboidal, or lacking distinct crystal faces (Popa et al. 2004). Although the presence of framboidal pyrite is not in itself positively indicative of sulfate-reducing metabolisms (Butler and Rickard 2000; Pósfai and Dunin-Borkowski 2006), there is a strong association between bacterial EPS and the formation of pyrite framboids (Maclean et al. 2008). Framboidal pyrite commonly occurs below the reduction-oxidation transition zone in subaqueous microbial mats (Popa et al. 2004). Focused ion beam SEM-EDX provides a novel view of the interior of low-temperature framboidal pyrite aggregates formed in microbial mats: organic matrix occurs between individual pyrite crystals, suggesting that nanocrystals nucleate directly within the organic matrix of bacterial EPS (MacLean et al. 2008). Extensive precipitation of pyrite, whether on cell surfaces or within EPS, can result in high-fidelity preservation of fossil morphology (Grimes et al. 2001, 2002; Gabbott et al. 2004; Brock et al. 2006; Darroch et al. 2012; Wang et al. 2012). In some cases, pyrite framboids form inside bacterial cells, replacing them, as is the case with the cyanobacteria reported by Tomescu et al. (2006, 2009) from the Early Silurian Massanutten Sandstone. Pyrite often completely replaces organics, as in the Jehol biota, where insects were initially preserved in pyrite that was later weathered to iron oxides (Wang et al. 2012), and cellularly preserved Devonian, Mississippian, and Eocene fossil plants that have been replaced with pyrite (e.g., Allison 1988b; Rothwell et al. 1989; Tomescu et al. 2001).

An actualistic experiment in organomineralization of a celery petiole (Grimes et al. 2001) has yielded important insights into authigenic pyrite formation in plant tissues. Grimes et al. (2001) demonstrated that pyrite readily precipitates on inner plant cell wall surfaces, within cell walls, and in the middle lamella between cells. Pyrite initially nucleates on the inner walls of parenchyma cells, before penetrating inward (Grimes et al. 2001). Inward penetration occurs through successive nucleation upon previously precipitated crystals, rather than by continued crystal growth (Grimes et al. 2001). Pyrite precipitates only between fibrils of cellulose and not on lignified surfaces; minerals do not replace the plant tissue but rather nucleate within fluid-filled spaces between cellulose fibrils (Grimes et al. 2001). Thus, pyritized plant tissues probably represent middle lamella regions, as opposed to replaced cellulose, and if present, lignin will be coalified (Grimes et al. 2001, 2002).

Taphonomic pathways hypothesized for the London Clay (one of the more diverse Eocene floras in Europe; Collinson et al. 2010), which invoke pyritic replacement of plant tissues in the presence of sulfate-reducing bacteria, have also been experimentally investigated (Grimes et al. 2001; Brock et al. 2006). In

both studies, the experimental system rapidly became driven by anaerobic respiration, with diffuse precipitation of iron sulfides into sediment surrounding *Platanus* twigs. Local pH also declined, but as decay tapered off—at 12 and 5 weeks (Grimes et al. 2001; Brock et al. 2006 respectively)—pH increased, reflecting a metabolic shift to sulfide oxidation (Brock et al. 2006). Although pyrite precipitated on plant surfaces, few of the twigs exhibited internal sulfide minerals (Grimes et al. 2001; Brock et al. 2006); these results may have been due to inherent heterogeneity of the system (Brock et al. 2006) or hydrophobic moieties in lignin molecules (Jung and Deetz 1993; Grimes et al. 2001).

Doushantuo fossils preserved in small cm-sized chert nodules represent a more specialized pyritization pathway. The chert nodules, which contain microbial mat fragments at their core, are surrounded by silica cortex and inner pyrite rim, with an exterior rim of late diagenetic blocky calcite (Xiao et al. 2010). Because pyrite crystals are immersed in groundmass silica, which exhibits no concentric growth zones, the two minerals were probably syngenetic and swiftly precipitated (Xiao et al. 2010). Formation of pyrite-silica rims was likely facilitated by local pH changes related to bacterial sulfate reduction (Xiao et al. 2010), consistent with diffusion-precipitation models that posit a spherical precipitation front formed at the boundary between diffusing H_2S and a surrounding Fe^{2+} reservoir (Raiswell et al. 1993; Coleman and Raiswell 1995). Pervasive marine anoxia and substantially higher levels of dissolved iron during the Ediacaran are thought to have encouraged proliferation of sulfate-reducing bacteria (Canfield et al. 2008; Li et al. 2010b). Sulfate reduction generates alkalinity (HCO_3^-), thereby promoting $CaCO_3$ precipitation, but because sulfate reduction and pyrite precipitation have a net increase of protons, pH declines (Xiao et al. 2010). Within a narrow window (pH 9.0–10.0), the solubilities of carbonate and silica behave inversely, and silica precipitates at the same time $CaCO_3$ enters solution; therefore, proton generation by sulfate-reducing bacteria led to silicification, while H_2S generated during metabolism led to pyrite precipitation in the Doushantuo nodules (Xiao et al. 2010).

Compression-Impression Leaf Fossilization

The presence of biofilms may be integral to preservation of leaves as compression-impression fossils. Two taphonomic pathways invoking microbially mediated preservation have been proposed for compression-impression plant macrofossils. The exceptional preservation of plant and insect biota at the Eocene Florissant locality is probably a special case and not widely replicated in the paleobotanical record: fossilization is thought to have been facilitated by extensive diatom blooms in response to increased levels of dissolved silica (derived from periodic volcanic ashfall) within a lacustrine system (O'Brien et al. 2002). When exposed along bedding planes, it is apparent that the fossils are encased within diatomaceous laminae; O'Brien et al. (2002) suggest that diatom biofilms were established on

floating plant and insect debris, with subsequent sinking and incorporation into the sediment.

