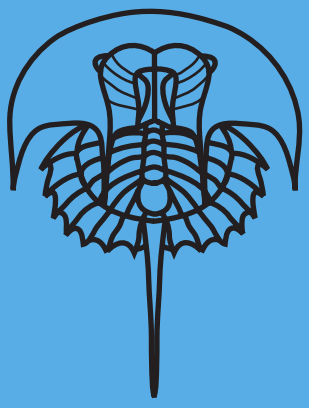

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PART B, VOLUME 2, CHAPTER 7
MICROFOSSILS OF PROKARYOTES (BACTERIA AND ARCHAEA): RESEARCH HISTORY, TAPHONOMY, AND PALEOBIOLOGY

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INTRODUCTION

Bacteria and archaea make up the paraphyletic group of prokaryotes, and together with eukaryotes they form the three major domains of life. One can easily envision a world without eukaryotes, but it is difficult to imagine a biosphere without prokaryotes. Today prokaryotes colonize virtually every corner of the surface Earth system, from human guts to oceanic gyres to hydrothermal vents. Earth is home to millions of prokaryote species (Schloss & others, 2016), which amount to a staggering number of individuals (Whitman, Coleman, & Wiebe, 1998; Flemming & Wuertz, 2019; Locey & Lennon, 2019) and account for ~14–50% of carbon in the biosphere (Whitman, Coleman, & Wiebe, 1998; Bar-On, Phillips, & Milo, 2018). In fact, the biochemical capability to fix carbon and to produce oxygen can be evolutionarily traced to prokaryotes (cyanobacteria to be exact), and nitrogen fixation in nature is exclusively carried out by prokaryotes. Thus, it is safe to say that there would not be a biosphere without prokaryotes.

There are no credible reasons to doubt that prokaryotes were as abundant and important in the geological past as they are today. Yet, the fossil record of prokaryotes is extremely poor. This poor record is largely related to the fact that most prokaryotes—with the prominent exception of magnetotactic bacteria (Bazylinski & Frankel, 2003) and some cyanobacteria (Benzerara & others, 2014)—do not perform biologically controlled mineralization. Thus, the preservation of prokaryotes as fossils requires specific taphonomic conditions. Furthermore, the microscopic size and simple morphology of prokaryotic fossils means that they are difficult to study because of potential problems related to contamination from younger microbes, conflation with abiotic structures, and convergence with eukaryotic microbes. Despite these challenges, there have been many reports of fossil prokaryotes since the late ninteenth century. This chapter is an overview of fossil prokaryotes, with a focus on bacteria, particularly cyanobacteria, preserved in Precambrian rocks.

HISTORY OF THE STUDY OF BACTERIAL FOSSILS

More detailed accounts of the history of fossil prokaryote research can be found in Fenton (1946), Banks and others (1967), Schopf (1992a), and Taylor, Taylor, and Krings (2009). Prokaryotic fossils had been reported in the literature by the late nineteenth century, although some were not originally identified as such, others may be eukaryotic, and still others were later proven abiotic. For example, the tubular microfossil *Girvanella* Nicholson & Etheridge, 1878 was first described as a foraminifer from Ordovician strata but later understood as a cyanobacterium (Wood, 1957; Riding,

Xiao, Shuhai, & Qing Tang. 2021. Part B, Volume 2, Chapter 7: Microfossils of Prokaryotes (Bacteria and Archaea): Research History, Taphonomy, and Paleobiology. Treatise Online 160:1–37, 9 fig., 1 table.

1991). Renault (1896) described coccoidal and rod-shaped microstructures preserved in Carboniferous-Permian plant fossils under the extant bacterial genera *Micrococcus* Cohn, 1872 and *Bacillus* Ehrenberg, 1835. These structures were originally interpreted and subsequently accepted as bacterial fossils (Pia, 1927; Banks & others, 1967), but many of them probably represent inorganic particles (Taylor & Krings, 2005). During the early twentieth century, definitively biogenic and possibly bacterial fossils were reported in the literature. Worth mentioning are *Gloeocapsomorpha* Zalessky, 1917 from Middle Ordoviclan kukersites of the Baltic Shale Basin in Estonia, as well as the middle Cambrian fossils *Morania* Walcott, 1919 and *Marpolia* Walcott, 1919 from the Burgess Shale in Canada. *Gloeocapsomorpha* was compared with extant chroococcalean cyanobacteria such as *Gloeocapsa* Kützing, 1843 and *Entophysalis* Kützing, 1843 (Foster, Reed, & Wicander, 1989; Stasiuk & Osadetz, 1990), but a cyanobacterial interpretation remains uncertain (Blokker & others, 2001) and some authors have interpreted *Gloeocapsomorpha* as a eukaryotic organism (e.g., a green alga) on the basis of organic geochemical evidence (Hoffmann & others, 1987; Derenne & others, 1991). The interpretation of *Marpolia* is also uncertain. It is commonly regarded as a cyanobacterium (Walcott, 1919; Steiner & Fatka, 1996), although Walcott (1919) also compared it with modern green and red algae, and fossils described as *Marpolia* may belong to different taxa or indeed different domains (LoDuca & others, 2017). *Morania*, on the other hand, has been generally accepted as a colonial organism consisting of cyanobacterial filaments (Walcott, 1919).

In addition to marine prokaryotes mentioned above, terrestrial cyanobacterial fossils have also been known from Phanerozoic deposits since the twentieth century. Among these, the most famous examples are various coccoidal and filamentous bacterial fossils from the Devonian Rhynie chert (Kidston & Lang, 1921; see also Croft & George, 1959; Edwards & Lyon, 1983; Krings & others, 2007; Krings, 2019; Krings & Harper, 2019).

By the first half of the twentieth century, alleged bacterial microfossils had been reported from Precambrian rocks (Walcott, 1914, 1915; Moore, 1918; Gruner, 1922, 1923, 1924, 1925; Ashley, 1937). Many of these were later confirmed to be pseudofossils. For example, tubular structures illustrated in Gruner (1923) and possibly those in Ashley (1937) are likely ambient pyrite trails (Tyler & Barghoorn, 1963; Knoll & Barghoorn, 1974). Such trails are common in cherts and phosphorites ranging from the Archean (Wacey & others, 2008) to the Ediacaran (Xiao & Knoll, 1999; She & others, 2016), and they were likely produced by pyrite crystal movement related to local build-up of degradational gas and pressure dissolution (Knoll & Barghoorn, 1974). However, some of these early reports likely included *bona fide* Precambrian microfossils from the Proterozoic Belcher Supergroup (Moore, 1918, fig. 14), Gunflint Formation (Gruner, 1922, pl. 7; Gruner, 1924, pl. 11), and Belt Supergroup (Walcott, 1914, pl. 20, *2–6*). In particular, Gruner's reports were from the same stratigraphic unit—the Gunflint Formation—where paradigm-shifting discoveries were reported three decades later (Tyler & Barghoorn, 1954; Barghoorn & Tyler, 1965; Cloud, 1965). But these earlier reports did not spark much interest at the time, perhaps because the quality of photomicrographs was poor (indeed, some reports had only camera lucida drawings), the great antiquity of these fossils was not appreciated, and preservation of bacterial fossils was not expected, as pointed out by Knoll, Barghoorn, and Awramik (1978).

During the second half of the twentieth century, the study of Precambrian prokaryotes opened a new chapter. This was initiated by several high-profile reports of silicified bacterial microfossils from the Paleoproterozoic (~1880 Ma) Gunflint chert in Canada (Tyler & Barghoorn, 1954; Barg-

hoorn & Tyler, 1965; Cloud, 1965). The Gunflint fossils include stromatolite-associated coccoidal and filamentous fossils (Fig. 1.1) (Barghoorn & Tyler, 1965), as well as coccoidal planktonic microbes (Knoll, Barghoorn, & Awramik, 1978). These fossils were compared with extant cyanobacteria, iron-oxidizing bacteria, and fungi (Barghoorn & Tyler, 1965; Cloud, 1965). Serving as a search image in the field and in the laboratory, Gunflint-type stromatolitic cherts and microfossils soon opened the floodgates to numerous discoveries of Precambrian microfossils. Within a decade, Precambrian microfossils had been reported from many Precambrian cherts in North America and Australia, including the Neoproterozoic Bitter Springs Formation in Australia (Fig. 1.7) (Barghoorn & Schopf, 1965; Schopf, 1968; Schopf & Blacic, 1971), the Neoproterozoic Skillogalee Dolomite in South Australia (Schopf & Barghoorn, 1969; Knoll, Barghoorn, & Golubic, 1975), the Neoproterozoic Beck Springs Formation in eastern California (Cloud & others, 1969), the Paleoproterozoic Belcher Supergroup in Canada (Hofmann, 1974; Hofmann, 1976), Archean strata in South Africa (Schopf & Barghoorn, 1967; Knoll & Barghoorn, 1977), and many other units. These were followed by reports of silicified microfossils, many of which are interpreted as cyanobacteria, from Precambrian cherts around the world (see summary in Schopf, 1983; Schopf & Klein, 1992; Sergeev, Sharma, & Shukla, 2012). Among these, Paleoarchean microfossils from Western Australia are the most contentious (Awramik, Schopf, & Walter, 1983; Buick, 1984; Schopf & Packer, 1987; Schopf, 1993; Brasier & others, 2002; Schopf & others, 2002). The combined geochemical, paleontological, and sedimentological data indicate the existence of a microbial ecosystem on Earth at ~3500 Ma or earlier (Rosing, 1999; Schopf, 2006b), perhaps with diverse microbial metabolic pathways (Schopf & others, 2018).

Since the 1960–1970s, paleontologists have also been investigating Precambrian organic-walled microfossils preserved in fine-grained siliciclastic rocks or shales using hydrofluoric acid maceration techniques (Xing & Liu, 1973; Timofeev, Hermann, & Mikhailova, 1976; Vidal, 1976), and some of these are filamentous microfossils that are interpreted as cyanobacteria (Hermann, 1974). This line of research opened a new taphonomic window onto the Precambrian microbial world (Vidal, 1981; Hofmann & Jackson, 1994; Grey, 2005; Tang & others, 2013). Together, microfossils preserved in cherts and shales provide a broader view of the paleoecology and taphonomy of Precambrian microbes.

MODES OF PRESERVATION

Because most prokaryotic microfossils are preserved in cherts and shales, silicification and carbonaceous compression are the main modes of preservation. However, prokaryotic microfossils can also be replicated by phosphate, pyrite, gypsum, and other minerals; and they have been reported from ambers. These taphonomic modes are briefly described below.

SILICIFICATION

As a major permineralization pathway, silicification is responsible for the preservation of the majority of prokaryotic microfossils (Fig. 1), including those preserved in cherts of the Gunflint Formation (Fig. 1.1–1.3) and Bitter Springs Group in Australia (Fig. 1.7). Generally understood as a taphonomic process through which organisms are replaced by diagenetic silica, silicification of microbes is neither molecule-by-molecule replacement of cellular structures by silica nor wholesale replacement of the entire organism by silica, as sometimes occurs in silicification of animal skeletons (Butts, 2014). Rather, at the microscopic level, silicification is fundamentally a casting and molding process, with silica precipitating on organic substrates, such as cell walls and laminae of cyanobacterial

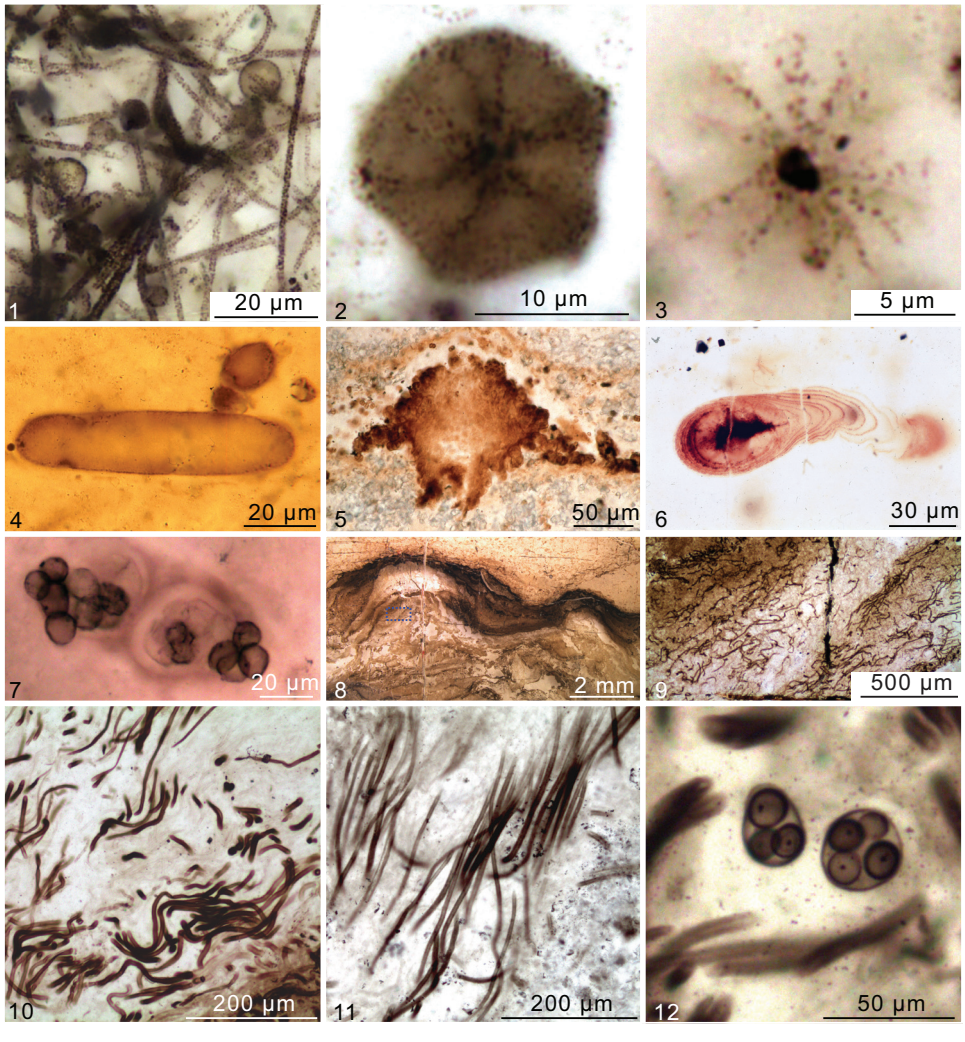

FIG. 1. Thin section photomicrographs of silicified prokaryotic microfossils from the ~1880 Ma Gunflint Formation in Canada (*1–3*), ~1400–1500 Ma Billyakh Group in Siberia (*4–5*), Tonian Draken Formation in Svalbard (*6*), Tonian Bitter Springs Group in Australia (*7*), and Tonian Jiudingshan Formation in North China (*8–12*). *1*, Coccoidal specimens of *Huroniospora* BARGHOORN in BARGHOORN & TYLER, 1965 and filamentous specimens of *Gunflintia* BARGHOORN in BARGHOORN & TYLER, 1965. Although *Gunflintia* was described as a multicellular filament (BARGHOORN & TYLER, 1965), most specimens do not preserve trichome structure and may be identified as *Siphonophycus*; *2*, *Kakabekia* BARGHOORN in BARGHOORN & TYLER, 1965; *3*, possibly *Eoastrion* BARGHOORN in BARGHOORN & TYLER,1965; *4*, *Archaeoellipsoides* HORODYSKI & DONALDSON, 1980; *5*, *Eoentophysalis* HOFMANN, 1976; *6*, *Polybessurus* GREEN & others, 1987; *7*, *Myxococcoides* SCHOPF, 1968; *8*, stromatolites consisting of filamentous *Siphonophycus* SCHOPF, 1968; *9–11*, close-up views of *Siphonophycus* filaments, *9* being a magnification of *8* (dotted line box); *12*, *Caryosphaeroides* SCHOPF, 1968 in the center, with coccoidal cells arranged in tetrads and enclosed in a common envelope. Note intracellular inclusions that were interpreted as degraded nuclei (SCHOPF, 1968; but see KNOLL & BARGHOORN, 1975). Also note *Siphonophycus* filaments co-occurring with *Caryosphaeroides*. Fig. *1.1–1.3* and *1.7–1.12*, new; Fig. *1.4–1.6* courtesy of Andrew H. Knoll, previously published as fig. 10,*2* and 17,*4* in Sergeev, Knoll, & Grotzinger, 1995, and fig. 12,*5* in Knoll, Swett, & Mark, 1991, respectively.

sheaths, through chemical bonds between organic functional groups and silicic acids (Leo & Barghoorn, 1976) and perhaps assisted by the presence of metallic ions (Ferris, Fyfe, & Beveridge, 1988), thus producing molds or casts of microbial cells and sheaths. Thus, the organic substrates are encased within the replicating silica and are subsequently degraded to various degrees. The taphonomic survival of the organic substrates, albeit in degraded forms and in trace amounts, aids the recognition and identification of these fossils in thin section microscopy and is regarded by some geologists as an indispensable criterion for affirmation of biogenicity (Buick, 1990).

A number of taphonomic experiments have been carried out to understand the silicification process. Degradation experiments have demonstrated that cyanobacterial cells degrade over periods of days to months but cyanobacterial sheaths are much more resistant and can remain recognizable over longer time (Golubic & Barghoorn, 1977; Bartley, 1996). These experiments have been borne out by field observations showing the degraded but still recognizable cyanobacterial cells and sheaths in pigment-poor layers of modern microbial mats (Gomes & others, 2020), and they indicate that fossil mineralization must have occurred rapidly during early diagenesis in order to preserve cellular structures. Indeed, field observations of microbial silicification in modern hot spring sinters, which are widely regarded as modern taphonomic analogs of microbial silicification in Precambrian oceans, indicate that cyanobacterial and other microbes can be silicified shortly after death or even *in vivo* (Renaut, Jones, & Tiercelin, 1998), and that cyanobacterial sheaths are preferentially preserved through silica encrustation and permeation (Renaut, Jones, & Tiercelin, 1998; Konhauser & others, 2003). Mineralization experiments have also demonstrated that silica and clay minerals can coat on cyanobacterial sheaths, and silica can permeate cyanobacterial sheaths and cell walls, thus rapidly replicating cyanobacterial morphology in three dimensions (Oehler & Schopf, 1971; Westall, Boni, & Guerzoni, 1995; Toporski & others, 2002; Newman & others, 2017). These encrustation and permeation processes may have been facilitated or accelerated by elevated silica concentrations in Precambrian seawaters and pore waters (Maliva, Knoll, & Simonson, 2005) and photosynthetic activity of cyanobacteria themselves (Moore & others, 2020). Thus, it is not surprising that microbial silicification was common in Precambrian marine environments, but as biosilification (e.g., in sponges, radiolarians, and diatoms) became more important and dissolved silica concentrations declined in Phanerozoic oceans (Conley & others, 2017), this taphonomic mode declined in and throughout the Phanerozoic, not only for bacterial silicification but for silicification in general (Schubert, Kidder, & Erwin, 1997). Nor is it surprising that microbial silicification is common in hydrothermal settings (e.g., modern hot spring and Devonian Rhynie chert) where dissolved silica concentrations are high.

Yet silicification is not ubiquitous in all Precambrian marine environments. Knoll (1985a) identified three sedimentary and geochemical factors that control microbial silicification: 1) sediment permeability, 2) silica availability in pore waters, and 3) local concentration of organic matter. It is possible that these factors can interact with each other to promote silicification. For example, the degradation of organic matter (and the partial degradation of organic substrates) can activate organic functional groups, thus facilitating the nucleation of silica. It can also drive down local pH values, thus promoting the precipitation of silica as the solubility of silica decreases with pH. These sedimentary and geochemical factors mean that silicification of microbes is environmentally restricted. Indeed, although there are notable exceptions (e.g., the Ediacaran Doushantuo Formation Zhang & others, 1998; Muscente, Hawkins, & Xiao, 2015), most silicified microbial

assemblages are preserved in either peritidal or hydrothermal environments (Knoll, 1985a; Knoll, 1985b; Trewin, Fayers, & Kelman, 2003). As such, silicification provides a limited and probably biased view of the environmental and ecological ranges of prokaryotic microbes (Knoll, 1985b; Butterfield & Chandler, 1992). Fortunately, this limitation is mitigated to some degree by other taphonomic modes, such as phosphatization and pyritization that are also known to preserve microbial fossils.

PHOSPHATIZATION

Although a different fossil mineralization process, phosphatization is mechanistically similar to silicification, and fossiliferous phosphorites tend to be siliceous (Yao & others, 2005; Dong & others, 2009; Sergeev, Schopf, & Kudryavtsev, 2020). Like silicification, phosphate encrustation and impregnation of organic substrates are key processes that are responsible for the three-dimensional preservation of microbial cell morphology (Xiao, Zhang, & Knoll, 1998; Xiao & Schiffbauer, 2009). Unlike silicification, however, the phosphatization is largely restricted to subtidal environments (Zhang & others, 1998; Muscente, Hawkins, & Xiao, 2015) and occurs mostly in the Ediacaran and the Phanerozoic (Schiffbauer & others, 2014a; Muscente & others, 2017). Phosphatized cyanobacteria, for example, are best known from Ediacaran-Cambrian strata, including the Ediacaran Doushantuo Formation in the South China Craton (Fig. 2) (Zhang & others, 1998; Yuan, Xiao, & Taylor, 2005), the early Cambrian (Terreneuvian) Yurtus Formation in the Tarim Basin of northwestern China (Yao & others, 2005; Dong & others, 2009) and equivalent strata in the South China Craton (Wang & others, 1984; Dong & others, 2009; Guo, Li, & Shu, 2010), and the middle Cambrian (Guzhuangian) Alum Shale Formation in Sweden (Castellani & others, 2018). In addition, many Phanerozoic coprolites and cololites contain micrometer-sized spherical and rod-shaped structures interpreted as bacteria (Lamboy & others, 1994; Cosmidis & others, 2013; Pesquero & others, 2014), although some of these spherical structures may be alternatively interpreted as phosphatic granules that may have been present in the digestive guts of some invertebrate animals (Butterfield, 2002; Hawkins & others, 2018).

Relative to silicification, taphonomic experiments of phosphatization have been less successful and mostly focused on invertebrate degradation and mineralization (Briggs & McMahon, 2016). Degradation experiments indicate that animal cells and tissues can be pseudomorphed by heterotrophic microbes and microbial biofilms (Raff & others, 2008; Raff & others, 2013; Butler & others, 2015), thus helping to stabilize anatomical details to be phosphatized during subsequent fossil mineralization. However, the giant sulfur bacterium *Thiomargarita* Schulz & others, 1999 subjected to similar experiments did not seem to be pseudomorphed by microbial biofilms during degradation (Cunningham & others, 2012). Mineralization experiments thus far are limited and have only been able to partially phosphatize invertebrate animals (Wilby & Briggs, 1997; Martin, Briggs, & Parkes, 2003; Hippler & others, 2011). To our knowledge, no mineralization experiments have been carried out on prokaryotic organisms, and this represents a key gap in the study of prokaryote phosphatization and an area for future research.

Exceptional preservation of microbial fossils through silicification and phosphatization depends on a delicate balance between rapid mineralization and over-mineralization. Over-mineralization results in thick mineral coats that bias and disguise microbial morphologies, making it difficult to recognize mineralized microfossils in microscopy, particularly when organic substrates, such as cell walls and sheaths are completely obliterated. This has been observed in modern hot spring sinters (Jones, Renaut, & Rosen, 2001; Peng & Jones, 2012) as well as phosphatized microbes in the

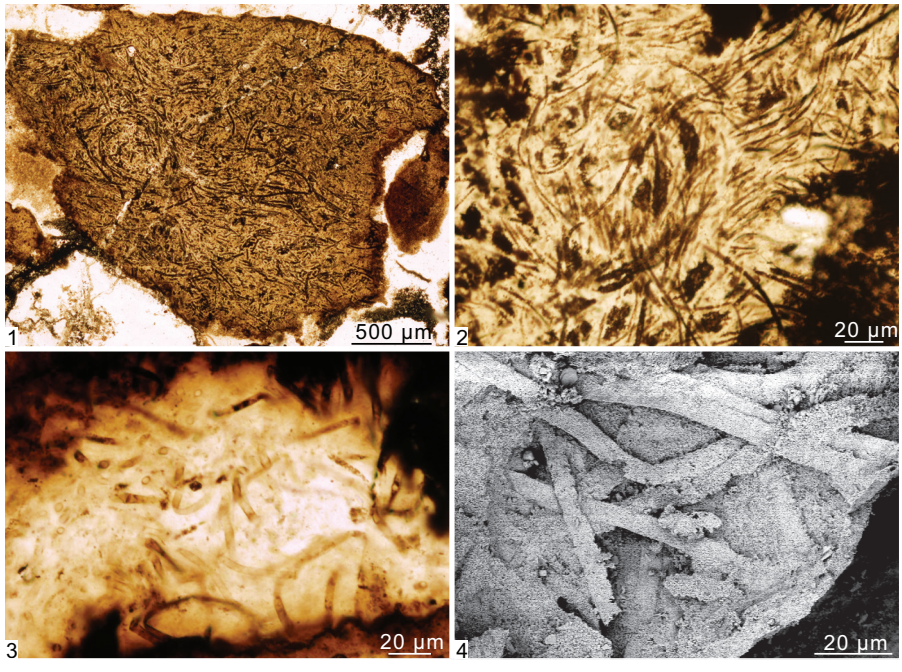

FIG. 2. Phosphatized *Siphonophycus* filaments from the Ediacaran Doushantuo Formation in South China. *1–3*, thin section photomicrographs (new; photos taken by and courtesy of Lei Chen); *4*, scanning electron microscopic (SEM) image (new; image by Shuhai Xiao).

Ediacaran Doushantuo Formation in South China (XIAO & SCHIFFBAUER, 2009).

The inhibition of post-mineralization recrystallization is also an integral part of exceptional preservation through phosphatization (XIAO & HOCHELLA, 2017). The successful fossilization of microscopic prokaryotic organisms, in particular, is critically dependent on the maintenance of fossilization minerals at micrometers or even nanometers in size; this is analogous to the achievement of the highest resolution in digital imaging by the smallest pixels. Exceptionally phosphatized microfossils from the Ediacaran Doushantuo Formation (Fig. 2), for example, are replicated by apatite minerals of tens to hundreds of nanometers in size (XIAO & SCHIFFBAUER, 2009). It is not completely understood why these apatite nanocrystals were prevented from dissolution and then recrystallization to become larger crystals. However, it is possible that the dissolution of phosphate nanocrystals in the size range of tens to hundreds of nanometers is self-suppressed or self-inhibited by the limited formation and growth of dissolution pits, the size of which is constrained by the nanocrystal size (TANG, NANCOLLAS, & ORME, 2001). This may be a fruitful area for future exploration of phosphatization (XIAO & HOCHELLA, 2017).

CALCIFICATION

Microbial calcification can occur as biologically controlled *in vivo* intracellular mineralization, biologically induced *in vivo* extracellular mineralization, or extrinsically induced *in vivo* or post-mortem extracellular mineralization. All three forms of mineralization can be found in cyanobacteria. Some cyanobacteria carry out biologically controlled mineralization and precipitate intracellular carbonates (COURADEAU & others, 2012; BENZERARA & others, 2014), but thus far these cyanobacterial biominerals are not known to be

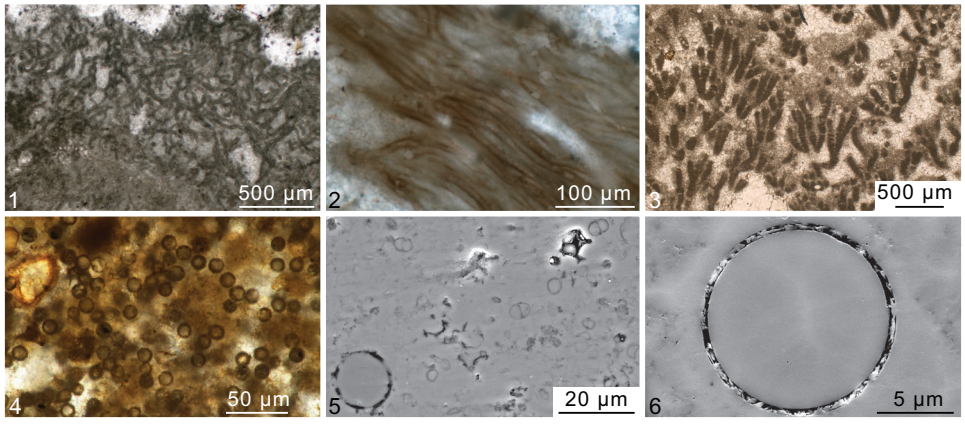

FIG. 3. Prokaryotic microfossils preserved in carbonate rocks. *1–2*, *Girvanella* NICHOLSON & ETHERIDGE, 1878 from the Lower Ordovician Fenhsiang Formation at the Liujiachang section, Songzi, Hubei Province, South China; *3*, *Epiphyton* BORNEMANN, 1886 from Cambrian Stage 3, Zhangxia Formation in Laiwu, Shandong Province, North China. Both *Girvanella* and *Epiphyton* have been interpreted as calcified cyanobacteria (RIDING, 1991); *4–6*, Coccoid microfossils, interpreted as methanogens on the basis of extremely high $\delta^{13}C_{carb}$ values up to 20‰ of the host dolomite concretions from the Middle Permian lacustrine deposits of the Lucaogou Formation in Xinjiang, northwestern China (SUN & others, 2020). Note two size classes in *5*, representing two different taxa. *1–4* are thin section photomicrographs and *5–6* are SEM images. Images *1–3,* new; photos taken by and courtesy of Jianbo Liu; *4–6,* courtesy of Funing Sun and Wenxuan Hu, previously published as fig. 2D, 2G, and 2F, respectively, in Sun & others, 2020.

preserved and identified in the fossil record. More commonly, metabolic activities of cyanobacteria, particularly photosynthesis and carbon dioxide concentration mechanisms, promote an increase in local pH values and induce *in vivo* precipitation of calcium carbonate that impregnate the sheath (RIDING, 2006). This form of biologically induced mineralization results in extracellular sheath calcification and may be responsible for the preservation of the majority of calcified cyanobacterial fossils, such as *Girvanella* NICHOLSON & ETHERIDGE, 1878 (Fig. 3.1–3.2), *Epiphyton* BORNEMANN, 1886 (Fig. 3.3), and *Renalcis* VOLOGDIN, 1932. Finally, microbes can be entombed *in-vivo* or postmortem in carbonate deposits (Fig. 3.4–3.6) (KREMER & others, 2012; SUN & others, 2020)—including tufas, travertines, and speleothems whose precipitation is primarily driven by abiotic processes such as CO_2 degassing, although it is not always possible to determine whether biological processes also play a secondary role in facilitating calcification (JONES & PENG, 2012; LI & others, 2013; JONES & PENG, 2014).

Microbial calcification is not uniformly distributed across geological time, sedimentary environments, and taxonomic groups. As calcification is critically dependent on carbonate supersaturation levels, it is not surprising that microbial calcification tends to be focused on tropical shallow marine realms, for example evaporitic, peritidal, and reefal or mud mound environments. In addition, because various microbial metabolisms have different impacts on the precipitation and dissolution of carbonate minerals (CANFIELD & RAISWELL, 1991), it is anticipated that different groups of microbes have different propensities to induce calcification. As mentioned earlier, photosynthesis and carbon dioxide concentration mechanisms of cyanobacteria facilitate fossilization through calcification (RIDING, 2006). But calcified cyanobacterial fossils have a non-uniform distribution in warm shallow marine environments across geological history. Although they range from the Meso-Neoproterozoic (KNOLL, FAIRCHILD, & SWETT, 1993; TURNER, NARBONNE, & JAMES, 1993; KAH & RIDING, 2007) to the Cenozoic (ARP,

Reimer, & Reitner, 2001), they are mostly concentrated in the Paleozoic and early Mesozoic (Arp, Reimer, & Reitner, 2001). Geochemical, atmospheric, and biological factors have been implicated as controlling factors for the non-uniform distribution of calcified cyanobacterial microfossils in marine environments. For example, Riding (2006) proposed that pCO_2 levels fell below ~0.4% (or 10× present atmospheric level) at 750–700 Ma, driving the evolution of CO_2-concentrating mechanisms and facilitating *in vivo* calcification of cyanobacterial sheaths in the Neoproterozoic and Paleozoic. Arp, Reimer, and Reitner (2001) suggested that the Paleozoic abundance of cyanobacterial calcification may be related to high calcium concentrations in Paleozoic oceans. Biological factors were in play too. Knoll, Fairchild, and Swett (1993), for example, suggested that, whereas the rarity of cyanobacterial calcification in the Precambrian may be attributed to the abundance of micrite (e.g., whiting) that outcompeted cyanobacterial sheaths as nucleation sites for calcite overgrowth in the sediment, the post-Mesozoic decline of cyanobacterial calcification was due to the ecological rise of calcareous phytoplankton.

PYRITIZATION AND RELATED PRESERVATION MODES

Bacteria and archaea are key players in the sulfur cycle (Ehrlich & Newman, 2009). Thus, it is not surprising that they play direct and indirect roles in the precipitation of sulfur-bearing minerals. Some sulfide-oxidizing bacteria (e.g., *Beggiatoa* Trevisan, 1842, *Thiomargarita* Schulz & others, 1999, and *Thioploca* Lauterborn, 1907) produce intracellular sulfur granules (Ehrlich & Newman, 2009; Bailey & others, 2013). Although such sulfur granules are not supposed to be stable in geological time scales, filamentous microfossils from the Ediacaran Doushantuo Formation in South China contain sulfur-rich granules that are interpreted as intracellular sulfur granules produced by sulfide-oxidizing bacteria (Bailey & others, 2013). More commonly, microbial sulfate reduction promotes the precipitation of pyrite, which can replicate microbes in the fossil record through pyritization; often, it is the organisms that are degraded by sulfate reducing microbes, rather than the sulfate reducing microbes themselves, that are pyritized (Schiffbauer & others, 2014b). Pyritized microfossils are common in the geological record (Schopf & others, 1965; Rasmussen, 2000; Moore & others, 2017). In some pyritized filamentous microfossils (e.g., those from the Ediacaran Krol Group in India; Fig. 4), pyrite crystals seem to precipitate within a tubular sheath, thus outlining the filamentous morphology but not faithfully replicating the diameter of the filaments until a full internal mold is formed. Thus, pyritization seems to be initiated within partially degraded filamentous microbes (perhaps after the degradation of trichomes but before the complete destruction of the sheath), and can proceed to form pyritic internal mold of microbes. Finally, microbial fossils can be replicated by gypsum (Vai & Lucchi, 1977; Schopf & others, 2012), the precipitation of which is primarily driven by abiotic processes such as evaporation.