The second taphonomic pathway implicating biofilms was first proposed by Spicer (1977) who recognized that iron was often precipitated on submerged surfaces of leaves prior to burial, and leaf compression fossils are often encrusted with iron oxides (Dunn et al. 1997). Leaf surfaces, however, are covered by hydrophobic cuticles that inhibit metal binding. Degradation of cuticle followed by authigenic mineralization of cellulose could account for this seeming oxymoron, but although exceptional instances of cellulose preservation have been demonstrated (Wolfe et al. 2012), cellulose typically degrades rapidly in comparison to cuticle (Spicer 1981). Dissimilatory iron-reducing bacteria have also been invoked to explain this oxymoron (Spicer 1977), but they are restricted to aerobic environments with abundant Fe^{3+} (Dunn et al. 1997). By contrast, leaf surfaces host a variety of microbes capable of forming biofilms (Morris et al. 1997). The anionic nature of bacterial EPS facilitates metal binding (Beveridge 1989), and experiments conducted by Dunn et al. (1997) show that mineral precipitation does not occur in the absence of biofilm formation.

3.6.3 Doushantuo "Embryos"

The Doushantuo biota, preserved in Ediacaran marine deposits, has been recently subject to intense debates, centering on the presence of microscopic multiloculate structures that have been interpreted as having bilateral symmetry and thus representing bilaterian embryos in varying stages of development (Xiao et al. 1998; Huldtgren et al 2011; Yin et al. 2014). A recent analysis using backscattered electron imaging, electron probe microanalysis, and synchrotron X-ray tomography microscopy (SRXTM) compared the so-called embryos to preserved cells of other Doushantuo fossils with uncontested affinities to distinguish between crystal structures of mineralized phases preserving (or replacing) original structure and those attributable to later diagenetic effects, including void filling (Cunningham et al. 2012a). Supposed nuclei exhibit crystal textures characteristic of void filling, and cells purported to represent later developmental stages are instead diagenetic artifacts (Cunningham et al. 2012a). In light of these analyses, the Doushantuo specimens are unlikely to actually represent fossilized embryos (trace fossil evidence, however, suggests that bilaterians may have evolved by this time; see Pecoits et al. 2012). Nevertheless, these enigmatic specimens triggered an intense period of research into taphonomic pathways that could replicate the structures.

Under abiotic conditions, invertebrate egg surfaces could be mineralized in solutions of calcium carbonate and calcium phosphate in as little as 1–2 weeks (Hippler et al. 2012) to 1 month (Martin et al. 2005). Sediments could also bind to the egg surfaces, similarly replicating exterior morphology (Martin et al. 2005). Although eggs may not exhibit substantial decay for up to a year, neither

experiment was able to induce internal mineralization (Martin et al. 2005; Hippler et al. 2012).

Unlike abiotic mineralization, bacterial pseudomorphing does replicate internal structure. A bacterial pseudomorph can be formed by establishment of a surface biofilm and then invasion of bacteria into the interior, where they consume cytoplasm, replacing it with EPS and bacterial biomass (Raff et al. 2008, 2013). Local biofilms are initially formed at structural boundaries (Stoodley et al. 2002) and then act as scaffolds, conjoining to form the full pseudomorphs (Raff et al. 2013). Localized surface heterogeneities promote generation of very small biofilms conformed to the local shape, and therefore a fully pseudomorphed structure is composed of numerous local biofilms (Raff et al. 2013). If autolysis of embryos is blocked by anoxia or reducing conditions (Raff et al. 2006), they are reliably pseudomorphed, in aerobic and anaerobic conditions, by natural seawater bacterial populations dominated by gammaproteobacteria (Raff et al. 2008, 2013). Furthermore, Raff et al. (2013) were able to identify the single species that could each replicate one of three taphonomic pathways observed in embryos exposed to natural seawater populations (Raff et al. 2013).

Because pseudomorphs initiate as minute biofilms, microbial flora may be heterogeneous across a specimen. Single-taxon experiments demonstrate that different colonizers will yield different taphonomic outcomes. *Pseudoalteromonas tunicata* produced high-fidelity pseudomorphs that replicated both external and internal structure within 2–3 days, a timeline comparable to pseudomorph generation in natural seawater. *Vibrio harveyi* generated pseudomorphs replicating external surfaces only, while *Pseudoalteromonas luteoviolacea* resulted in complete degradation within a few days (Raff et al. 2013). Finally, although *Pseudoalteromonas atlantica* is known to form surface biofilms, it did not interact with the embryos, suggesting that not all biofilm formers are competent pseudomorphers (Raff et al. 2013). Species identity may not be foremost in determining taphonomic outcomes (Raff et al. 2013), but rather may depend on the suite of genetic capabilities (Burke et al. 2011).

Competition experiments (Raff et al. 2013) illustrated that the products of an initial pseudomorphing strain could be obliterated by tissue-destructive strains, but once formed, bacterial pseudomorphs of *Artemia* embryos and nauplius larvae were stable for up to 19 months. These experiments demonstrated that if *Pseudoalteromonas luteoviolacea* comprised more than 5 % of a mixed population, pseudomorphing was inhibited. This suggests that preservation of soft tissue may depend upon favorable competitive outcomes between closely related species.

Hypotheses regarding the taxonomic affinities of the Doushantuo "embryos" have also been tested using actualistic experiments. Bailey et al. (2007) suggested that the Doushantuo fossils could represent fossilized giant sulfur bacteria similar to *Thiomargarita*, in which a large central vacuole accounts for 98 % of the cell volume. *Thiomargarita* reproduces by reductive cell division (Kalanetra et al. 2005) and thus provides a morphological analogue to "cleaving cells" seen in the putative embryos. During laboratory decay of *Thiomargarita*, however, cell membranes decayed in advance of mucus sheaths, which may remain stable for

months or years prior to degradation (Cunningham et al. 2012b). Furthermore, when *Thiomargarita* cells were inoculated with pseudomorphing bacteria of the type used in experiments by Raff et al. (2008), the cells collapsed into their central vacuole (Cunningham et al. 2012b). Despite similar morphologies, it is thus unlikely that the Doushantuo specimens represent giant sulfur bacteria.

3.6.4 Microbial Mats

Microbial mats, which are composed of biofilms with microbial cells spatially organized in EPS (Stoodley et al. 2002), are vertically stratified communities defined by light penetration and vertical redox gradients generated by microbial metabolic activities (Wierzchos et al. 1996). The upper surfaces are dominated by photosynthetic cyanobacteria, with aerobic heterotrophic microbes in the oxidized upper layer (Visscher and Stolz 2005). These overlie a deeper anoxic layer characterized by anoxygenic photosynthetic bacteria, fermenters, and chemolithoautotrophic sulfur bacteria; lowermost layers contain dissimilatory sulfate and sulfur-reducing bacteria and methanogens (Dupraz and Visscher 2005; Visscher and Stolz 2005). Transitions between these zones may occur within millimeters. Oxygenation and carbon dynamics within mats are also subject to temporal shifts: in daylight, photosynthesis results in supersaturated O_2 concentrations and high carbon production. After dark, microbes employing aerobic respiratory pathways rapidly consume the accumulated carbon and render much of the mat anoxic; thereafter, respiration switches to sulfate reduction, and sulfides accumulate, peaking near dawn (Canfield and Des Marais 1991; Visscher et al. 1991; Canfield et al. 2004). Microbial mats induce precipitation of both iron sulfides and carbonates, and because they grow continually, mats also trap sedimentary particles and organic remains (Krumbein 1979; Visscher and Stolz 2005).

3.6.4.1 Death Masks

First proposed by Gehling (1999), the microbial death mask model of fossil preservation invokes anaerobic sulfate-reducing metabolisms, which induce formation of pyritic shrouds that drape the decaying carcass and preserve features as mineralized casts (Gehling 1999; Gehling et al. 2005; Callow and Brasier 2009). Pyrite precipitation through death masks formed beneath active microbial mats constitutes the leading hypothesis for Ediacaran-type preservation (Gehling 1999; Gehling et al. 2005; Darroch et al. 2012). In Ediacaran-type deposits, framboidal pyrite is found in direct association with some three-dimensionally preserved fossils (Laflamme et al. 2011), and beds commonly contain oxidized weathering products of pyrite (goethite and limonite) as well as sedimentary textures characteristic of preserved microbial mats (Gehling 1999; Laflamme et al. 2012). It has also been suggested that some Ediacaran morphologies may even be taphomorphs,

preservational variants of structures produced during postmortem microbial decay (Liu et al. 2011).

Microbial mats were probably extensive across Proterozoic seafloors, where they substantially contributed to sediment lithification (Gehling et al. 2005; Droser et al. 2006). Although the rise of metazoan grazers diminished the extent to which microbial mats influenced sedimentary structure on global scale (Orr et al. 2003), they remained important agents in the formation of Konservat-Lagerstätten (Gall et al. 1985; Gall 1990; Seilacher et al. 1985; Briggs 2003a, b; Fregenal-Martínez and Buscalioni 2010). Mats contribute to fossilization through biostratinomic and early diagenetic processes. The former include envelopment of carcasses in which the microbial mat can replicate the body surface on the underside of the mat and protect the body from scavengers and disarticulation. Anoxic conditions within the mat can also inhibit microbial decay, and mineral precipitation can stabilize the specimen (Gall 1990; Wilby et al. 1996; Gehling 1999; Briggs 2003a, b; Briggs et al. 2005; Martill et al. 2008; Iniesto et al. 2013). Although iron sulfide precipitation is usually invoked in death mask preservation, microbial mats also precipitate carbonates and phosphates (Reid et al. 2000; Decho and Kawaguchi 2003; Dupraz et al. 2009; Cosmidis et al. 2013).

In the first experiment to test death mask hypotheses, Darroch et al. (2012) followed the taphonomic pathways of lepidopteran larvae placed on top of microbial mats, marine sand, and sterilized sand, which were allowed to decay over a 6-week period. By the end of the experiment, only specimens from microbial mat arrays consistently exhibited Ediacaran-type epirelief structure that replicated morphology. Iron sulfides precipitated within a day, reaching their maximum extent within 2 weeks and reentering solution by the end of the experiment (Darroch et al. 2012), likely due to a shift to sulfide-oxidizing metabolism. These results suggest that the temporal window in which Ediacaran-type preservation can occur is short. The formation of abundant iron sulfides, despite negative stoichiometric bias due to the use of low-sulfate freshwater, provides substantial support for the importance of sulfate-reducing bacteria in Ediacaran-type preservation. However, there is little evidence for iron sulfides precipitating as finely grained cements capable of replicating morphology (sensu Gehling 1999). Instead, sediments and some clay minerals appear to have been stabilized by microbial EPS (Darroch et al. 2012), which may play a critical role in early cementation of grains and preservation of morphological detail (Briggs and Kear 1994; Wilby et al. 1996; Briggs et al. 2005; Laflamme et al. 2011).