PRESERVATION OF BIOMINERALS PRODUCED BY MAGNETOTACTIC BACTERIA

A number of iron bacteria can produce biologically controlled and biologically induced biominerals (Bazylinski & Frankel, 2003; Frankel & Bazylinski, 2003). Magnetotactic bacteria, for example, produce intracellular minerals such as magnetite (Fe_3O_4) and greigite (Fe_3S_4) that can have distinct morphologies and crystallographic features (Fig. 5) (Bazylinski & Frankel, 2003; Li & others, 2013, 2020). These distinct crystals allow their identification in the fossil record, and indeed fossil magnetotactic bacteria have been reported in Mesozoic and Cenozoic sediments (Chang & Kirschvink, 1989; Kopp & Kirschvink, 2008). Some iron bacteria can also

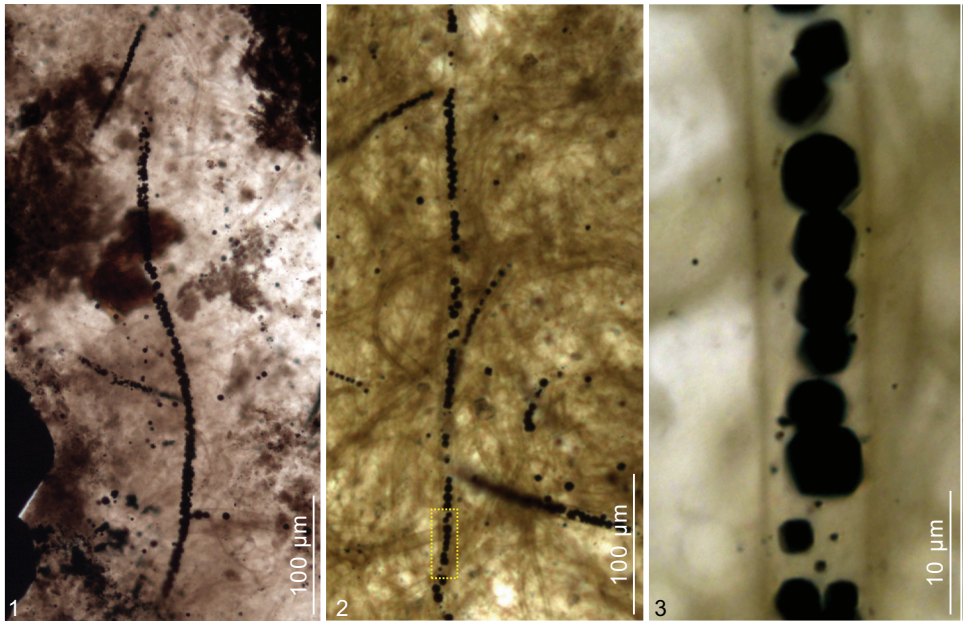

Fig. 4. Thin section photomicrographs of pyritized Siphonophycus filaments from the Ediacaran Krol Group in northern India. 3 is magnified view of 2 (yellow dotted-line box). Note that organic sheath is largely degraded in 1 and well preserved in 2–3. All images are new and were taken by Shuhai Xiao.

produce biologically induced biominerals with distinct morphologies. For example, the iron bacteria *Gallionella* Ehrenberg, 1838 and *Mariprofundus* Emerson & others, 2007 can produce extracellular ferric-oxyhydroxide stalks that are twisted, branched, or organized into ribbon-like bands (Frankel & Bazylinski, 2003; Chan & others, 2011; Krepski & others, 2013). Morphologically similar stalks have also been identified in the fossil record and interpreted as evidence for iron bacteria (Hofmann & others, 2008; Krepski & others, 2013; Crosby, Bailey, & Sharma, 2014).

CARBONACEOUS PRESERVATION

Although traces of carbonaceous material are commonly found in mineralized prokaryotic fossils, they are typically impregnated or penetrated by replicating minerals such as microquartz and apatite, so that extraction of coherent organic-walled microfossils using hydrofluoric (HF) digestion method is difficult. In contrast, carbonaceous preservation of prokaryotic fossils in fine-grained siliciclastic rocks may manifest as compressed organic-walled structures with little mineral permeation or impregnation (Xiao & others, 2002; Callow & Brasier, 2009), and these fossils can be extracted from the rock matrix using hydrofluoric acid digestion methods without compromising their structural integrity (Fig. 6) (Tang & others, 2013; Tang & others, 2015). In addition to carbonaceous compressions, structurally recognizable organic residues of prokaryotic microbes can also be preserved in ambers (Poinar, Waggoner, & Bauer, 1993; Waggoner, 1994; Dörfelt, Schmidt, & Wunderlich, 2000; Schmidt & Schäfer, 2005). Finally, carbonaceous coccoids, filaments, and sheets have been reported on the basis of scanning electron microscopic observation of fractured rock surface (sometimes after acid etching), and these have been interpreted as fossil microbes or as extracellular polymeric substances (Westall & Folk, 2003; Dai, Song, & Shen, 2004; Rozanov & Astafieva, 2009; Lan & others, 2020), although it is a significant challenge to

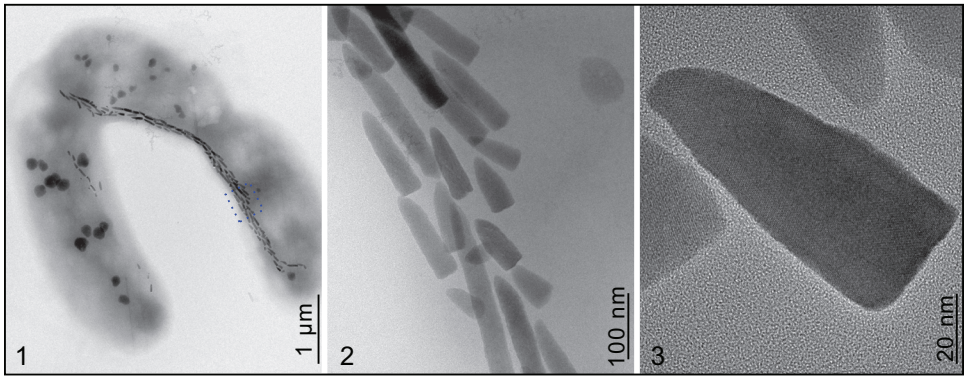

Fig. 5. Bright-field TEM (transmission electron microscopy) images (*1–2*) and high-resolution TEM image (*3*) of chains of straight bullet-shaped magnetite nanocrystals produced by extant magnetotactic deltaproteobacteria (strain WYHR-1) collected from Weiyang Lake, north of Xi'an city, Shaanxi Province, North China (Li & others, 2020). Images are new and courtesy of Jinhua Li.

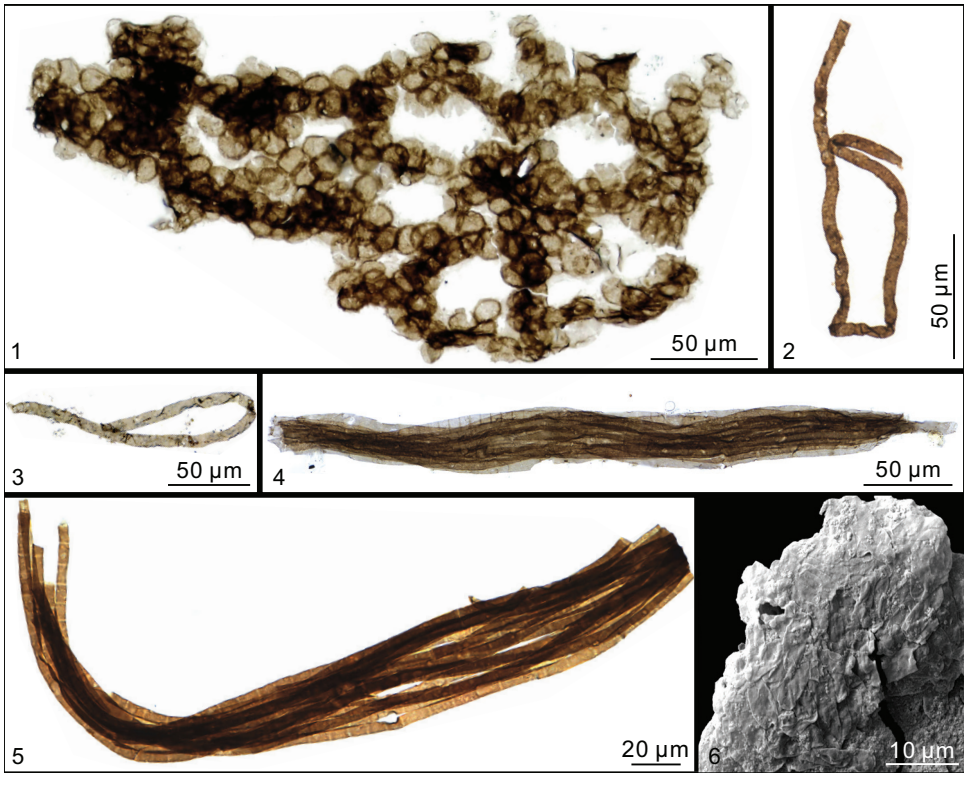

Fig. 6. Prokaryotic microfossils preserved as carbonaceous compressions in fine-grained sediments. *1*, *Ostiana microcystis* Hermann in Timofeev, Hermann, & Mikhailova, 1976, a possible cyanobacterium (Butterfield, Knoll, & Swett, 1994); *2–3*, *Siphonophycus typicum* (Hermann, 1974; transferred to the genus *Siphonophycus* by Butterfield in Butterfield, Knoll, & Swett, 1994); *4–5*, *Polytrichoides lineatus* Hermann, 1974; *6*, ellipsoidal cells of *Eosynechococcus moorei* Hofmann, 1976. All specimens were extracted from shale samples using hydrofluoric acid digestion method. *1–4* are from the Tonian Liulaobei Formation in the North China Craton (Tang & others, 2013, fig. 5G, 13C, 13D, and 14A, respectively), and *5–6* are from the Tonian Gouhou Formation in the North China Craton (Tang & others, 2015, fig. 19E and 5B, respectively). Fig. *1–5* are transmitted light photomicrographs; *6* is an SEM image.

demonstrate their syngenicity (Altermann, 2001; Edwards & others, 2006).

TRACE FOSSILS

Some prokaryotic micro-organisms, particularly cyanobacteria, can bore into hard substrates and leave a trace fossil record (Golubic, Perkins, & Lukas, 1975; Cockell & Herrera, 2008). Tunnels and galleries of tunnels interpreted as traces of euendolithic cyanobacteria have been reported from many phosphatic small shelly fossils from the Cambrian Period (Runnegar, 1985; Li, 1997). These tunnels typically have smooth walls and a constant diameter along their length, but they are otherwise simple in morphology, and the distinction between cyanobacterial, fungal, and green algal borings can be difficult (Golubić, Perkins, & Lukas, 1975). However, they can be easily differentiated from ambient pyrite trails in phosphorites and cherts, which are characterized by striated walls and commonly terminated by a pyrite grain (Xiao & Knoll, 1999; She & others, 2016; Yang & others, 2017). They can also be easily differentiated from tubular structures in Paleoarchean pillow basalts that were controversially interpreted as putative bioerosional structures of early microbes (Furnes & others, 2004; Staudigel & others, 2006).

CHALLENGES IN THE INTERPRETATION OF PROKARYOTIC MICROFOSSILS

To unambiguously demonstrate the syngenicity, biogenicity, and affinity of purported prokaryotic microfossils is a significant challenge, particularly in the study of Precambrian micropaleontology because of the poor age constraints, difficulty in stratigraphic correlation, and simple (and sometimes exotic) morphologies of ancient microorganisms. This challenge is highlighted in the debate on the earliest traces of microbial life on Earth (Buick, 1990; Brasier & others, 2005; Brasier & others, 2006; Javaux, 2019). Below, indigenicity, syngenicity, biogenicity, and affinity are discussed separately for clarity purpose, although these are often intimately related.

INDIGENICITY AND SYNGENICITY

Syngenicity refers to the provenance of the purported microfossils. Syngenetic microfossils must be indigenous; they should be demostrated to be enclosed within and thus have the same age of the host rock, rather than later contaminants. Contaminants can be introduced in the geological past, in the field, or in the laboratory (Cloud & Morrison, 1979). In early studies of Precambrian microfossils, there were numerous cases of contamination. Such examples included modern chasmolithic filaments or extracellular polysaccharide strands, seemingly indigenous as they pass beneath mineral grains in sediment (Cloud & Morrison, 1979). Other examples involved modern fungal spores and hyphae that were introduced in the field and laboratory, particularly when samples were processed using acid digestion methods. Mendelson and Schopf (1992) provided a comprehensive assessment of these contaminants.

An accepted criterion for indigenicity is to demonstrate—typically through petrographic observation of thin sections cut from freshly collected rock samples—that the purported microfossils are encased in rock matrix. In order to confirm syngenicity in thin sections, care must be taken to distinguish whether the purported microfossils were buried in the rock matrix at the time of deposition or are embedded in secondary cements/crystals that fill voids, fractures, veins, dikes, or volcanic vesicles (i.e., amygdales). In the latter case, the secondary cements/crystals should be independently dated because they can be markedly younger than the host rock. This can be achieved through relative dating using cement stratigraphy and cross-cutting relationships (Zhou & others, 2015; Gan & others, 2021), analysis of mineral assemblages tied

to dated metamorphic events (Bengtson & others, 2017), or (when carbonaceous material is available) Raman spectroscopic analysis of carbonaceous material to determine maximum metamorphic temperatures (Schopf & others, 2005; Schiffbauer & others, 2007; Javaux, Marshall, & Bekker, 2010).

BIOGENICITY

Biogenicity refers to the biological origin of the purported microfossils. It should be emphasized that, to prove biogenicity, the morphologies of the microfossils must be shown to be biological in origin. This is a distinction between morphological and chemical biosignatures. For example, a pyrite concretion may preserve chemical biosignatures because its sulfur isotopic composition indicates the involvement of microbial sulfate reduction, but this by itself does not offer evidence for a biological origin of the pyrite concretion.

Cloud (1965, p. 27) argued that the null hypothesis in Precambrian micropaleontology should be that purported microfossils be initially regarded as abiotic in origin. He wrote, "... in considering what we may accept as unequivocal Precambrian fossils, the crucial point is not whether materials observed might conceivably be of vital origin, but whether they could have been produced by non-vital processes; and, if not, whether they are sure endemic to authentic Precambrian rocks." Only after an abiotic origin can be ruled out and syngenicity is confirmed can Precambrian microfossils be accepted. This restrictive approach is necessary because of the possibility of biomorphs that are abiotic in origin but morphologically mimic microfossils (García-Ruiz & others, 2003; Javaux, 2019) and also because the profound ramifications of false positives in the study of Precambrian (particularly Archean) microfossils.

In early debates on putative microfossils from the Paleoarchean Warrawoona Group in Western Australia, Buick (1990) proposed a seven-point test to assess their syngenicity and biogenicity. He argued that *bona-fide* microfossils should be observed in petrographic thin sections, preserved in sedimentary rocks or low-grade metasediments, no smaller than the smallest extant modern microbes (i.e., >0.01 μm^3), comprised of kerogen, part of a larger population of similar morphologies, hollow structures, and show cellular elaborations. Subsequently, a number of authors proposed additional criteria to assess the morphology, ontogeny, metabolism, behavior, taphonomy, chemistry, and geological context of purported microfossils (Schopf & others, 2010; Brasier & Wacey, 2012; Rouillard & others, 2018; Javaux, 2019; Rouillard & others, 2021). For example, *bona fide* microfossils should have a stable species-specific morphology with a unimodal size distribution and would exhibit evidence of development (e.g., cell division and development of branching filaments), distinct cell wall ultrastructures, taphonomic degradation (e.g., degradation of cytoplasm, deflation of cell vesicles, and deformation of cell walls and sheaths), ecological interactions (e.g., aggregations and attachment to substrates), and metabolic activities (e.g., organic C and N isotope signatures, trace metal enrichment) (Lepot, 2020).

Recent exploration of ancient microfossils have pushed the envelope beyond the preservation of organic-walled structures in sedimentary rocks as stipulated by Buick (1990). Coccoidal, rod-shaped, and filamentous structures preserved in igneous rocks, sometimes with no traces of organic walls, may represent evidence for ancient life, including both prokaryotes and eukaryotes (Fig. 7.1) (Bengtson & others, 2017; Ivarsson & others, 2020). More controversial are micrometer-sized titanite filaments or microtextures in altered volcanic glass of Paleoarchean pillow basalts that have been interpreted as bioerosional structures or trace fossils produced by chasmoendolithic and euendolithic microbes (Fig. 7.2) (Furnes & others, 2004; Staudigel & others, 2006) and micrometer-sized hematitic tubular

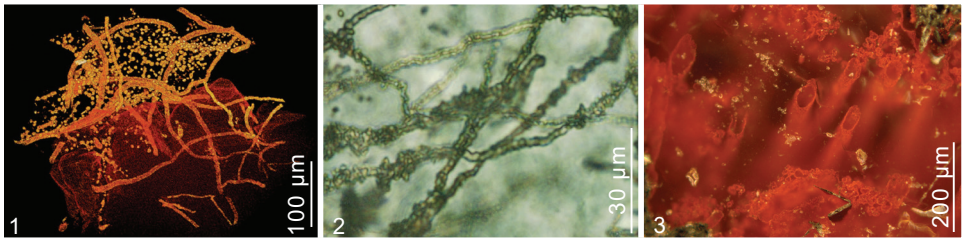

Fig. 7. Coccoidal, filamentous, and tubular structures with no preservation of organic walls. *1*, synchrotron-based X-ray tomographic rendition of coccoidal structures (interpreted as unicellular prokaryotes) suspended in filamentous cobweb-like structures (interpreted as fungal hyphae) from Koko Seamount (Ivarsson & others, 2020, fig. 4C); *2*, titanite microtextures from the ~3350 Ma Euro Basalt in Western Australia (see McLoughlin & others, 2020) (new; image by Nicola McLoughlin); *3*, hematitic tubes in chert from jasper banded iron formation in hydrothermal vent deposits of the Nuvvuagittuq Supracrustal Belt (NSB) in Québec, Canada, constrained between ~3750 and ~4280 Ma (Dodd & others, 2017, fig. 2e). Photographed in a one-cm-thick polished slab under dark-field reflected light. *1* is courtesy of Magnus Ivarsson and Stefan Bengtson; *2* courtesy of Nicola McLoughlin; and *3* courtesy of Matthew Dodd and Dominic Papineau.

structures from >3.77 Ga ferruginous sedimentary rocks in the Nuvvuagittuq supracrustal belt in Canada that are regarded as putative microfossils, possibly representing iron-oxidizing bacteria (Fig. 7.3) (Dodd & others, 2017). Given that inorganic and morphologically simple tubes and spheres can be produced abiotically (García-Ruiz & others, 2003; García-Ruiz & others, 2017; McMahon, 2019), extra efforts must be made to affirm the biogenicity of these purported microfossils, and alternative abiotic origins must be ruled out before they can be considered evidence for ancient life (Staudigel & others, 2008; Grosch & McLoughlin, 2014; McMahon, 2019; McLoughlin & others, 2020). Controversies notwithstanding, igneous rocks and inorganic preservation may represent underexplored archives of microbes in deep time and deep Earth (Ivarsson & others, 2020).