The progression of decay in vertebrates has also been assessed in the context of microbial mats. Neon tetra carcasses were maintained on microbial mats and control sediment over a 27-month period (Iniesto et al. 2013). Control fish exhibited advanced decay by 15 days, and by day 50 the entire specimen was readily disarticulated. By comparison, structural integrity of mat fish was stable between 7 and 30 days; organized scales and tegument persisted at least 3 months in the mat fish, whereas control fish were almost entirely decomposed to a few fragmentary skeletal remains by the end of three months (Iniesto et al. 2013). The proliferation of the microbial mat over decaying fish had significant implications for

preservation: by day 30, carcasses had been almost entirely covered by cyanobacterial filaments, which thickened over time such that by day 270, fish carcasses were immersed in the mat to the depth of transition zone between oxic and anoxic layers, with full incorporation into the anoxic layer by day 540 (Iniesto et al. 2013). SEM-EDX analyses also demonstrated that despite Ca- and Mg-enriched water chemistry, the major mineral precipitated in experimental mats was calcium carbonate, with spherules appearing in localized patches by day 7 and a thin film of calcium carbonate covering the whole carcass by day 15. Iniesto et al. (2013) also examined several decayed microbial mat carcasses using magnetic resonance imaging, which revealed that internal skeletal organization and soft organs were readily apparent even at day 270, indicating that immersion in the mat inhibited decomposition. This experiment illustrated that microbial mats directly contribute to preservation of fish in two major ways: formation of a cyanobacterial sarcophagus which prevents disarticulation and inhibits decay and early biostratinomic precipitation of a calcium-rich film (Iniesto et al. 2013).

3.6.4.2 Trackways

Microbial mats have long been understood as integral to preservation of vertebrate trackways and footprints (Thulborn 1990; Conti et al. 2005; Marty et al. 2009). However, there has been only one actualistic examination of track preservation in modern microbial mats (Marty et al. 2009), despite the fact that debate in vertebrate ichnology (study of trace fossils) often hinges on whether a track is a primary imprint, an underprint, or an overprint. Primary imprints, discernable by the presence of skin or claw impressions, are relatively rare in the fossil record. By contrast, underprints, where the act of impression distorts underlying sediments which then lithify, are thought to have been readily incorporated into the fossil record (Lockley 1991). Overtracks, on the other hand, are formed when tracks are stabilized by microbial mats and are then infilled with sediments; as this may happen multiple times, with each new lamina stabilized by a successive mat, a number of smaller-perimeter and less-detailed surfaces will develop (Thulborn 1990). Tracks preserved in this fashion could break along any fissile plane, and the exposed surface might therefore represent a later infill and not the original impression surface. Observations of footprints along modern tidal flats suggest that most of the vertebrate fossil track record comprises modified true tracks and overtracks (Marty et al. 2009). Furthermore, footprints are generally only produced during wet periods; when dry, microbial mats are resistant to pressures, and even large tracemakers will leave no impression. Because microbial mats are densely consolidated once dried, they rarely disintegrate even under heavy rainfall, and surfaces which retain impressions are therefore those which are subject to repeated inundations, rarely drying (Marty et al. 2009). This suggests that tracks represent narrow taphonomic windows—those on the same bedding plane are likely to have been emplaced within hours to a few days of each other. Understanding essential factors leading to fossilization of tracks has important implications for

biomechanical modeling and behavioral interpretations (e.g., Currie and Sarjeant 1979; Lockley 1986).

3.6.5 Microbial Interactions with Bone

Microbial degradation of buried bones is not necessarily immediate (Hedges 2002), especially in waterlogged and humid sites (Jans et al. 2004). Because most environments are not geochemically stable with respect to the apatite (calcium phosphate) they contain, bones are not in thermodynamic equilibrium with soil solution, and biological attack generally precedes demineralization (Collins et al. 2002). Under normal environmental parameters, collagen is recalcitrant (Collins et al. 2002). Deterioration of collagen, which is enhanced by a variety of microbial collagenases (McDermid et al. 1988; Harrington 1996), follows demineralization (Collins et al. 2002). Although the low permeability and high mineral content of bone can initially inhibit substantial decomposition prior to demineralization (Child 1995), microbial "bone taint" can begin as early as 6 h postmortem (Roberts and Mead 1985), owing to proliferation of gut and muscle flora, which initially propagate along foramina housing vessels and nerves (Child 1995). Soft tissue decay reduces pH, accelerating demineralization that continues as bones are incorporated into sediment (Child 1995). In addition to bacteria, common soil fungi, including *Mucor*, are also capable of producing microscopic focal destructions (Child 1995). Mycelial proliferation may facilitate bacterial proliferation within bone because fungal hyphae readily cross voids in cancellous bone (Daniel and Chin 2010). Fungal proliferation in bone is often inhibited by accumulating NH_4^+ and nitrogen which result from autolysis, microbial degradation, and acid hydrolysis of collagen (Child 1995).

Microbial decay is the ultimate fate of most bone incorporated into sediment, and several studies have demonstrated that biofilm establishment is imperative for preservation. Carbonates can substitute in bone lattice for PO_4^{3-} (Timlin et al. 2000). Carpenter (2005) demonstrated that carbonate minerals develop on bone when it is exposed to calcium carbonate solutions in the presence of bacteria, whereas $CaCO_3$ did not precipitate in sterile solution. Daniel and Chin (2010) built on this study, defining the temporal window in which precipitation commences. Cubes of bone which were not surface-sterilized prior to suspension in a sand matrix exhibited extensive mineral deposition, particularly within interior cancellous bone. Samples that had been washed, but not sterilized, showed a similar pattern, although interior deposition was lower. By contrast, sterilized samples showed little deposition that was limited to the exterior surfaces (Daniel and Chin 2010). These studies confirm the importance of biofilms that both induce mineral precipitation and trap sediment around bone and also indicate that early diagenetic mineralization is more likely to initiate in cancellous bone than compact bone (Daniel and Chin).

Bones deposited in marine settings are subject to colonization by anaerobic-oxidizing archaeans and sulfate-reducing bacteria (Shapiro and Spangler 2009). High-sulfide concentrations occur in the proximity of skeletons as a result of oxidation of lipids by sulfate-reducing bacteria, and carbonates precipitate readily (Allison et al. 1991; Shapiro and Spangler 2009). Epifluorescence bacterial counts show that highest concentrations of bacteria occur at bone surfaces, with no statistical difference between bone buried in sediment or exposed at the sediment–water interface (Deming et al. 1997). Rich mats of microbial biofilms cover up to 50 % of the bone surface, and destruction of the outer edges of bones is facilitated by bacterial boring (Allison et al. 1991). Features consistent with microboring and bacteriogenic precipitation of carbonates and iron sulfides have been observed in fossil whale falls from the Eocene through Pleistocene and in some Cretaceous plesiosaurs (Amano and Little 2005; Shapiro and Spangler 2009). Aragonite with botryoidal fabrics, associated with methane oxidation (Campbell et al. 2002), also occurs in some specimens (Shapiro and Spangler 2009).

3.7 Microbial Symbioses in the Fossil Record

Symbiotic associations of different trophic consequences (mutualistic, parasitic, etc.) involving microbes continue to be discovered in high numbers in all modern ecosystems, and they are probably even more widely spread than we could imagine. Therefore, it is not surprising that their fossil counterparts are also being discovered at high rates in the rock record. As a result, many symbiotic associations known from the modern biota have been reported from the fossil record. Some of these associations fit into well-circumscribed categories, such as the lichen symbioses and mycorrhizal associations, which are very briefly addressed here because of the imminent publication of a book that will provide an exhaustive treatment of the fungal fossil record (Taylor et al. 2014). Other associations described in the fossil record belong to more loosely circumscribed types, such as the endophytic syndrome or the bacterial-cyanobacterial mat consortia (the oldest record of which has been described in ca. 440 Ma Silurian cyanobacterial colonies; Tomescu et al. 2008).

3.7.1 Lichen Symbioses

Lichens are symbioses between a phylogenetically heterogeneous assemblage of mycobionts—predominantly ascomycete fungi (Gargas et al. 1995; Grube and Winka 2002; Prieto and Wedin 2013)—and photobionts, the majority of which are chlorophyte algae (Honegger 2009). A smaller number of mycobionts, perhaps 10 %, form symbioses with cyanobacteria (Honegger 2009). The lichenized habit has been independently gained and lost multiple times (Lutzoni et al. 2001, 2004;

Nelsen et al. 2009), and few characters used in traditional morphological classification are phylogenetically informative (e.g., Stenroos and DePriest 1998; Grube and Kroken 2000). Thus, although the fossil record of lichens [comprehensively reviewed by Rikkinen and Poinar (2008) and Matsunaga et al. (2013)] is stratigraphically extensive, the phylogenetic affinities of most fossil lichen symbionts cannot be determined with confidence. Several Paleogene specimens preserved in amber have been attributed to living lineages (e.g., Peterson 2000; Poinar et al. 2000; Rikkinen 2003; Rikkinen and Poinar 2002, 2008), but few fossils exhibit the key reproductive features that would allow identification of the mycobiont.

The oldest record of a putative lichen is a ca. 585 Ma phosphatized algal mat from the Doushantuo Formation containing several 0.5–0.9 μm wide filaments that are interpreted as coenocytic hyphae with terminal sporulation, thought to be comparable to those of the glomeromycete *Geosiphon* (Yuan et al. 2005), which forms an endosymbiotic association with *Nostoc* cyanobacteria (Gehrig et al. 1996; Kluge et al. 2003). Yuan et al. (2005) interpreted these Ediacaran hyphae as evidence of a presymbiotic syndrome defined by facultative use of algal products by a marine fungus. The fungal affinities of the filaments are, however, rather suspect due to their small diameter: hyphae of *Geosiphon* are significantly larger, as are those of Mucoromycota (Schüssler and Kluge 2001; Deacon 2006). New techniques, including Raman spectroscopy or time-of-flight mass spectrometry, and confocal laser scanning microscopy may provide more insight into the nature of these earliest lichen-like specimens. No other evidence exists for lichen symbioses prior to the Devonian: suggestions that some Ediacaran fossils conventionally considered metazoans instead represent lichens (Retallack 1994, 2013) have been refuted (Antcliffe and Hancy 2013a, b; Xiao et al. 2013).

Other contenders for the earliest lichens include those described from early Devonian of Scotland and Wales. Honneger et al. (2013a, b) have described two fossil lichens preserved in siltstone from the Welsh borderlands; the specimens consist of septate hyphae of probable ascomycete affinity, which hosted cyanobacteria and unicellular chlorophyte algae. As in some extant lichens (Cardinale et al. 2006; Grube and Berg 2009), the latter also appears to have been colonized by non-photosynthetic bacteria, including actinomycetes (Honegger et al. 2013a). More important to our understanding of the fossil record of lichen symbioses, both Welsh lichens are dorsiventrally organized with internal stratification consistent with modern lichens. This stands in contrast to another Devonian structure, the enigmatic *Winfrenatia reticulata* of Scotland's Rhynie Chert. *Winfrenatia* was described as a morphologically primitive crustose cyanolichen (Taylor et al. 1995a, 1997). It lacks internal stratification, and cyanobacteria are thought to have been housed in depressions pocking the surface of the thallus (Taylor et al. 1995a, 1997).