AFFINITY

With syngenicity and biogenicity established, the next challenge is to assess the affinity of the microfossils: whether they are prokaryotes or eukaryotes, and which group of prokaryotes they belong to. The most common microfossils are filaments, bacilloids, and coccoids, but these morphotypes occur in both eukaryotes and prokaryotes. To complicate interpretations further, subcellular structures such as melanosomes can be superficially similar in size and shape to bacilloidal and coccoidal bacteria (Moyer & others, 2014; Vinther, 2015), although they are less relevant in the study of Precambrian microfossils. Eukaryotic cells are typically larger than prokaryotic cells, but there is a significant overlap (Schopf, 1992b; Pang & others, 2018). Thus, cell size is a suggestive but inconclusive criterion. Other morphological features, such as branching filaments, fused filaments, anastomosed filaments, coccoidal diads and tetrads, cell differentiation, and cell wall ornaments can be useful in distinguishing eukaryotic from prokaryotic microfossils. Typically, eukaryotic cells are morphologically more complex than prokaryotic cells. However, many of the features listed above may occur in bacterial cells. For example, actinobacteria can develop branching filaments and some of them (e.g., *Streptomyces* Waksman & Henrici, 1943) have been reported to form anastomosis of network (Erikson, 1949; Gregory, 1956). A number of cyanobacteria can develop branching filaments (e.g., *Fischerella* Gomont, 1895), coccoidal diads and tetrads (e.g., *Chroococcus* Nägeli, 1849 and *Gloeocapsa* Kützing, 1843), and morphologically and functionally differentiated cells (e.g., heterocysts and akinetes in *Anabaena* Bory *ex* Bornet & Flahault, 1886b) (Castenholz, 2001). Thus, these features are not exclusively eukaryotic, and

only more complex features such as spinose cell wall ornaments, differentiated holdfast, apical meristem, and parenchymatous thallus are regarded diagnostic characters for eukaryotes (Knoll & others, 2006). Cell wall ultrastructures can also be useful. For example, the trilaminar structure with two electron-dense layers around a thicker electron-tenuous layer is said to be characteristic of eukaryotic cell walls (Javaux, Knoll, & Walter, 2004; Moczydłowska, Schopf, & Willman, 2010), although cell wall ultrastructures of modern eukaryotes and prokaryotes have not been thoroughly surveyed. Geochemical evidence can also be used to infer the prokaryotic versus eukaryotic affinities of microfossils. For example, combined micro-FTIR (Fourier-transform infrared spectroscopy) and Raman spectroscopic data—that is, FTIR CH3/CH2 absorbance ratio and Raman I-1350/I-1600 ratio of carbonaceous material—may be useful in distinguishing prokaryotic from eukaryotic microfossils (Igisu & others, 2009; Qu & others, 2015; Qu & others, 2018; Bonneville & others, 2020), although diagenetic and thermal alteration of these parameters has not been completely understood (Igisu & others, 2018). As another example, methanogenic archaea can generate large carbon isotope fractionations that can be preserved in the geological record (Stueken & others, 2017; Lepot, 2020). The assignment of prokaryotic microfossils to the various phylogenetic and physiological groups is another major challenge; but ecological, morphological, and chemical comparison with modern prokaryotic groups can provide some insights. This is discussed below for selected groups of prokaryotic microfossils.

SELECTED GROUPS OF PROKARYOTIC MICROFOSSILS

CYANOBACTERIA

Modern cyanobacteria consist of five morphological groups (Castenholz, 2001). Subsection I includes unicellular/colonial cyanobacteria that reproduce by binary fission (e.g., *Prochlorococcus* Chisholm & others, 1992, *Synechococcus* Nägeli, 1849, *Gloeocapsa*, *Entophysalis* Kützing, 1843, *Chroococcus*). Subsection II includes unicellular/colonial cyanobacteria that reproduce by internal multiple fissions and formation baeocytes (e.g., *Pleurocapsa* Thuret in Hauck, 1885, *Hyella* Bornet & Flahault, 1888). Subsection III (e.g., *Lyngbya* Agardh *ex* Gomont, 1892b, *Microcoleus* Desmazières *ex* Gomont, 1892a, *Oscillatoria* Vaucher *ex* Gomont, 1892b, *Spirulina* Turpin *ex* Gomont, 1892b, *Trichodesmium* Ehrenberg *ex* Gomont, 1892b) and Subsection IV (e.g., *Anabaena, Nostoc* Vaucher *ex* Bornet & Flahault, 1886b, *Calothrix* Agardh *ex* Bornet & Flahault, 1886a) are both characterized by uniseriate and unbranched trichomes produced by binary fission in one plane, but the latter have differentiated cells (e.g., specialized N_2-fixing heterocysts and resting akinetes). Subsection V is characterized by multiseriate or branching trichomes produced by binary fission in more than one plane, with some members having differentiated heterocysts (e.g., *Stigonema* Agardh *ex* Bornet & Flahault 1886c, *Fischerella*). Recent Phylogenetic analyses indicate that Subsections IV and V are monophyletic groups, whereas the other three are paraphyletic (Sánchez-Baracaldo, 2015; Schirrmeister, Gugger, & Donoghue, 2015).

Cyanobacteria play a major role in modern ecosystems and in the global carbon and oxygen cycles. The cyanobacteria *Prochlorococcus* and *Synechococcus* are the most abundant photosynthetic organisms in modern oceans, accounting for about 10% of the total ocean picoplankton cells in the euphotic zone and responsible for as much as 25% of ocean net primary productivity (Flombaum & others, 2013). A single cyanobacterial genus, *Trichodesmium*, is responsible for nearly 50% of global marine N_2 fixation (Sohm, Webb, & Capone, 2011; Bergman & others, 2013). Benthic cyanobacteria are also important sedimentary agents. They build microbial mats and stromatolites (Stal, 2012), stabilize sediments (Noffke, 2010), and perform bioerosion and

biodegradation (Golubic, Pietrini, & Ricci, 2015). Cyanobacteria also played a transformative role in Earth history. The origin of oxygenic photosynthesis in a common ancestor of cyanobacteria is the geobiological foundation of the Great Oxidation Event and the origin of photosynthetic eukaryotes (Knoll, 2008). Thus, it is expected that cyanobacteria should be richly archived in the geological record. Indeed, they are the most common and widespread prokaryotic microfossils in the geological record, and some of the Precambrian microfossils first reported in the literature were compared and identified with cyanobacteria (Barghoorn & Tyler, 1965; Cloud, 1965).

A number of researchers have reviewed Precambrian cyanobacterial microfossils from different perspectives (Knoll & Golubic, 1992; Golubic & Lee, 1999; Schopf, 2012; Sergeev, Sharma, & Shukla, 2012; Knoll, 2015; Schirrmeister, Sánchez-Baracaldo, & Wacey, 2016; Demoulin & others, 2019). The identification of cyanobacterial microfossils is based on their combined morphologic, taphonomic, paleoecological, paleoenvironmental, and behavioral features that are considered with modern counterparts (Knoll & Golubic, 1992; Golubic & Lee, 1999). Relative to other bacteria, cyanobacteria are typically larger in size and more complex in morphologies, some have sheaths, many are associated with stromatolites, and they commonly live in the photic zone or shallow marine environments where silicification occurs, although there are aspects of morphological and ecological convergences between cyanobacteria and some mat-forming sulfide-oxidizing bacteria. Some purported cyanobacterial fossils are morphologically simple. Examples include micrometer-sized coccoids such as *Myxococcoides* Schopf, 1968 (Fig. 1.7) and tubular filaments such as *Siphonophycus* Schopf, 1968 (Fig. 1.9–1.12; Fig. 2.4). Their cyanobacterial interpretation is primarily based on their preservation, sometimes in life position (Fig. 1.8–1.9) in stromatolitic laminae (Golubic & Lee, 1999; Cao, Yuan, & Xiao, 2001)—it is assumed that these stromatolites were likely constructed by cyanobacteria. Others have a combination of morphologies and ecologies that support a cyanobacterial interpretation. These include *Eoentophysalis* Hofmann, 1976 with colonial coccoidal cells forming microbial crusts (Fig. 1.5); *Eohyella* Zhang & Golubic, 1987 being euendolithic and psuedofilamentous; and *Polybessurus* Green & others, 1987, with a stalk consisting of stacked cup-like gelatinous material (Fig. 1.6). Still others are character-rich and have distinctive, if not diagnostic, cyanobacterial features such as fossilized akinetes. The co-occurrence of *Archaeoellipsoides* Horodyski & Donaldson, 1980 and *Filiconstrictosus* Schopf & Blacic, 1971—which are interpreted as akinetes and short-trichome germlings, respectively—from the Mesoproterozoic Billyakh Group in Siberia provides a plausible case for fossil akinetes (Golubic, Sergeev, & Knoll, 1995; Sergeev, Knoll, & Grotzinger, 1995). Akinetes also occur in the Tonian fossil *Anhuithrix* Pang & others, 2018, and both akinetes and heterocysts have been reported in the Devonian microfossils *Langiella* Croft & George, 1959 and *Kidstoniella* Croft & George, 1959. These features facilitate morphological comparisons with modern cyanobacteria, where akinetes and heterocysts occur only in Subsections IV–V (Castenholz, 2001; Uyeda, Harmon, & Blank, 2016, fig. S7). Various ecological and morphological comparisons have been proposed for a number of well-known cyanobacterial fossils (Table 1, p. 18–19), many of which were named after their modern counterparts (Schopf, 1994; Knoll, 2015). Accepting the interpretations presented in Table 1, all five cyanobacterial subdivisions are represented in the fossil record.

When did cyanobacteria first evolve? This question can be addressed from the perspectives of molecular clocks, geochemical signatures, and fossils, but currently available data do not provide a tight constraint on this important evolutionary event. Molec-

ular clocks give divergent results, with the estimated divergence time of crown-group cyanobacteria ranging widely from more than 3600 Ma to less than 2000 Ma, with very large error bars (Schirrmeister, Gugger, & Donoghue, 2015; Shih & others, 2017; see summary in Demoulin & others, 2019; Garcia-Pichel & others, 2019). Stable carbon isotope signatures of Archean organic carbon are consistent with but are not uniquely diagnostic of cyanobacterial metabolism (Demoulin & others, 2019), although Lyons, Reinhard, and Planavsky (2014) argue that the total organic carbon content in Archean shales presents strong evidence for oxygenic photosynthesis (and perhaps cyanobacteria) before the Great Oxidation Event at 2320–2450 Ma (Bekker & others, 2004; Holland, 2006; Luo & others, 2016). The report of 2-methylhopanoids—which were regarded as a biomarker of cyanobacteria—from the ~2700 Ma Jeerinah Formation in Western Australia (Brocks & others, 1999) was later shown to be compromised by contaminations (Rasmussen & others, 2008; French & others, 2015), leaving the 1.64 Barney Creek Formation in Western Australia as the oldest known unit to contain appreciable amount of 2-methylhopanoids (Summons & others, 1999; Brocks & others, 2005). More recent studies, however, have brought uncertainty to the interpretation of 2-methylhopanoids as a cyanobacterial biomarker; it seems that 2-methylhopanoids can also be produced by diverse alphaproteobacteria, including the anoxygenic purple nonsulfur phototroph *Rhodopseudomonas palustris* (Rashby & others, 2007) and the nitrifying bacterium *Nitrobacter vulgaris* (Elling & others, 2020). Thus, it is possible that the biochemical capability to synthesize 2-methylhopanoids may have a broader phylogenetic distribution and a deeper evolutionary history than cyanobacteria. More convincing biomarker evidence for cyanobacteria comes from fossil porphyrins, coupled with compound-specific nitrogen isotope data, from the ~1100 Ma El Mreïti Group in the Taoudeni Basin of Mauritania in northwestern Africa (Gueneli & others, 2018).

The Archean micropaleontological record is sparse and intensely debated. Various microfossils have been reported from the ~3400–3500 Ma Warrawoona Group and Strelley Pool Formation in Western Australia (Schopf, 2006a; Schopf, 2006b; Sugitania & others, 2013), and some have been compared with and interpreted as cyanobacteria (Awramik, Schopf, & Walter, 1983; Schopf & Packer, 1987; Schopf, 1993), although their biogenicity is a continual debate (Buick, 1984; Brasier & others, 2002; Wacey, Eiloart, & Saunders, 2019). More convincing Archean and early Paleoproterozoic filamentous microfossils have been known from ~3235 Ma volcanogenic massive sulfide deposit in in Sulfur Spring Group (Rasmussen, 2000) and the 2450–2210 Ma Kazput Formation of the Turee Creek Group in Western Australia (Schopf & others, 2015; Fadel & others, 2017; Barlow & Kranendonk, 2018), but none of these have been interpreted as cyanobacterial filaments. Filamentous microfossils described as *Siphonophycus transvaalensis* Beukes, Klein, & Schopf in Klein, Beukes, & Schopf, 1987 from the ~2500 Ma Gamohaan Formation and the ~2600 Ma Campbellrand Group of the Transvaal Supergroup in South Africa are among the oldest microfossils that have been interpreted as cyanobacteria (Klein, Beukes, & Schopf, 1987; Altermann & Schopf, 1995), but the simple morphology of *Siphonophycus* (see Fig. 1.9–1.12, 2, 4, 6.2–6.3) means that this interpretation is open to scrutiny. Indeed, among the genera listed in Table 1, only *Eoentophysalis* (Fig. 1.5), *Eohyella*, and *Polybessurus* (Fig. 1.6) are regarded as uncontested cyanobacteria (Demoulin & others, 2019), although several others are likely or probable cyanobacteria when additional paleonenvironmental and taphonomic conditions are considered together with morphological features (Knoll, 2015). As such, *Eoentophysalis belcherensis* Hofmann, 1976 from the 2015–2018 Ma Belcher

Table 1. Selected microfossils that have been interpreted as cyanobacteria. With the exception of *Anhuithrix* Pang & others, 2018, most are a few to a few tens of micrometers in cell/trichome diameter/width. See Demoulin & others (2019) for a more complete list of occurrences.

Fossil genus	Proposed cyanobacterial features	Oldest occurrence	Proposed modern analogs	Cyanobacteria?
Eosynechococcus Hofmann, 1976 (Fig. 6.6)	Rod-shaped cells, no sheath, sometimes two cells attached end-to-end, indicating symmetrical transverse binary fission in a single plane	2015–2018 Ma Belcher Supergroup, Canada (Hofmann, 1976; Hodgskiss & others, 2019)	*Synechococcus,* Subsection I	Probable
Gloeocapsomorpha Zalessky, 1917	Nested planar cell aggregates surrounded by multilaminated sheaths	Middle Ordovician oil shale, Baltic Shale Basin, Estonia (Zalessky, 1917; Foster, Reed, & Wicander, 1989)	*Gloeocapsa* & *Entophysalis,* Subsection I	Possible
Eoentophysalis Hofmann, 1976	Layers or crusts consisting of solitary cells, paired cells, planar tetrads, or irregular clusters of cells embedded in multilaminated sheaths	2015–2018 Ma Belcher Supergroup, Canada (Golubic & Hofmann, 1976; Hofmann, 1976; Hodgskiss & others, 2019)	*Entophysalis,* Subsection I	Likely
Palaeopleurocapsa Knoll, Barghoorn, & Golubic, 1975.	Sheathed pseudofilamentous cell packets	~800 Ma Skillogalee Dolomite, Adelaide Geosyncline, southern Australia (Knoll, Barghoorn, & Golubic, 1975).	*Pleurocapsa,* Subsection II	Probable
Eohyella Zhang & Golubic, 1987	euendolithic pseudofilamentous cyanobacterium	~1625 Ma Dahongyu Formation, North China (Zhang & Golubic, 1987)	*Hyella,* Subsection II	Likely
Polybessurus Green & others, 1987 (Fig. 1.6)	Spherical cell subtended by a cylindrical stalk consisting of stacked cup-like envelopes and may have reproduced by baeocytes	~1200 Ma Avzyan Formation, Ural Mountains, Russia (Sergeev, 1994); ~1050 Ma Uluksan Group (Kah & Knoll, 1996; Gibson & others, 2018); Tonian Eleanor Bay Supergroup in eastern Greenland (Green & others, 1987); Tonian Draken Formation in Svalbard (Knoll, Swett, & Mark, 1991)	*Cyanostylon,* Subsection II	Likely
Palaeolyngbya Schopf, 1968	Cellular trichome singularly enclosed in sheath	Tonian (~825 Ma) Bitter Springs Group, Australia (Schopf, 1968; Normington & others, 2019)	*Lyngbya,* Subsection III	Probable
Oscillatoriopsis Schopf, 1968	Unsheathed uniseriate trichome, cells wider than long, slightly differentiated apical cells	Tonian (~825 Ma) Bitter Springs Group, Australia (Schopf, 1968; Normington & others, 2019)	*Oscillatoria,* Subsection III	Probable
Obruchevella Reitlinger, 1948	Helical tubular filaments	~1560 Ma Gaoyuzhuang Formation, North China (Shi & others, 2017)	*Spirulina,* Subsection III	Possible

Table 1 *continued on next page*

Fossil genus	Proposed cyanobacterial features	Oldest occurrence	Proposed modern analogs	Cyanobacteria?
Siphonophycus Schopf, 1968 (Fig. 1.9–1.12, 2,4)	Tubular filament interpreted as cyanobacterial sheaths; form genus	~2600 Ma Campbellrand Group (Altermann & Schopf, 1995) and ~2500 Ma Gamohaan Formation (Klein, Beukes, & Schopf, 1987), both of Transvaal Supergroup, South Africa	Tubular sheath of Subsection III filaments	Probable
Eoschizothrix	Sheathed multitrichomous filaments	~1560 Ma Gaoyuzhuang Formation, North China Craton (Lee & Golubic, 1998)	*Microcoleus* & *Schizothrix* Subsection III	Probable
Archaeoellipsoides Horodyski & Donaldson, 1980 (Fig. 1.4)	Large (~100 µm) elongate sausage-shaped vesicles interpreted as isolated akinetes, sometimes co-occurring with short trichomes interpreted as germlings (Sergeev, Knoll, & Grotzinger, 1995)	(?) ~2100–2040 Ma Francevillian Group (Amard & Beertrand-Sarfati, 1997); ~1560 Ma Gaoyuzhuang Formation, North China Craton (Shi & others, 2017); 1653–1647 Ma McArthur Group, Australia (Tomtani & others, 2006); 1400–1500 Ma Billyakh Group, Siberia (Golubic, Sergeev, & Knoll, 1995; Sergeev, Knoll, & Grotzinger, 1995; Gorokhov & others, 2019); ~1400 Ma Dismal Lake Group, Canada (Horodyski & Donaldson, 1980)	Akinetes of Member IV cyanobacteria	Likely
Veteronostocale Schopf & Blacic, 1971	Unsheathed uniseriate trichome with rounded cells, no apical attenuation	Tonian (~825 Ma) Bitter Springs Group, Australia (Schopf & Blacic, 1971; Normington & others, 2019)	*Nostoc,* Subsection IV according to Schopf & Blacic (1971)	Probable
Anhuithrix Pang & others, 2018	Unbranched, uniseriate trichomes with sheathed vegetative cells and akinetes	Tonian Liulaobei Formation, North China (Pang & others, 2018)	*Anabaena* & *Nostoc,* Subsection IV	Likely
Langiella Croft & George, 1959 & *Kidstoniella* Croft & George, 1959	Branching trichomes with sheathed cells as well as differentiated heterocysts and (in *Langiella*) akinetes	Early Devonian (~400–412 Ma) Rhynie Chert, Scotland (Croft & George, 1959)	*Stigonema,* Subsection V	Likely

Supergroup in Canada (Hofmann, 1976; Hodgskiss & others, 2019) represents the oldest unequivocal cyanobacterial fossil and provides a minimum age constraint on cyanobacterial divergence (Fig. 8).

Stromatolites have been reported from a number of Archean successions. Putative stromatolites are known from the ~3470 Ma Dresser Formation in Western Australia (Fig. 9.1) (Buick, Dunlop, & Groves, 1981). Conical stromatolites from the ~3430 Ma Strelley Pool Formation in Western Australia (Fig. 9.2) are regarded as biosedimentary structures (Hofmann & others, 1999; Allwood & others, 2006), possibly related to cyanobacterial activities (Schopf, 2012). More convincing evidence for cyanobacterial metabolism comes from disrupted stromatolitic laminae due to bubble formation related to oxygenic photosynthesis (Bosak & others, 2009), and such evidence first appears in stromatolites from the ~2700 Ma Tumbiana Formation in Western Australia (Fig. 9.3). Consistent with

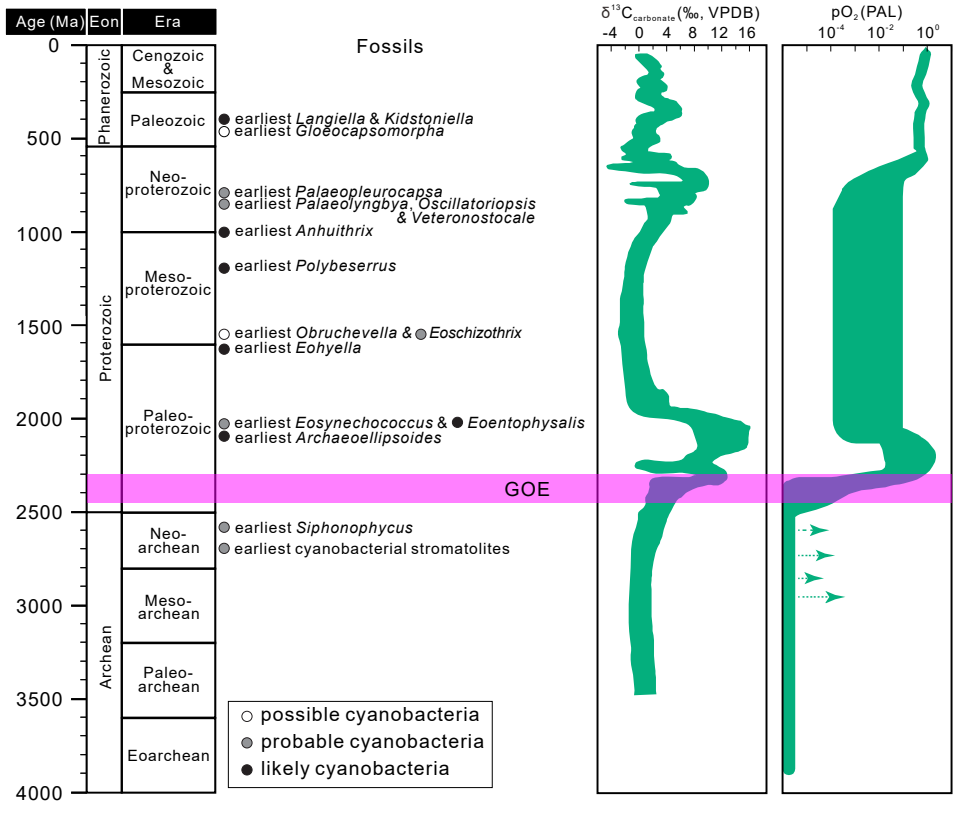

FIG. 8. Geological distribution of cyanobacterial microfossils. Hollow, gray, and solid circles represent the oldest known occurrence of possible, probable, and likely cyanobacterial microfossils. Purple bar represents the Great Oxidation Event (GOE) (adapted from Xiao & Tang, 2018 and Demoulin & others, 2019, and based on data in Table 1).

this inference, limited evidence for Fe and S cycling in strata hosting the Tumbiana stromatolites indicates photoautotrophy using water rather than iron or sulfur as electron donors (BUICK, 1992; STUEKEN & others, 2017). Overall, microfossils and stromatolites indicate that cyanobacteria may have diverged between 2700 Ma and 2000 Ma. If one accepts that the origin of cyanobacteria must predate the Great Oxidation Event (BEKKER & others, 2004; HOLLAND, 2006; LUO & others, 2016), this window can be further narrowed to be 2700–2450 Ma (Fig. 8).

NON-CYANOBACTERIAL MICROBES

The identification of non-cyanobacterial microbes in the geological record is usually based only on geochemical data (e.g., carbon, iron, and sulfur isotopes) indicative of specific physiology or metabolism (e.g., STUEKEN & others, 2017; LEPOT, 2020). Thus, unlike cyanobacterial fossils, these inferred physiologies—because of their diverse phylogenetic distributions—do not define monophyletic groups. For example, iron oxidation (EMERSON, FLEMING, & MCBETH, 2010), dissimilatory iron reduction (LOVLEY, 2013), dissimilatory sulfate/sulfur reduction (CANFIELD & RAISWELL, 1999), and methanotrophy (HANSON & HANSON, 1996; KNITTEL & others, 2005) occur in both bacteria and archaea. And methanogensis occurs in multiple archaeal groups (LYU & LIU, 2018). Nonetheless, there are reports of body fossils of non-cyanobacterial prokaryotes, and their interpretations are sometimes based

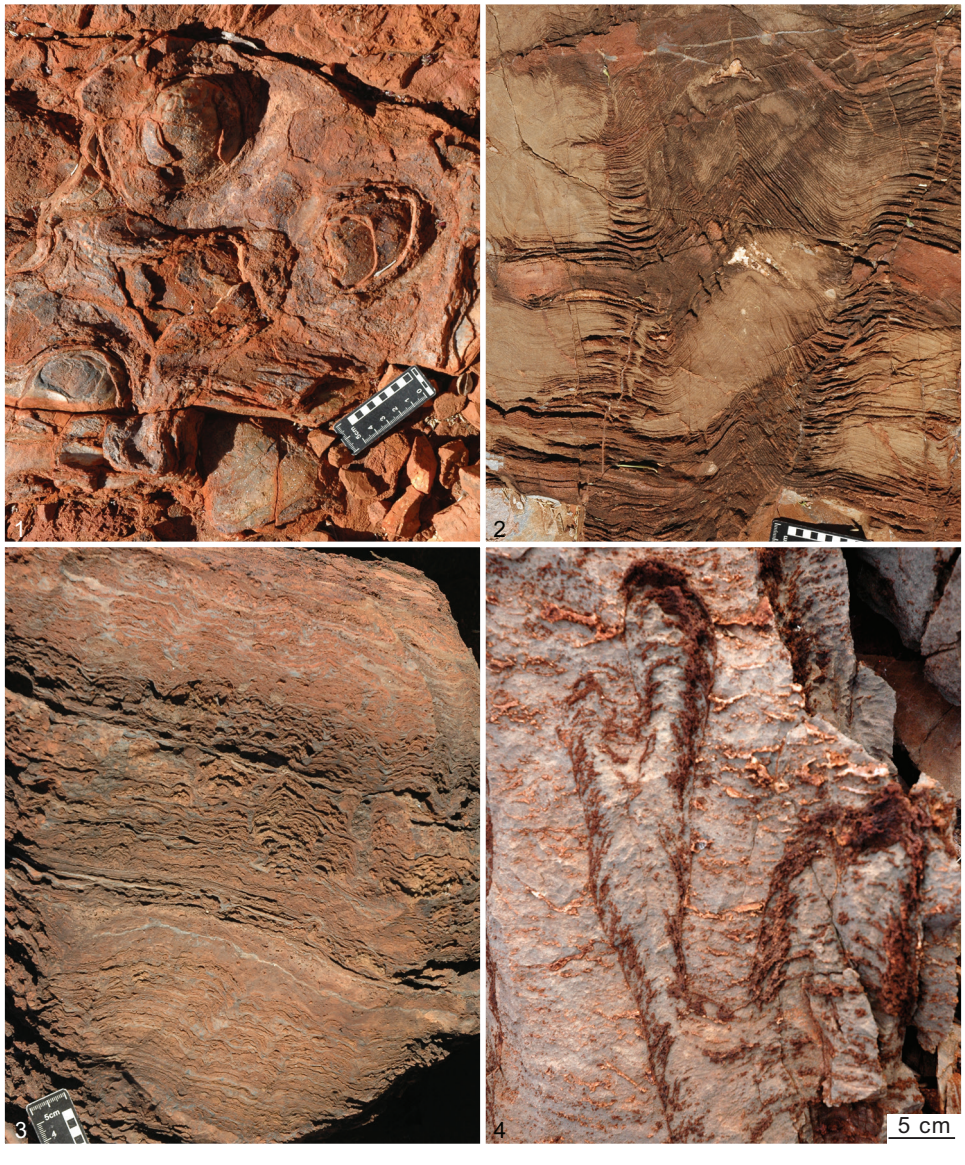

FIG. 9. Field photographs of representative Archean and Paleoproterozoic stromatolites. 1, possible coniform stromatolites (top view) from the ~3470 Ma Dresser Formation, North Pole, Western Australia (Buick, Dunlop, & Groves, 1981); 2, Conical stromatolite (vertical cross-sectional view) from the ~3430 Ma Strelley Pool Formation in Western Australia (Hofmann & others, 1999; Allwood & others, 2006); 3, microbial stromatolites (cross-sectional view) from the ~2700 Ma Tumbiana Formation of the Fortescue Group in Western Australia (AWRAMIK & BUCHHEIM, 2009); 4, branching stromatolites (cross-sectional view) from the ~2450–2210 Ma Kazput Formation of the Turee Creek Group in Western Australia (Martindale & others, 2015). All photos are new and by Shuhai Xiao.

on characteristic morphological features and aided by geochemical data. These are briefly described below.

IRON-METABOLIZING MICROBES

Iron is involved in the metabolism of diverse bacteria and archaea, including dissimilatory Fe^{3+} reducing or Fe^{3+} respiring bacteria (Lovley, 2013) such as *Geobacter* Lovley & others, 1993 and *Shewanella* MacDonell & Colwell, 1985, Fe^{2+} oxidizing bacteria (some of which are anoxygenic phototrophs) (Brock & others, 1994), and magnetotactic bacteria (Bazylinski & Frankel, 2003). There are a number of reports of iron-oxidizing microbial fossils. For example, *Frutexites*-like microstromatolites in Cenozoic basaltic seafloor are interpreted as structures produced by biofilms involving iron-oxidizing bacteria (Heim & others, 2017; Ivarsson & others, 2020). Some filamentous microfossils from the Ediacaran Qigebulake Formation in China (Zhou & others, 2015), the ~1880 Ma Gunflint Formation in Canada (Barghoorn & Tyler, 1965; Cloud, 1965), and the ~2450–2210 Ma Kazput Formation of the Turee Creek Group in northwestern Australia(Fadel & others, 2017) were compared with iron-oxidizing bacteria, but these microfossils do not seem to have diagnostic features uniquely characteristic of iron bacteria. Similarly, the Gunflint microfossil *Eoastrion* Barghoorn in Barghoorn & Tyler, 1965 (Fig. 1.3) has been compared with the extant Fe- and Mn-oxidizing bacterium *Metallogenium* Perfilev & Gabe, 1961 (Cloud, 1965; Zavarzin, 1981), although the nature of *Metallogenium* remains enigmatic (Klaveness, 1999), and a recent study of *Eoastrion*-like structures from the ~2100 Ma FC Formation of the Francevillian in Gabon was unable to unequivocally confirm its biogenicity (Lekele Baghekema & others, 2017). Additionally, tubular structures from the >3750 Ma Nuvvuagittuq supracrustal belt in Canada (Fig. 7.3) were tentatively compared with iron-oxidizing bacteria (Dodd & others, 2017), but their biogenicity has been debated (McMahon, 2019). Some extant iron-oxidizing bacteria do produce morphologically distinct stalks (e.g., branching and twisted Fe-oxyhydroxide stalks in *Gallionella*) (Chan & others, 2011) that can be preserved in the fossil record and thus offer promising diagnostic features for this group of bacteria (Johannessen & others, 2020). Morphologically similar stalks have been reported from Jurassic hydrothermal deposits at ODP site 801 in the western Pacific Ocean (Krepski & others, 2013), Pennsylvanian coal beds in Ohio, USA (e.g., Schopf & others, 1965, fig. 12), the late Paleoproterozoic (~1700 Ma) Jhamarkotra Formation in India (Crosby, Bailey, & Sharma, 2014), the late Paleoproterozoic Chuanlinggou Formation in the North China Craton (Lin & others, 2019), and late Paleoproterozoic (1.74 Ga) jasper in the lower Cleopatra Rhyolite in central Arizona, USA (Little & others, 2021). These are intriguing and more convincing evidence for iron-oxidizing bacteria in the fossil record.

Both microaerophilic iron-oxidizing bacteria and anoxygenic photoferrotrophs have been implicated in the deposition of Precambrian banded iron formations (Kappler & others, 2005; Konhauser & others, 2002; Chi Fru & others, 2013; Chan, Emerson, & Luther, 2016). If so, then Archean and Paleoproterozoic banded iron formations can be regarded as indirect evidence for iron-oxidizing bacteria (see Heimann, 2021, Chapter 6). In fact, Chi Fru and others (2013) reported what appears to be anoxygenic photoferrotroph fossils from a Quaternary hydrothermal vent field on Milos Island, Greece.

Magnetotactic bacteria represent a special group of iron bacteria that can uptake complexed ferric iron and, through reduction and partial oxidation of Fe, precipitate intracellular magnetite (Fe_3O_4) or greigite (Fe_3S_4) nanocrystals in membranous magnetosomes (Bazylinski & Frankel, 2003). Magnetite crystals produced by magnetotactic bacteria have distinct morphologies

and crystallographic features that allow their identification in the fossil record (see Fig. 5) (Bazylinski & Frankel, 2003; Li & others, 2020). Magnetofossils have been reported from Mesozoic and Cenozoic sediments (Chang & Kirschvink, 1989; Kopp & Kirschvink, 2008; Roberts & others, 2011) and even Precambrian stromatolites (Chang & others, 1989).