As described, the architecture of *Winfrenatia* is unlike that of any living lichen (Taylor et al. 1997; Honegger et al. 2013b). Additional specimens of *Winfrenatia*, described by Karatygin et al. (2009), suggest that much of the thallus is composed of sheaths of extracellular polymeric substances of filamentous biofilm-forming cyanobacteria. While some modern lichens contain multiple photobiont species,

several authors have suggested that *Winfrenatia* instead represents opportunistic fungal parasitism of cyanobacterial colonies (Poinar et al. 2000; Karatygin et al. 2009). While this interpretation accounts for multiple cyanobacteria, and the lack of internal stratification, the three-dimensional complexity of the specimens remains problematic. We suggest instead that *Winfrenatia* represents a microbial mat with intrinsic fungal biota. Cantrell and Duval-Pérez (2012) have isolated 43 species of fungi from a hypersaline microbial mat, including *Aspergillus*, *Cladosporium*, and *Acremonium* species. Microbial mats are composed of aggregated biofilms, which are themselves highly structured multispecies communities with complex internal architecture: most cells are arranged in sessile microcolonies surrounded by EPS and separated by minute water channels (Costerton et al. 1995; Stoodley et al. 2002). Such channelization would have aided percolation of silica-rich water of the hydrothermal pools in which the Rhynie Chert was deposited (Rice et al. 2002). Furthermore, microbial mats have complex three-dimensional morphology resulting from desiccation, gas production, and water flow (Gerdes et al. 1993), accounting for the pocket-like depressions evident in *Winfrenatia*.

3.7.2 Mycorrhizal Symbioses

Of the microbes that colonize root tissue, mycorrhizal fungi in particular are thought to have been integral to the evolution of land plants and their successful exploitation of terrestrial soils (Pirozynski and Malloch 1975; Humphreys et al. 2010; Wang et al. 2010; Bidartondo et al. 2011). Three highly conserved genes (DMI1, DMI3, and IPD3) found in all major land plant lineages are necessary for mycorrhizal formation, suggesting that this symbiotic relationship evolved with the common ancestor of liverworts and vascular plants (Wang et al. 2010). Arbuscular mycorrhizal fungi are known from at least the Ordovician (Redecker et al. 2000) and were highly diverse by the Devonian (e.g., Remy et al. 1994; Taylor et al. 1995b; Taylor and Taylor 2000; Dotzler et al. 2006, 2009; Garcia Massini 2007; Krings et al. 2012; Strullu-Derrien et al. 2014). Despite the ephemeral nature of absorptive arbuscules, they have been observed in numerous fossil plants, including the Triassic *Antarcticycas* (Phipps and Taylor 1996) and the seed fern *Glossopteris* (Harper et al. 2013), as well as the Eocene conifer *Metasequoia milleri* (Stockey et al. 2001). The fossil record for ectomycorrhizae, on the other hand, is exceedingly sparse: a *Suillus*- or *Rhizopogon*-like fungus is known from the Eocene Princeton Chert, where it formed an ectomycorrhizal association with the extinct pine, *Pinus arnoldii* (LePage et al. 1997; Klymiuk et al. 2011).

3.7.3 Microbial Endophytes

In paleobotanical and paleomycological literature, it has become common practice to use the term "endophyte" to refer to any fossil microbe occurring within plant tissues (Krings et al. 2009). This usage is intended to be purely descriptive (Krings pers. comm.) and does not imply ecology of the microbe in question. Mycologists and microbial ecologists, however, use the term in an explicitly ecological context, defining an endophyte as a microbe that grows asymptomatically within its host plant (for a discussion of endophyte definitions, see Stone et al. 2000); mycorrhizal fungi and nitrogen-fixing bacteria, while endophytic, are not always classified within the "endophyte catch-all." While some endophytes may be engaged in cryptic mutualism with their hosts, as has been hypothesized of some dark septate endophytes (a heterogeneous assemblage of predominantly ascomycetous fungi), others may be latent pathogens or become saprotrophs upon the death of their host (Jumpponen and Trappe 1998; Saikkonen et al. 1998; Jumpponen 2001; Rodriguez et al. 2009; Maciá-Vicente et al. 2009; Newsham 2011). Some fossil fungi described as endophytes (as defined by Krings et al. 2009) elicited host responses characteristic of infection or parasitism (e.g., Krings et al. 2007; Schwendemann et al. 2010; Taylor et al. 2012). Recently, a study of the Early Devonian vascular plant *Horneophyton lignieri*, eliciting comparisons with modern basal land plants (embryophytes), has demonstrated the presence of endophytes belonging to two major fungal lineages, the Glomeromycota and Mucoromycotina, and revealed previously undocumented diversity in the fungal associations of basal embryophytes (Strullu-Derrien et al. 2014).

Endophytes, excluding mycorrhizal symbionts, have yet to be conclusively demonstrated in the fossil record. A cyanobacterial "endophyte" has also been described, from the Rhynie chert: cyanobacterial colonization of *Aglaophyton major*, a nonvascular plant that was extensively colonized by arbuscular mycorrhizae, has been observed in sections cut from two blocks of chert (Krings et al. 2009). The presence of aquatic species, including the charophyte alga *Palaeonitella*, indicates that these blocks represent a part of the system that experienced sustained inundation. Cyanobacteria within the specimens have morphology consistent with living Oscillatoriales and appear to have colonized the tissue by invading via stomata (Krings et al. 2009). While acknowledging that the specimens exhibited no explicit evidence for mutualism, Krings et al. (2009) suggest that they may represent a model for precursory or initial stages of a mutualistic interaction. Although some extant plants like cycads are known to form stable mutualisms with N_2-fixing cyanobacteria, these photobionts are usually *Anabaena* or *Nostoc* (Rai 1990; Costa et al. 1999; Adams and Duggan 2008). By contrast, a number of oscillatorian cyanobacteria are known to produce toxins (Chorus and Bartram 1999), including microcystins, which have inhibitory effects on plant growth, photosynthetic capacity, and seedling development (McElhiney et al. 2001).