SULFUR-METABOLIZING MICROBES

Sulfur cycling in the water column and sediments can be inferred from geochemical data. For example, sulfate reduction, sulfide oxidation, and sulfur disproportionation can be inferred from sulfur isotope data (Canfield & Raiswell, 1999; Shen & Buick, 2004; Johnston & others, 2005), and anoxygenic photosynthesizers such as green and purple sulfur bacteria can be inferred from biomarker data (Brocks & others, 2005). The body fossil record of sulfur-metabolizing microbes is scarce, primarily because they generally do not have diagnostic morphological features. Nonetheless, sulfur-metabolizing microbial fossils have been reported in the literature. For example, Schopf and others (2015) reported filamentous microbial communities from the Paleoproterozoic Turee Creek Group and Duck Creek Formation in Australia, and interpreted them as sulfureta in which sulfate/sulfur-reducing and sulfide-oxidizing microbes worked together to cycle sulfur species. This interpretation is based on inferred community ecology and the cobweb-like microbial fabrics that are often found in sulfureta. It is possible that these microbes also recycled iron species (Fadel & others, 2017). Additionally, Bailey and others (2013) reported septate filamentous microfossils with sparse intracellular sulfur globules from the Ediacaran Doushantuo Formation and interpreted them as sulfide-oxidizing bacteria analogous to the extant *Beggiatoa*. Finally, Bailey and others (2007) interpreted the animal embryo-like microfossil *Megasphaera* Chen & Liu, 1986 from the Ediacaran Doushantuo Formation in the South China Craton as a giant sulfide-oxidizing bacterium analogous to the extant genus *Thiomargarita*, but this interpretation has been refuted (Xiao, Zhou, & Yuan, 2007; Cunningham & others, 2012).

METHANOGENS AND METHANOTROPHS

Microbial activities of methanogens in the geological record are chiefly inferred from $\delta^{13}C$ data, because they produce a CH_4 pool extremely depleted in ^{13}C and correspondingly a CO_2 pool enriched in ^{13}C (Lepot, 2020). This isotopic signal can be recorded as extremely high $\delta^{13}C_{carb}$ values of carbonate sourced from the CO_2 pool as long as CH_4 is effectively removed from the system (Sun & others, 2020) or as extremely negative $\delta^{13}C_{carb}$ values of carbonate related to anaerobic oxidation of methane (Jiang, Kennedy, & Christie-Blick, 2003; Wang & others, 2008), or as extremely negative $\delta^{13}C_{org}$ values of organic carbon produced by methanotrophs or methylotrophs in general (Stueken & others, 2017; Xiao & others, 2017). Thus, extremely negative $\delta^{13}C_{org}$ values (as low as −57‰) from the ~2700 Ma Fortescue Group in Western Australia indicate that both methanogens and methanotrophs must have evolved by the Neoarchean. Body fossils of methanotrophs or methylotrophs, however, are extremely rare, although Sun and others (2020) recently reported micrometer-sized coccoidal methanogens from dolomite concretions in Permian lacustrine deposits of northwestern China. These coccoids are morphologically indistinct and their interpretation as fossil methanogens was largely based on the extremely positive $\delta^{13}C_{carb}$ values of the host dolomite concretions.

SUMMARY AND FUTURE PROSPECTS

Prokaryotes (bacteria and archaea) are ubiquitous, abundant, and physiologically diverse. They play essential roles in modern Earth systems and were likely as important in the geological past as they are today. Yet,

their fossil record is rather sparse, and the prokaryote paleontology is a relatively young science. Since the 1950s, however, we have learned a great deal about prokaryotes in the geological past and the field continues to grow rapidly. Prokaryotic microfossils are known in a number of taphonomic modes: silicification, phosphatization, calcification, pyritization, carbonaceous compression in fine-grained siliciclastic sediments and in amber, biomineral preservation, and trace fossil preservation. The study of prokaryotic microfossils faces many challenges. Given their microscopic sizes, simple morphologies, and possible confusion with biomorphs and eukaryotic microbes, it is a difficult task to demonstrate the syngenicity, biogenicity, and phylogenetic affinity of purported prokaryotic microfossils. Nonetheless, authentic prokaryotic microfossils are known in the geological record, and they extend as far back as 3200 Ma and perhaps 3500 Ma. Some of these microfossils can be assigned to phylogenetic or physiological groups, including cyanobacteria, iron-oxidizing bacteria, magnetotactic bacteria, sulfur-oxidizing bacteria, and methanogens. Of these, cyanobacteria have the richest record, one that goes back to 2000 Ma and perhaps 2700 Ma, and their identification is aided by ecological association with stromatolites and sometimes diagnostic morphological features.

Despite notable progress in the study of prokaryotic fossils since the 1950s, there remain enormous opportunities for future research. Prokaryotic micropaleontology continues to be a frontier in scientific investigation. The vast majority of prokaryotic groups are poorly (or not at all) represented in the fossil record, including archaea and various nitrogen-metabolizing microbes, which are fundamental in the origin and function of the biosphere. The full spectrum of environmental distribution of prokaryotes is poorly documented in the geological record. This is particularly true for microbes in the terrestrial realm, cryptic spaces, deep-sea settings, deep lithosphere, and other extreme environments. We know very little about how prokaryotes interacted with the environment and with other organisms in the geological record. It is likely that new advances will be made in the study of prokaryote micropaleontology at the interface with other sciences (e.g., geochemistry, sedimentology, microbiology, big data science) and advanced analytical techniques. Ultimately, the vast phylogenetic, physiological, and ecological diversity of bacteria and archaea evident today must surely have substantial geological and evolutionary roots, and much more awaits discovery.

REFERENCES

Allwood, A. C., M. R. Walter, B. S. Kamber, C. P. Marshall, & I. W. Burch. 2006. Stromatolite reef from the Early Archaean era of Australia. Nature 441:714–718 [doi:10.1038/nature04764].

Altermann, Wladyslaw. 2001. The oldest fossils of Africa: A brief reappraisal of reports from the Archean. Journal of African Earth Sciences 33:427–436 [doi:10.1016/S0899-5362(01)00089-6].

Altermann, Wladyslaw, & J. W. Schopf. 1995. Microfossils from the Neoarchean Campbell Group, Griqualand West Sequence of the Transvaal Supergroup, and their paleoenvironmental and evolutionary implications. Precambrian Research 75:65–90.

Amard, Bertrand, & Janine Bertrand-Sarfati. 1997. Microfossils in 2000 Ma old cherty stromatolites of the Franceville group, Gabon. Precambrian Research 81:197–221 [doi:10.1016/S0301-9268(96)00035-6].

Arp, Gernot, Andreas Reimer, & Joachim Reitner. 2001. Photosynthesis-induced biofilm calcification and calcium concentrations in Phanerozoic oceans. Science 292:1071–1074.

Ashley, B. E. 1937. Fossil algae from the Kundelungu Series of Northern Rhodesia. Journal of Geology 45:332–335.

Awramik, S. M., & H. P. Buchheim. 2009. A giant, Late Archean lake system: The Meentheena Member (Tumbiana Formation; Fortescue Group), Western Australia. Precambrian Research 174:215–240 [doi:10.1016/j.precamres.2009.07.005].

Awramik, S. M., J. W. Schopf, & M. R. Walter. 1983. Filamentous fossil bacteria from the Archean of Western Australia. Precambrian Research 20:357–374.

Bailey, J. V., F. A. Corsetti, S. E. Greene, C. H. Crosby, Pengju Liu, & V. J. Orphan. 2013. Filamentous sulfur bacteria preserved in modern and ancient phosphatic sediments: implications for the role of oxygen and bacteria in phosphogenesis. Geobiology 11:397–405 [doi:10.1111/gbi.12046].

Bailey, J. V., S. B. Joye, K. M. Kalanetra, B. E. Flood, & F. A. Corsetti. 2007. Evidence of giant sulphur bacteria in Neoproterozoic phosphorites. Nature 445:198–201.

Banks, H. P., K. I. M. Chesters, N. F. Hughes, G. A. L. Johnson, H. M. Johnson, & L. R. Moore. 1967. Chapter 1 Thallophyta–1. Geological Society of London Special Publications 2:163–180 [doi:10.1144/GSL.SP.1967.002.01.18].

Barghoorn, E. S., & J. W. Schopf. 1965. Microorganisms from the late Precambrian of central Australia. Science 150:337–339.

Barghoorn, E. S., & S. A. Tyler. 1965. Microorganisms from the Gunflint Chert. Science 147:563–577.

Barlow, E. V., & M. J. van Kranendonk. 2018. Snapshot of an early Paleoproterozoic ecosystem: Two diverse microfossil communities from the Turee Creek Group, Western Australia. Geobiology 16:445–479 [doi:10.1111/gbi.12304].

Bar-On, Y. M., Rob Phillips, & Ron Milo. 2018. The biomass distribution on Earth. Proceedings of the National Academy of Sciences, USA 115:6506–6511 [doi:10.1073/pnas.1711842115].

Bartley, J. K. 1996. Actualistic taphonomy of cyanobacteria: Implications for the Precambrian fossil record. Palaios 11:571–586.

Bazylinski, D. A., & R. B. Frankel. 2003. Biologically controlled mineralization in prokaryotes. Reviews in Mineralogy and Geochemistry 54:217–247.

Bekker, Andrey, H. D. Holland, P.-L. Wang, Douglas Rumble III, H. J. Stein, J. L. Hannah, L. L. Coetzee, & N. J. Beukes. 2004. Dating the rise of atmospheric oxygen. Nature 427:117–120 [doi:10.1038/nature02260].

Bengtson, Stefan, Birger Rasmussen, Magnus Ivarsson, Janet Muhling, Curt Broman, Federica Marone, Marco Stampanoni, & Andrey Bekker. 2017. Fungus-like mycelial fossils in 2.4-billion-year-old vesicular basalt. Nature Ecology & Evolution 1:0141 [doi:10.1038/s41559-017-0141].

Benzerara, Karim, Feriel Skouri-Panet, Jinhua Li, Céline Férard, Muriel Gugger, Thierry Laurent, Estelle Couradeau, Marie Ragon, Julie Cosmidis, Nicolas Menguy, Isabel Margaret-Oliver, Rosaluz Tavera, Purificación López-García, & David Moreira. 2014. Intracellular Ca-carbonate biomineralization is widespread in cyanobacteria. Proceedings of the National Academy of Sciences, USA 111:10933–10938 [doi:10.1073/pnas.1403510111].

Bergman, Birgitta, Gustaf Sandh, Senjie Lin, John Larsson, & E. J. Carpenter. 2013. *Trichodesmium*: A widespread marine cyanobacterium with unusual nitrogen fixation properties. FEMS Microbiology Reviews 37:286–302 [doi:10.1111/j.1574-6976.2012.00352.x].

Blokker, Peter, Pim van Bergen, Rich Pancost, M. E. Collinson, J. W. de Leeuw, & J. S. Sinninghe damsté. 2001. The chemical structure of *Gloeocapsomorpha prisca* microfossils: Implications for their origin. Geochimica et Cosmochimica Acta 65:885–900.

Bonneville, S. C., Frank Delpomdor, Alain Préat, Clément Chevalier, Tohru Araki, M. Kazemian, Andrew Steele, Anja Schreiber, Rainer Wirth, & L. G. Benning. 2020. Molecular identification of fungi microfossils in a Neoproterozoic shale rock. Science Advances 6:eaax7599 [doi:10.1126/sciadv.aax7599].

Bornemann, J. G. 1886. Die Versteinerungen des Cambrischen Schichten-Systems der Insel Sardinien nebst vergleichenden Untersuchungen iiber analoge Vorkommnisse aus andern Landern. Verhandlungen Der Kaiserlich Leopoldinisch-Carolinischen Deutschen Akademie Der Naturforscher 51: 1–147.

Bornet, Édouard, & Charle Flahault. 1886a. Revision des Nostocacées hétérocystées contenues dans les principaux herbiers de France. Annales des Sciences Naturelles, Botanique, Septième Série 3:323–381.

Bornet, Édouard, & Charles Flahault. 1886b. Revision des Nostocacées hétérocystées contenues dans les principaux herbiers de France (quatrième et dernier fragment). Annales des Sciences Naturelles, Botanique, Septième Série 7:177–262.

Bornet, Édouard, & Charles Flahault. 1886c. Revision des Nostocacées hétérocystées contenues dans les principaux herbiers de France (Troisième fragment). Annales des Sciences Naturelles, Botanique, Septième série 5:51–129.

Bornet, Édouard, & Charles Flahault. 1888. Note sur deux nouveaux genres d'algues perforantes. Journal de Botanique Morot 2:161–165.

Bosak, Tanja, Biqing Liang, M. S. Sim, & A. P. Petroff. 2009. Morphological record of oxygenic photosynthesis in conical stromatolites. Proceedings of the National Academy of Sciences, USA 106:10939–10943 [doi:10.1073pnas.0900885106].

Brasier, M. D., O. R. Green, A. P. Jephcoat, A. K. Kleppe, M. J. V. Kranendonk, J. F. Lindsay, Andrew Steele, & N. V. Grassineau. 2002. Questioning the evidence for Earth's oldest fossils. Nature 416:76–81.

Brasier, M. D., O. R. Green, J. F. Lindsay, Nicola McLoughlin, Andrew Steele, & Cris Stoakes. 2005. Critical testing of Earth's oldest putative fossil assemblage from the 3.5 Ga Apex chert, Chinaman Creek, Western Australia. Precambrian Research 140:55–102.

Brasier, M. D., Nicola McLoughlin, O. R. Green, & David Wacey. 2006. A fresh look at the fossil evidence for early Archaean cellular life. Philosophical Transactions of the Royal Society of London B (Biological Sciences) 361:887–902.

Brasier, M. D., & David Wacey. 2012. Fossils and astrobiology: new protocols for cell evolution in deep time. International Journal of Astrobiology 11:217–228 [doi:10.1017/S1473550412000298].

Briggs, D. E. G., & Sean McMahon. 2016. The role of experiments in investigating the taphonomy of exceptional preservation. Palaeontology 59:1–11 [doi:10.1111/pala.12219].

Brock, T. D., M. T. Madigan, J. M. Martinko, & Jack Parker. 1994. Biology of Microorganisms. Prentice Hall. Englewood Cliffs, NJ. 909 p.

Brocks, J. J., G. A. Logan, Roger Buick, & R. E. Summons. 1999. Archean molecular fossils and the early rise of eukaryotes. Science 285:1033–1036.

Brocks, J. J., G. D. Love, R. E. Summons, A. H. Knoll, G. A. Logan, & S. A. Bowden. 2005. Biomarker evidence for green and purple sulphur bacteria in a stratified Palaeoproterozoic sea. Nature 437:866–870.

Buick, Roger. 1984. Carbonaceous filaments from North Pole, Western Australia: Are they fossil bacteria in Archean stromatolites? Precambrian Research 24:157–172.

Buick, Roger. 1990. Microfossil recognition in Archean rocks: An appraisal of spheroids and filaments from a 3500 My old chert-barite unit at North Pole, Western Australia. Palaios 5:441–459.

Buick, Roger. 1992. The antiquity of oxygenic photosynthesis: evidence from stromatolites in sulfur-deficient Archean lakes. Science 255:74–77.

Buick, Roger, J. S. R. Dunlop, & D. I. Groves. 1981. Stromatolite recognition in ancient rocks: an appraisal of irregularly laminated structures in an Early Archaean chert-barite unit from North Pole, Western Australia. Alcheringa 5:161–181 [doi:10.1080/03115518108566999].

Butler, A. D., J. A. Cunningham, G. E. Budd, & P. C. J. Donoghue. 2015. Experimental taphonomy of *Artemia* reveals the role of endogenous microbes in mediating decay and fossilization. Proceedings of the Royal Socity B (Biological Sciences) 282:(20150476) [doi:10.1098/rspb.2015.0476].

Butterfield, N. J. 2002. *Leanchoilia* guts and the interpretation of three-dimensional structures in Burgess Shale-type fossils. Paleobiology 28:155–171 [doi:10.1666/0094-8373(2002)028<0155:LGATIO>2.0.CO;2].

Butterfield, N. J., & F. W. Chandler. 1992. Paleoenvironmental distribution of Proterozoic microfossils, with an example from the Agu Bay Formation, Baffin Island. Palaeontology 35:943–957.

Butterfield, N. J., A. H. Knoll, & Keene Swett. 1994. Paleobiology of the Neoproterozoic Svanbergfjellet Formation, Spitsbergen. Fossils and Strata 34:1–84 [doi:10.1111/j.1502-3931.1994.tb01558.x].

Butts, S. H. 2014. Silicification. *In* Marc Laflamme, J. D. Schiffbauer, & S. A. F. Darroch, eds., Reading and Writing of the Fossil Record: Preservational Pathways to Exceptional Fossilization. The Paleontological Society Papers, Volume 20. p. 15–33.

Callow, R. H. T., & M. D. Brasier. 2009. Remarkable preservation of microbial mats in Neoproterozoic siliciclastic settings: Implications for Ediacaran taphonomic models. Earth-Science Reviews 96:207–219 [doi:10.1016/j.earscirev.2009.07.002].

Canfield, D. E., & Rob Raiswell. 1991. Carbonate precipitation and dissolution, its relevance to fossil preservation. *In* P. A. Allison, & D. E. G. Briggs, eds., Taphonomy: Releasing the Data Locked in the Fossil Record, Topics in Geobiology. (Vol. 9) Plenum Press. New York. p. 411–453

Canfield, D. E., & Rob Raiswell. 1999. The evolution of the sulfur cycle. American Journal of Science 299:697–723.

Cao, Ruiji, Xunlai Yuan, & Shuhai Xiao. 2001. On morphogenesis of *Conophyton* stromatolites. Acta Palaeontologica Polonica 40:318–329.

Castellani, Christopher, Andreas Maas, M. E. Eriksson, J. T. Haug, Joachim Haug, & Dieter Waloszek. 2018. First record of Cyanobacteria in Cambrian Orsten deposits of Sweden. Palaeontology 61:855–880 [doi:10.1111/pala.12374].

Castenholz, R. W. 2001. Phylum BX. Cyanobacteria. *In* D. R. Boone, R. W. Castenholz, & G. M. Garrity, eds., Bergey's Manual of Systematic Bacteriology. Volume 1. Springer New York. p. 473–599 [doi:10.1007/978-0-387-21609-6_27].

Chan, C. S., David Emerson, & G. W. Luther, III. 2016. The role of microaerophilic Fe-oxidizing micro-organisms in producing banded iron formations. Geobiology 14:509–528 [doi:10.1111/gbi.12192].

Chan, C. S., S. C. Fakra, David Emerson, E. J. Fleming, & K. J. Edwards. 2011. Lithotrophic iron-oxidizing bacteria produce organic stalks to control mineral growth: implications for biosignature formation. The ISME Journal 5:717–727 [doi:10.1038/ismej.2010.173].

Chang, S. B. R., & J. L. Kirschvink. 1989. Magnetofossils, the magnetization of sediments, and the evolution of magnetite biomineralization. Annual Review of Earth and Planetary Sciences 17:169–195 [doi:10.1146/annurev.ea.17.050189.001125].

Chang, S. B. R., J. F. Stolz, J. L. Kirschvink, & S. M. Awramik. 1989. Biogenic magnetite in stromatolites. II. Occurrence in ancient sedimentary environments. Precambrian Research 43:305–315.

Chen, Menge, & Kuiwu Liu. 1986. The geological significance of newly discovered microfossils from the upper Sinian (Doushantuo age) phosphorites. Scientia Geologica Sinica 1:46–53.

Chi Fru, Ernest, Magnus Ivarsson, S. P. Kilias, Stefan Bengtson, Veneta Belivanova, Federica Marone, Danielle Fortin, Curt Broman, & Marco Stampanoni. 2013. Fossilized iron bacteria reveal a pathway to the biological origin of banded iron formation. Nature Communications 4:2050 [doi:10.1038/ncomms3050].

Chisholm, S. W., S. L. Frankel, Ralf Goericke, R. J. Olson, Brian Palenik, J. B. Waterbury, Lisa West-Johnsrud, & E. R. Zettler. 1992. *Prochlorococcus marinus* nov. gen. nov. sp.: an oxyphototrophic marine prokaryote containing divinyl chlorophyll a and b. Archives of Microbiology 157:297–300.

Cloud, P. E., Jr. 1965. Significance of the Gunflint (Precambrian) microflora. Science 148:27–35.

Cloud, P. E., G. R. Licari, L. A. Wright, & B. W. Troxel. 1969. Proterozoic eucaryotes from eastern California. Proceedings of the National Academy of Sciences, USA 623–630 [doi:10.1073/pnas.62.3.623].

Cloud, P. E., & Karen Morrison. 1979. On microbial contaminants, micropseudofossils, and the oldest records of life. Precambrian Research 9:81–91.

Cockell, C. S., & Aude Herrera. 2008. Why are some microorganisms boring? Trends in Microbiology 16:101–106 [doi:10.1016/j.tim.2007.12.007].

Cohn, Ferdinand. 1872. Untersuchungen über Bakterien. Beiträge zur Biologie der Pflanzen Heft II:127–224.

Conley, D. J., P. J. Frings, Guillaume Fontorbe, Wim Clymans, Johanna Stadmark, K. R. Hendry, A. O. Marron, & C. L. De La Roch. 2017. Biosilicification drives a decline of dissolved Si in the oceans through geologic time. Frontiers in Marine Science 4:397 [doi:10.3389/fmars.2017.00397].

Cosmidis, Julie, Karim Benzerara, Emmanuel Gheerbrant, Imène Estève, Baadi Bouya, & Mbarek

Amaghzaz. 2013. Nanometer-scale characterization of exceptionally preserved bacterial fossils in Paleocene phosphorites from Ouled Abdoun (Morocco). Geobiology 11:139–153 [doi:10.1111/gbi.12022].

Couradeau, Estelle, Karim Benzerara, Emmanuelle Gérard, David Moreira, Sylvain Bernard, G. E. Brown, Jr., & P. López-García. 2012. An early-branching microbialite cyanobacterium forms intracellular carbonates. Science 336:459–462 [doi:10.1126/science.1216171].

Croft, W. N., & E. A. George. 1959. Blue-green algae from the Middle Devonian of Rhynie, Aberdeenshire. Bulletin of the British Museum (Natural History). Geology Series 3:341–353.

Crosby, C. H., J. V. Bailey, & Mukund Sharma. 2014. Fossil evidence of iron-oxidizing chemolithotrophy linked to phosphogenesis in the wake of the Great Oxidation Event. Geology 42:1015–1018 [doi:10.1130/G35922.1].

Cunningham, J. A., C.-W. Thomas, S. Bengtson, F. Marone, M. Stampanoni, F. R. Turner, J. V. Bailey, R. A. Raff, E. C. Raff, & P. C. J. Donoghue. 2012. Experimental taphonomy of giant sulphur bacteria: Implications for the interpretation of the embryo-like Ediacaran Doushantuo fossils. Proceedings of the Royal Society B (Biological Sciences) 279:1857–1864.

Dai, Y. D., H. M. Song, & J. Y. Shen. 2004. Fossil bacteria in Xuanlong iron ore deposits of Hebei Province. Science in China Series D (Earth Sciences) 47:347–356 [doi:10.1360/02yd0178].

Demoulin, C. F., Y. J. Lara, Luc Cornet, Camille François, Denis Baurain, Annick Wilmotte, & E. J. Javaux. 2019. Cyanobacteria evolution: Insight from the fossil record. Free Radical Biology and Medicine 140:206–223 [doi:10.1016/j.freeradbiomed.2019.05.007].

Derenne, Sylvie, Peter Metzger, Claude Largeau, P. F. van Bergen, J. P. Gatellier, J. S. Sinninghe Damsté, J. W. de Leeuw, & Claire Berkaloff. 1991. Similar morphological and chemical variations of *Gloeocapsomorpha prisca* in Ordovician sediments and cultured *Botryococcus braunii* as a response to changes in salinity. Organic Geochemistry 19:299–313.

Dodd, M. S., Dominic Papineau, Tor Grenne, J. F. Slack, Martin Rittner, Franco Pirajno, J. O. O'Neil, & C. T. Little. 2017. Evidence for early life in Earth's oldest hydrothermal vent precipitates. Nature 543:60–64 [doi:10.1038/nature21377].

Dong, Lin, Shuhai Xiao, Bing Shen, Chuanming Zhou, Guoxiang Li, & Jinxian Yao. 2009. Basal Cambrian microfossils from the Yangtze Gorges area (South China) and the Aksu area (Tarim Block, northwestern China). Journal of Paleontology 83:30–44 [doi:10.1017/S0022336000058108].

Dörfelt, Heinrich, A. R. Schmidt, & Jörg Wunderlich. 2000. *Rosaria succina* spec. nov.: A fossil cyanobacterium from Tertiary amber. Journal of Basic Microbiology 40:327–332 [doi:10.1002/1521-4028(200012)40:5/6<327::AID-JOBM327>3.0.CO;2-E].

Edwards, Dianne, Lindsey Axe, John Parkes, & David Rickard. 2006. Provenance and age of bacteria-like structures on mid-Palaeozoic plant fossils. International Journal of Astrobiology 5:109–142 [doi:10.1017/S147355040600303X].

Edwards, D. S., & A. G. Lyon. 1983. Algae from the Rhynie chert. Botanical Journal of the Linnean Society 86:37–55.

Ehrenberg, C. G. 1835. Die Akalephen des rothen Meeres und der Organismus der Medusen der Ostsee. Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin. p. 181–260.

Ehrenberg, C. G. 1838. Die Infusionsthierchen als vollkommene Organismen. L. Voss. Leipzig. 547 p.

Ehrlich, H. L., & D. K. Newman. 2009. Geomicrobiology (5th edition). CRC Press/Taylor & Francis. Boca Raton. 606 p.

Elling, F. J., J. D. Hemingway, T. W. Evans, J. J. Kharbush, Eva Spieck, R. E. Summons, & Ann Pearson. 2020. Vitamin B12-dependent biosynthesis ties amplified 2-methylhopanoid production during oceanic anoxic events to nitrification. Proceedings of the National Academy of Sciences, USA 117:32996–33004 [doi:10.1073/pnas.2012357117].

Emerson, David, E. J. Fleming, & J. M. McBeth. 2010. Iron-oxidizing bacteria: An environmental and genomic perspective. Annual Review of Microbiology 64:561–583 [doi:10.1146/annurev.micro.112408.134208].

Emerson, David, J. A. Rentz, T. G. Lilburn, R. E. Davis, Henry Aldrich, Clara Chan, & C. L. Moyer. 2007. A novel lineage of Proteobacteria involved in formation of marine fe-oxidizing microbial mat communities. PLoSOne 2:e667 [doi:10.1371/journal.pone.0000667].

Erikson, Dagny. 1949. The morphology, cytology, and taxonomy of the Actinomycetes. Annual Review of Microbiology 3:23–54 [doi:10.1146/annurev.mi.03.100149.000323].

Fadel, Alexandre, Kevin Lepot, Vincent Busigny, Ahmed Addad, & David Troadec. 2017. Iron mineralization and taphonomy of microfossils of the 2.45–2.21 Ga Turee Creek Group, Western Australia. Precambrian Research 298:530–551 [doi:10.1016/j.precamres.2017.07.003].

Fenton, C. L. 1946. Algae of the Pre-Cambrian and Early Paleozoic. The American Midland Naturalist 36:259–263.

Ferris, F. G., W. S. Fyfe, & T. J. Beveridge. 1988. Metallic ion binding by Bacillus subtilis: Implications for the fossilization of microorganisms. Geology 16:149–152 [doi:10.1130/0091-7613(1988)016<0149:MIBBBS>2.3.CO;2].

Flemming, H.-C., & Stefan Wuertz. 2019. Bacteria and archaea on Earth and their abundance in biofilms. Nature Reviews Microbiology 17:247–260 [doi:10.1038/s41579-019-0158-9].

Flombaum, Pedro, J. L. Gallegos, R. A. Gordillo, José Rincón, L. L. Zabala, Nianzhi Jiao, D. M. Karl, W. K. W. Li, M. W. Lomas, Daniele Veneziano, C. S. Vera, J. A. Vrugt, & A. C. Martiny. 2013. Present and future global distributions of the marine Cyanobacteria *Prochlorococcus* and *Synechococcus*. Proceedings of the National Academy of Sciences, USA 110:9824–9829 [doi:10.1073/pnas.1307701110].

Foster, C. B., J. D. Reed, & Reed Wicander. 1989. *Gloeocapsomorpha prisca* Zalessky, 1917: A new study part I: Taxonomy, geochemistry, and paleoecology. Geobios 22:735–759.

Frankel, R. B., & D. A. Bazylinski. 2003. Biologically induced mineralization by bacteria. Reviews in Mineralogy and Geochemistry. Biomineralization 54:95–114.

French, K. L., C. Hallmann, J. M. Hope, P. L. Schoon, J. A. Zumberge, Yosuke Hoshino, C. A. Peters, S. C. George, G. D. Love, J. J. Brocks, Roger Buick, & R. E. Summons. 2015. Reappraisal of hydrocarbon biomarkers in Archean rocks. Proceedings of the National Academy of Sciences, USA 112:5915–5920 [doi:10.1073/pnas.1419563112].

Furnes, Harald, N. R. Banerjee, Karlis Muehlenbachs, Hubert Staudigel, & Maarten de Wit. 2004. Early life recorded in Archean pillow lavas. Science 304:578–581.

Gan, Tian, Taiyi Luo, Ke Pang, Chuanming Zhou, Guanghong Zhou, Bin Wan, Gang Li, Qiru Yi, A. D. Czaja, & Shuhai Xiao. 2021. Cryptic terrestrial fungus-like fossils of the early Ediacaran Period. Nature Communications 12:641 [doi:10.1038/s41467-021-20975-1].

Garcia-Pichel, Ferran, Jonathan Lombard, Tanya Soule, Sean Dunaj, S. H. Wu, & M. F. Wojciechowski. 2019. Timing the evolutionary advent of cyanobacteria and the later Great Oxidation Event using gene phylogenies of a sunscreen. mBio 10:e00561–00519 [doi:10.1128/mBio.00561-19].

García-Ruiz, J. M., S. T. Hyde, A. M. Carnerup, A. G. Christy, M. J. van Kranendonk, & N. J. Welham. 2003. Self-assembled silica-carbonate structures and detection of ancient microfossils. Science 302:1194–1197.

García-Ruiz, J. M., Elias Nakouzi, Electra Kotopoulou, Leonardo Tamborrino, & Oliver Steinbock. 2017. Biomimetic mineral self-organization from silica-rich spring waters. Science Advances 3:e1602285 [doi:10.1126/sciadv.1602285].

Gibson, T. M., P. M. Shih, V. M. Cumming, W. W. Fischer, P. W. Crockford, M. S. W. Hodgskiss, Sarah Wörndle, R. A. Creaser, R. H. Rainbird, T. M. Skulski, & G. P. Halverson. 2018. Precise age of *Bangiomorpha pubescens* dates the origin of eukaryotic photosynthesis. Geology 46:135–138 [doi:10.1130/G39829.1].

Golubic, Stjepko, & E. S. Barghoorn. 1977. Interpretation of microbial fossils with special reference to the Precambrian. *In* Erik Flügel, ed., Fossil Algae: Recent Results and Developments. Springer-Verlag. Berlin. p. 1–14

Golubic, Stjepko, & H. J. Hofmann. 1976. Comparison of Holocene and mid-Precambrian Entophysalidaceae (Cyanophyta) in stromatolitic algal mats: Cell division and degradation. Journal of Paleontology 50:1074–1082.

Golubic, Stjepko, & S.-J. Lee. 1999. Early cyanobacterial fossil record: preservation, palaeoenvironments and identification. European Journal of Phycology 34:339–348 [doi:10.1080/09670269910001736402].

Golubic, Stjepko, R. D. Perkins, & K. J. Lukas. 1975. Boring microorganisms and microborings in carbonate substrates. *In* R. W. Frey, ed., The Study of Trace Fossils. Springer-Verlag. Berlin. p. 229–259

Golubic, Stjepko, A. M. Pietrini, & Sandra Ricci. 2015. Euendolithic activity of the cyanobacterium *Chroococcus lithophilus* Erc. in biodeterioration of the Pyramid of Caius Cestius, Rome, Italy. International Biodeterioration & Biodegradation 100:7–16 [doi:10.1016/j.ibiod.2015.01.019].

Golubic, Stjepko, V. N. Sergeev, & A. H. Knoll. 1995. Mesoproterozoic *Archaeoellipsoides*: akinetes of heterocystous cyanobacteria. Lethaia 28:285–298 [doi:10.1111/j.1502-3931.1995.tb01817.x].

Gomes, M. L., L. A. Riedman, Shane O'Reilly, Usha Lingappa, Kyle Metcalfe, D. A. Fike, J. P. Grotzinger, W. W. Fischer, & A. H. Knoll. 2020. Taphonomy of biosignatures in microbial mats on Little Ambergris Cay, Turks and Caicos Islands. Frontiers in Earth Science 8:576712 [doi:10.3389/feart.2020.576712].

Gomont, M. A. 1892a. Monographie des Oscillariées (Nostocacées homocystées). Annales des Sciences Naturelles, Botanique (Série 7) 15:263–368, pl. 266–214.

Gomont, M. A. 1892b. Monographie des Oscillariées (Nostocacées Homocystées). Deuxième partie. Lyngbyées. Annales des Sciences Naturelles, Botanique (série 7) 16:91–264, pl 261–267.

Gomont, M. A. 1895. Note sur le Scytonema ambiguum Kützing. Journal de Botanique 9:49–52.

Gorokhov, I. M., A. B. Kuznetsov, M. A. Semikhatov, I. M. Vasil'eva, N. G. Rizvanova, G. V. Lipenkov, & E. O. Dubinina. 2019. Early Riphean Billyakh Group of the Anabar Uplift, north Siberia: C–O isotopic geochemistry and Pb–Pb age of dolomites. Stratigraphy and Geological Correlation 27:514–528 [doi:10.1134/S0869593819050022].

Green, J. W., A. H. Knoll, Stjepko Golubic, & Keene Swett. 1987. Paleobiology of distinctive benthic microfossils from the upper Proterozoic Limestone-Dolomite "Series," central East Greenland. American Journal of Botany 74:928–940 [doi:10.2307/2443874].

Gregory, K. F. 1956. Hyphal anastomosis and cytological aspects of *Streptomyces scabies*. Canadian Journal of Microbiology 2:649–655 [doi:10.1139/m56-077].

Grey, Kathleen. 2005. Ediacaran palynology of Australia. Memoirs of the Association of Australasian Palaeontologists 31:1–439.

Grosch, E. G., & Nicola McLoughlin. 2014. Reassessing the biogenicity of Earth's oldest trace fossil with implications for biosignatures in the search for early life. Proceedings of the National Academy of Sciences 111:8380–8385 [doi:10.1073/pnas.1402565111].