In the course of paleomycological investigations of the Eocene Princeton Chert of British Columbia, Canada, Klymiuk et al. (2013b) described vegetative mycelia

and microsclerotia characteristic of some dark septate endophytes (e.g., Currah et al. 1988; Ahlich and Sieber 2006; Fernández et al. 2008; Stoyke and Currah 1991). Intracellular microsclerotia were found in the outer cortex of the aquatic angiosperm *Eorhiza arnoldii* (Klymiuk et al. 2013b); extant dark septate endophytes also produce microsclerotia within host cortex, typically in response to stress or host senescence (Fernando and Currah 1995; Jumpponen and Trappe 1998; Barrow 2003). Because the host-fungus interface of living dark septate endophytes involves a network of nonchitinous mucilaginous hyphae intimately associated with host sieve elements (Barrow 2003), Klymiuk et al. (2013b) indicated that it is unlikely that this interface will be observed in the fossil record. Although conidiogenesis can be diagnostic for a number of root endophytes (Fernando and Currah 1995; Addy et al. 2005), Klymiuk et al. (2013b) did not observe conidia in association with the putative endophytes. Furthermore, at the time of preservation, the host tissue was probably moribund, and it is possible that the fungi represent saprotrophs.

3.8 Future Directions

Studies of microbial fossils are poised to reveal the timing of the advent of cellular life and to contribute to understanding of the early evolution of life and its role as a component of Earth systems; additionally, they can illuminate the origin and early evolution of eukaryotes, as well as clarify aspects of the genesis of fossils as records of past life and of the evolution of symbioses involving microbial participants. These contributions are important as the geologic record provides the only direct evidence and, thus, independent tests for hypotheses on the timing and tempo of events and processes that otherwise can only be inferred based on the modern earth systems and biota.

Looking into the future, it is immediately apparent that continued work in the field and in the lab to document in more detail known fossil occurrences and to identify new fossil localities, as well as to recognize more potential fossils and confirm them as bona fide microfossils, will always have their place in the study of the microbial fossil record. In discussing the fossil record of Archean microbial life, Knoll (2012) reiterated the general acceptance of the fact that life existed at least as far back as 3.5 Ga and suggested two major areas of inquiry for future research. One of these involves continued discovery and application of analytical tools to resolve the biogenicity of increasingly older putative fossils and to elucidate the physiology or phylogenetic relationships of the earliest life forms. But studies coming from the opposite direction, that of modern microbes in their host ecosystems, are also needed. Such studies will lead to better understanding of the roles and products of microbial components in the chemical cycles of different ecosystems and in different geologic or petrologic contexts. The findings can lead to the development of new methods to more reliably assess indigenousness, syngenicity, and biogenicity of putative body fossils and to unequivocally identify microbial fossils

of all types (stromatolites, alteration textures, etc.) even in the absence of body fossils, which will ultimately improve our ability to trace the trajectory of microbial life through the rock record. Such actualistic studies also benefit from the application of cutting-edge analytical tools and can point the way to applications in fossil contexts. For example, Schmid et al. (2014) used a combination of advanced complementary three-dimensional microscopy tomography techniques (focused ion beam—scanning electron microscopy tomography, transmission electron microscopy tomography, scanning-transmission X-ray microscopy tomography, and confocal laser scanning microscopy) to characterize bacterial cell-(iron) mineral aggregates formed during Fe(II) oxidation by nitrate-reducing bacteria. Their study showed that only in combination did the different techniques provide a comprehensive understanding of structure and composition of the various precipitates and their association with bacterial cells and EPS; such an approach is directly applicable to the discovery and characterization of similar structures and relationships in the fossil record.

Another major area of inquiry identified by Knoll (2012) concerns the rise of cyanobacteria and aerobic photosynthesis in terms of the timing of these events, as they relate to the oxygenation of the atmosphere to stable levels. In this context, Knoll asks whether cyanobacteria (aerobic photosynthesizers) could be counted among the primary producers in Neoarchean (2.8–2.5 Ga) ecosystems. This is relevant to the issue of small positive oscillations recorded in atmospheric oxygen concentrations toward the end of the Neoarchean, before the 2.5–2.3 Ga Great Oxidation Event, in a context in which documented biosignatures (stromatolites, stable isotopes, hydrocarbon biomarkers) don't exclude the presence of cyanobacteria, but they don't require it either (Knoll 2012). Some answers may come from studies such as that recently published by Planavsky et al. (2014) who document chemical biosignatures for oxygenic photosynthesis in 2.95 Ga Sinqeni Formation (Pongola Supergroup, South Africa), at least a half billion years before the Great Oxidation Event. In the Sinqeni Formation, rocks deposited in a nearshore environment yielded molybdenum isotopic signatures consistent with interaction with manganese oxides, which imply presence of oxygen produced through oxygenic photosynthesis.

More precise constraints on the dating of environmental changes are also needed for the Proterozoic, to draw less tentative conclusions on the causes and mechanisms of early eukaryote evolution and diversification. This was pointed out by Javaux (2007), who reviewed the different ideas proposed to explain the observed pattern of diversification of early eukaryote-like fossils, concluding that no event in particular explained it. For example, some unanswered questions are whether early eukaryotes diversifying in the marine realm displaced a preexisting cyanobacterial biota or evolved in an ecologically undersaturated environment and whether eukaryotes remained in minority while diversifying or they quickly formed eukaryote-dominated communities (Knoll and Awramik 1983), or when eukaryotes did invade the continents. In terms of recognition of early (unicellular) eukaryotes, Peat et al. (1978) discussed critically the value of an actualistic approach which can bias interpretations of ancient microfossils under the assumption that prokaryotes in

the Precambrian were morphologically similar to modern prokaryotes and suggested that it is not out of the realm of possibility to discover disproportionately large (eukaryote-like) prokaryote microfossils in Precambrian rocks.

Like in the case of prokaryote evolution, answers to questions concerning early eukaryotes will come both from continued studies of the fossil record and from better understanding of their taphonomy and modes of preservation based on actualistic studies. Early on, Golubic and Barghoorn (1977) emphasized the need for ultrastructural studies of diagenetic alteration in the cell walls of extant microorganisms, for application in the microbial fossil record. Conversely yet convergently, Javaux et al. (2003) pointed out that taphonomic studies [like those conducted by Knoll and Barghoorn (1975) or Bartley (1996) on prokaryotes] are needed to elucidate the probability of preservation of intracellular—components such as pyrenoids, starch, and cytoplasm—which, contrary to conventional wisdom, is far from vanishingly small (e.g., Bomfleur et al. 2014). By improving understanding of fossils and their mode of formation, such studies will lead to more detailed and accurate interpretations of the fossils' implications for the taxonomy, ecology, and evolution of ancient microbes.

Microbially induced sedimentary structures have entered the sphere of interest of Precambrian biological evolution studies relatively recently, benefiting fully from well-developed and articulated concepts of sedimentology, an outlook emphasizing actualistic studies, and the breadth of modern environments in which they are formed. Recently, Wilmeth et al. (2014) documented domal sand structures of putative microbial origin in the 1.09 Ga Copper Harbor Conglomerate of Michigan, expanding the fossil record of continental microbialites to siliciclastic fluvial environments.

In contrast to MISS, stromatolites, although recognized and studied for more than a century, lack extensive modern analogues and have ranked among the more contentious Precambrian fossil biosignatures. It is therefore exciting to note a resurgence of actualistic studies addressing stromatolite structures and the microbial communities that build them from several perspectives. Kremer et al.'s (2012a) studies of microbial taphonomy and fossilization potential in modern stromatolites in Tonga are such a study (see "Stromatolites" in sect. 3.2.2.1). Related to this, a study by Knoll et al. (2013) documented in detail both the composition of microfossil assemblages and the sedimentary structures (petrofabrics) in Mesoproterozoic carbonate platform microbialites of the Angmaat/Society Cliffs Formation (Baffin and Bylot Islands). Their study revealed covariation of microfossil assemblages with petrofabrics, supporting hypotheses that link stromatolite microstructure to the composition and diversity of microbial mat communities.

Mirroring Knoll et al.'s (2013) work in modern microbialites, Russell et al. (2014) studied the microbial communities building microbialites in Pavilion Lake (Canada). Using molecular analyses, Russell et al. (2014) documented diverse communities including phototrophs (cyanobacteria) as well as heterotrophs and photoheterotrophs. They also showed that the microbialite-building communities are more diverse than the non-lithifying microbial mats in the lake and that microbial community composition does not correlate with depth-related changes

in microbialite morphology, suggesting that microbialite structure may not be under strict control of microbial community composition. Finally, in a study of extracellular polymeric substances and functional gene diversity within biofilm communities of modern oolitic sands (analogous in genesis to stratiform stromatolites) from Great Bahama Bank, Diaz et al. (2014) suggest that carbonate precipitation in marine oolitic biofilms is spatially and temporally controlled by a consortium of microbes with diverse physiologies (photosynthesizers, heterotrophs, denitrifiers, sulfate reducers, and ammonifiers) and point to a role of EPS-mediated microbial calcium carbonate precipitation in the formation of the microlaminated oolitic structures.

Long time considered ill positioned to make independent contributions beyond merely documenting historical confirmation of events and processes, paleontology (including Precambrian paleobiology; Schopf 2009) witnessed in the 1970s–1980s the "paleobiological revolution" that reinstated it at the "high table" of evolutionary biology (Sepkoski and Ruse 2009). Building on this newfound identity and adding to it a developmental anatomy - comparative morphology twist, today paleontology is poised to make meaningful contributions to the field of evolutionary-developmental biology by documenting in fossils and tracing through time the anatomical and morphological fingerprints of genetic pathways that regulate development (e.g., Rothwell et al. 2014). In this context, a recent study by Flood et al. (2014) inspires some exciting ideas. These authors used comparative genomics to study phylogenetically distant bacteria that induce formation of wrinkle structures (a type of MISS) in modern sediments. Their results suggest that horizontally transferred genes may code for phenotypic traits that underlie similar biostabilizing influences of these organisms on sediments. On the one hand, this implies that the ecological utility of some phenotypic traits such as the construction of mats and biofilms, along with the lateral mobility of genes in the microbial world, render inferences of phylogenetic relationships from gross morphological features preserved in the rock record uncertain (Flood et al. 2014). On the other hand, this study expands the range of phenotypic traits that can be used as morphological fingerprints for shared genetic pathways, to the realm of micro- and macroscale sedimentary structures.

Deep in the rock record, the fossil evidence may not look spectacular by most standards—tiny microfossils, wrinkles on a rock face, readings of chemical composition on a computer screen, or a spectrometer curve. Yet the studies of the microbial fossil record can have tremendous outcomes, as they can bring key contributions to addressing two of the most profound and perennial questions that have puzzled humanity and science. On the one hand, tracing the microbial fossil record is our only direct way of catching a glimpse of the beginnings and early evolution of life, and this chapter has attempted to provide an introduction and overview of the paradigms that underpin such studies. On the other hand, the methods and ideas developed as a result of studies of the microbial fossil record for recognizing ancient and inconspicuous traces of life, as well as the knowledge and experience accumulated in the process, have crystallized in an approach that is directly applicable to the search for traces of life on other planets (e.g., Brasier and

Wacey 2012). Although the connections of paleomicrobiological work with astrobiology are not explored in this chapter, it is noteworthy that this relatively new field of research has already produced an impressive body of publications, including several books (e.g., Seckbach and Walsh 2009), and has two dedicated journals (*Astrobiology* and *International Journal of Astrobiology*) which host some of the references cited throughout this chapter. It is only fitting to conclude, then, that from the deepest reaches of time and of Earth's crust, to the landscapes of other worlds, paleomicrobiology can open unprecedented perspectives in the study of life.

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