Gruner, J. W. 1922. The origin of sedimentary iron formations: The Biwabik Formation of the Mesabi Range. Economic Geology 17:407–460.

Gruner, J. W. 1923. Algae believed to be Archean. Journal of Geology 31:146–148.

Gruner, J. W. 1924. Contributions to the geology of the Mesabi Range, with special reference to the magnetites of the iron-bearing formation west of Mesaba. Minnesota Geological Survey Bulletin 19:1–71.

Gruner, J. W. 1925. Discovery of life in the Archean. Journal of Geology 33:151–152 [doi:10.1086/623182].

Gueneli, Nur, A. M. McKenna, Naohiko Ohkouchi, C. J. Boreham, Jérémie Beghin, E. J. Javaux, & J. J. Brocks. 2018. 1.1-billion-year-old porphyrins establish a marine ecosystem dominated by bacterial primary producers. Proceedings of the National Academy of Sciences, USA 115:E6978–E6986 [doi:10.1073/pnas.1803866115].

Guo, Jun-feng, Yong Li, & De-gan Shu. 2010. Cyanobacteria fossils from the Yanjiahe Formation, Terreneuvian, Cambrian, Yichang, Hubei. Acta Micropalaeontologica Sinica 27:144–149.

Hanson, R. S., & T. E. Hanson. 1996. Methanotrophic bacteria. Microbiological Reviews 60:439–471.

Hauck, Ferdinand. 1885. Die Meeresalgen Deutschlands und Österreichs. *In* L. Rabenhorst, ed., Kryptogamen-Flora von Deutschland, Österreich und der Schweiz. Zweite Auflage (Vol. 2). Eduard Kummer. Leipzig. p. i-xxiv, 513–575.

Hawkins, A. D., H. P. Liu, D. E. G. Briggs, A. D. Muscente, R. M. McKay, B. J. Witzke, & Shuhai Xiao. 2018. Taphonomy and biological affinity of three-dimensionally phosphatized bromalites from the Middle Ordovician Winneshiek Lagerstätte, northeastern Iowa, USA. Palaios 33:1–15 [doi:10.2110/palo.2017.053].

Heim, Christine, N.-V. Quéric, Danny Ionescu, Nadine Schäfer, & Joachim Reitner. 2017. *Frutexites*-like structures formed by iron oxidizing biofilms in the continental subsurface (Äspö Hard Rock Laboratory, Sweden). PLOS One 12:e0177542 [doi:10.1371/journal.pone.0177542].

Heimann, Adriana. 2021. Part B, Volume 1, Chapter 6: Banded iron formations. Treatise Online 158:1–48, 4 fig., 2 tables.

Hermann, T. N. 1974. Findings of mass accumulations of trichomes in the Riphean. *In* B. V. Timofeev, ed., Proterozoic and Paleozoic microfossils of the USSR. Nauka. Moscow. p. 6–10.

Hippler, Dorothee, Nanjie Hu, Michael Steiner, Gerhard Scholtz, & Gerhard Franz. 2011. Experimental mineralization of crustacean eggs: New implications for the fossilization of Precambrian–Cambrian embryos. Biogeosciences 9:1765–1775 [doi:10.5194/bg-9-1765-2012].

Hodgskiss, M. S. W., O. M. J. Dagnaud, J. L. Frost, G. P. Halverson, M. D. Schmitz, N. L. Swanson-Hysell, & E. A. Sperling. 2019. New insights on the Orosirian carbon cycle, early Cyanobacteria, and the assembly of Laurentia from the Paleoproterozoic Belcher Group. Earth and Planetary Science Letters 520:141–152 [doi:10.1016/j.epsl.2019.05.023].

Hoffmann, C. F., C. B. Foster, T. G. Powell, & R. E. Summons. 1987. Hydrocarbon biomarkers from Ordovician sediments and the fossil alga *Gloeocapsomorpha prisca* Zalessky 1917. Geochimica et Cosmchimica 51:2681–2697.

Hofmann, B. A., J. D. Farmer, Friedhelm von Blanckenburg, & A. E. Fallick. 2008. Subsurface filamentous fabrics: an evaluation of origins based on morphological and geochemical criteria, with implications for exopaleontology. Astrobiology 8:87–117 [doi:10.1089/ast.2007.0130].

Hofmann, H. J. 1974. Mid-Precambrian prokaryotes (?) from the Belcher Islands, Canada. Nature 249:87–88.

Hofmann, H. J. 1976. Precambrian microflora, Belcher Island, Canada: Significance and systematics. Journal of Paleontology 50:1040–1073.

Hofmann, H. J., Kathleen Grey, A. H. Hickman, & R. I. Thorpe. 1999. Origin of 3.45 Ga coniform stromatolites in Warrawoona Group, Western Australia. Geological Society of America Bulletin 111:1256–1262.

Hofmann, H. J., & G. D. Jackson. 1994. Shale-facies microfossils from the Proterozoic Bylot Supergroup, Baffin Island, Canada. Paleontological Society Memoir 37:1–35.

Holland, H. D. 2006. The oxygenation of the atmosphere and oceans. Philosophical Transactions of the Royal Society of London B (Biological Sciences) 361:903–915.

Horodyski, R. J., & J. A. Donaldson. 1980. Microfossils from the middle Proterozoic Dismal Lakes Group, Arctic Canada. Precambrian Research 11:125–159.

Igisu, Motoko, Yuichiro Ueno, Mie Shimojima, Satoru Nakashima, S. M. Awramik, Hiroyuki Ohta, & Shigenori Maruyama. 2009. Micro-FTIR spectroscopic signatures of bacterial lipids in Proterozoic microfossils. Precambrian Research 173:19–26 [doi:10.1016/j.precamres.2009.03.006].

Igisu, Motoko, Tadashi Yokoyama, Yuichiro Ueno, Satoru Nakashima, Mie Shimojima, Hiroyuki Ohta, & Shigenori Maruyama. 2018. Changes of aliphatic C-H bonds in cyanobacteria during experimental thermal maturation in the presence or absence of silica as evaluated by FTIR microspectroscopy. Geobiology 4:412–428 [doi:10.1111/gbi.12294].

Ivarsson, Magnus, Henrik Drake, Anna Neubeck, Therese Sallstedt, Stefan Bengtson, N. M. W. Roberts, & Birger Rasmussen. 2020. The fossil record of igneous rock. Earth-Science Reviews 210:103342 [doi:10.1016/j.earscirev.2020.103342].

Javaux, E. J. 2019. Challenges in evidencing the earliest traces of life. Nature 572:451–470 [doi:10.1038/s41586-019–1436-4].

Javaux, E. J., A. H. Knoll, & M. R. Walter. 2004. TEM evidence for eukaryotic diversity in mid-Proterozoic oceans. Geobiology 2:121–132.

Javaux, E. J., C. P. Marshall, & Andrey Bekker. 2010. Organic-walled microfossils in 3.2-billion-year-old shallow-marine siliciclastic deposits. Nature 463:934–938.

Jiang, Ganqing, M. J. Kennedy, & Nicholas Christie-Blick. 2003. Stable isotopic evidence for methane seeps in Neoproterozoic postglacial cap carbonates. Nature 426:822–826.

Johannessen, K. C., Nicola McLoughlin, P. E. Vullum, & I. H. Thorseth. 2020. On the biogenicity of Fe-oxyhydroxide filaments in silicified low-temperature hydrothermal deposits: Implications for the identification of Fe-oxidizing bacteria in the rock record. Geobiology 18:31–53 [doi:10.1111/gbi.12363].

Johnston, D. T., B. A. Wing, James Farquhar, A. J. Kaufman, Harald Strauss, T. W. Lyons, L. C. Kah,

& D. E. Canfield. 2005. Active microbial sulfur disproportionation in the Mesoproterozoic. Science 310:1477–1479 [doi:10.1126/science.1117824].

Jones, Brian, & Xiaotong Peng. 2012. Intrinsic versus extrinsic controls on the development of calcite dendrite bushes, Shuzhishi Spring, Rehai geothermal area, Tengchong, Yunnan Province, China. Sedimentary Geology 249–250:45–62 [doi:10.1016/j.sedgeo.2012.01.009].

Jones, Brian, & Xiaotong Peng. 2014. Signatures of biologically influenced $CaCO_3$ and Mg-Fe silicate precipitation in hot springs: Case study from the Ruidian geothermal area, western Yunnan Province, China. Sedimentology 61:56–89 [doi:10.1111/sed.12043].

Jones, Brian, R. W. Renaut, & M. R. Rosen. 2001. Taphonomy of silicified filamentous microbes in modern geothermal sinters: Implications for identification. Palaios 16:580–592.

Kah, L. C., & A. H. Knoll. 1996. Microbenthic distribution of Proterozoic tidal flats: Environmental and taphonomic considerations. Geology 24:79–82.

Kah, L. C., & Robert Riding. 2007. Mesoproterozoic carbon dioxide levels inferred from calcified cyanobacteria. Geology 35:799–802.

Kappler, Andreas, Claudia Pasquer, K. O. Konhauser, & D. K. Newman. 2005. Deposition of banded iron formations by anoxygenic phototrophic Fe(II)-oxidizing bacteria. Geology 33:865–868. [doi:10.1130/G21658.1].

Kidston, Robert, & W. H. Lang. 1921. On old red sandstone plants showing structure, from the Rhynie chert bed, Aberdeenshire. Part V. The Thallophyta occurring in the peat-bed; the succession of the plants through a vertical section of the bed, and the conditions of accumulation and preservation of the deposit. Transaction of the Royal Society of Edinburgh 52:855–902.

Klaveness, Dag. 1999. *Metallogenium*: A microbial enigma. *In* Joseph Seckbach, ed., Enigmatic Microorganisms and Life in Extreme Environments. Springer. Dordrecht. p. 541–548.

Klein, Cornelis, N. J. Beukes, & J. W. Schopf. 1987. Filamentous microfossils in the early Proterozoic Transvaal Supergroup: Their morphology, significance, and paleoenvironmental setting. Precambrian Research 36:81–94.

Knittel, Katrin, Tina Lösekann, Antje Boetius, Renate Kort, & Rudolf Amann. 2005. Diversity and distribution of methanotrophic archaea at cold seeps. Microbial Ecology 71:467–479 [doi:10.1128/AEM.71.1.467-479.2005].

Knoll, A. H. 1985a. Exceptional preservation of photosynthetic organisms in silicified carbonates and silicified peats. Philosophical Transactions of the Royal Society of London B (Biological Sciences) 311:111–122.

Knoll, A. H. 1985b. A paleobiological perspective on sabkhas. *In* G. M. Friedman, & W. E. Krumbein, eds., Hypersaline Ecosystems: The Gavish Sabkha. p. 407–425.

Knoll, A. H. 2008. Cyanobacteria and Earth history. *In* Antonia Herrero, & Enrique Flores, eds., The Cyanobacteria: Molecular Biology, Genomics and Evolution. Horizon Scientific. Heatherset. p. 1–19.

Knoll, A. H. 2015. Paleobiological perspectives on early microbial evolution. Cold Spring Harbor Perspectives in Biology 7:a018093 [doi:10.1101/cshperspect.a018093].

Knoll, A. H., & E. S. Barghoorn. 1974. Ambient pyrite in Precambrian chert: New evidence and a theory. Proceedings of the National Academy of Sciences, USA 71:2329–2331.

Knoll, A. H., & E. S. Barghoorn. 1975. Precambrian eukaryotic organisms: A reassessment of the evidence. Science 190:52–54.

Knoll, A. H., & E. S. Barghoorn. 1977. Archean microfossils showing cell-division from Swaziland System of South Africa. Science 198:396–398.

Knoll, A. H., E. S. Barghoorn, & S. M. Awramik. 1978. New microorganisms from the Aphebian Gunflint Iron Formation, Ontario Journal of Paleontology 52:976–992.

Knoll, A. H., E. S. Barghoorn, & Stjepko Golubic. 1975. *Paleopleurocapsa wopfnerii* gen. et sp. nov.: A late Precambrian alga and its modern counterpart. Proceedings of the National Academy of Sciences, USA 72:2488–2492.

Knoll, A. H., I. J. Fairchild, & Keene Swett. 1993. Calcified microbes in Neoproterozoic carbonates: implications for our understanding of the Proterozoic/Cambrian Transition. Palaios 8:512–525.

Knoll, A. H., & Stjepko Golubic. 1992. Proterozoic and living cyanobacteria. *In* Manfred Schidlowski, Stjepko Golubic, M. M. Kimberley, D. M. McKirdy, & P. A. Trudinger, eds., Early Organic Eyolution: Implications for Mineral and Energy Resources. Springer-Verlag. Berlin & Heidelberg. p. 450–462.

Knoll, A. H., E. J. Javaux, David Hewitt, & Phoebe Cohen. 2006. Eukaryotic organisms in Proterozoic oceans. Philosophical Transactions of the Royal Society of London B (Biological Sciences) 361:1023–1038.

Knoll, A. H., Keene Swett, & Jonathan Mark. 1991. Paleobiology of a Neoproterozoic tidal flat/lagoonal complex: The Draken Conglomerate Formation, Spitsbergen. Journal of Paleontology 65:531–570.

Konhauser, K. O., Tristan Hamade, Rob Raiswell, R. C. Morris, F. G. Ferris, Gordon Southam, & D. E. Canfield. 2002. Could bacteria have formed the Precambrian banded iron formations? Geology 30:1079–1082 [doi:10.1130/0091-7613(2002)030<1079:CBHFTP>2.0.CO;2].

Konhauser, K. O., Brian Jones, A. L. Reysenbach, & R. W. Renaut. 2003. Hot spring sinters: keys to understanding Earth's earliest life forms. Canadian Journal of Earth Sciences 40:1713–1724.

Kopp, R. E., & J. L. Kirschvink. 2008. The identification and biogeochemical interpretation of fossil magnetotactic bacteria. Earth-Science Reviews 86:42–61 [doi:10.1016/j.earscirev.2007.08.001].

Kremer, B., J. Kazmierczak, Maja Łukomska-Kowalczyk, & Stephan Kempe. 2012. Calcification and Silicification: Fossilization Potential of Cyanobacteria from Stromatolites of Niuafo'ou's Caldera Lakes (Tonga) and Implications for the Early Fossil

Record. Astrobiology 12:535–548 [doi:10.1089/ast.2011.0742].

Krepski, S. T., David Emerson, P. L. Hredzak-Showalter, G. W. Luther, III, & C. S. Chan. 2013. Morphology of biogenic iron oxides records microbial physiology and environmental conditions: toward interpreting iron microfossils. Geobiology 11:457–471 [doi:10.1111/gbi.12043].

Krings, Michael. 2019. *Palaeolyngbya kerpii* sp. nov., a large flamentous cyanobacterium with affinities to Oscillatoriaceae from the Lower Devonian Rhynie chert. PalZ 93:377–386 [doi:10.1007/s12542-019-00475-w].

Krings, Michael, & C. J. Harper. 2019. A microfossil resembling Merismopedia (Cyanobacteria) from the 410-million-yr-old Rhynie and Windyfield cherts: *Rhyniococcus uniformis* revisited. Nova Hedwigia 108:17–35 [doi:10.1127/nova_hedwigia/2018/0507 0029-5035/2018/0507].

Krings, Michael, Hans Kerp, Hagen Hass, T. N. Taylor, & Nora Dotzler. 2007. A filamentous cyanobacterium showing structured colonial growth from the Early Devonian Rhynie chert. Review of Palaeobotany and Palynology 146:265–276 [doi:10.1016/j.revpalbo.2007.05.002].

Kützing, F. T. 1843. Phycologia generalis oder Anatomie, Physiologie und Systemkunde der Tange. Mit 80 farbig gedruckten Tafeln, gezeichnet und gravirt vom Verfasser. F. A. Brockhaus. Leipzig. [part 1, i-xxxii, 1–142; part 2, 143–458].

Lamboy, Michel, V. P. Rao, Ezzat Ahmed, & Nasreddine Azzouzi. 1994. Nannostructure and significance of fish coprolites in phosphorites. Marine Geology 120:373–383 [doi:10.1016/0025-3227(94)90068-X].

Lan, Zhongwu, Shujing Zhang, Maurice Tucker, Zhensheng Li, & Zhuoya Zhao. 2020. Evidence for microbes in early Neoproterozoic stromatolites. Sedimentary Geology 398:105589 [doi:10.1016/j.sedgeo.2020.105589].

Lauterborn, Robert. 1907. A new genus of sulfur bacteria *(Thioploca schmidlei* nov. gen. nov. spec.). Berichte der Deutschen Botanischen Gesellschaft 25:238–242.

Lee, S.-J., & Stjepko Golubic. 1998. Multi-trichomous cyanobacterial microfossils from the Mesoproterozoic Gaoyuzhuang Formation, China: Paleoecological and taxonomic implications. Lethaia 31:169–184.

Lekele Baghekema, S. G., Kevin Lepot, Armelle Riboulleau, Alexandre Fadel, Alain Trentesaux, & Abderrazak El Albani. 2017. Nanoscale analysis of preservation of ca. 2.1 Ga old Francevillian microfossils, Gabon. Precambrian Research 301:1–18 [doi:10.1016/j.precamres.2017.08.024].

Leo, R. F., & E. S. Barghoorn. 1976. Silicification of wood. Botanical Museum Leaflets, Harvard University 25:1–47.

Lepot, Kevin. 2020. Signatures of early microbial life from the Archean (4 to 2.5 Ga) eon. Earth-Science Reviews 209:103296 [doi:10.1016/j.earscirev.2020.103296].

Li, Guoxiang. 1997. Early Cambrian phosphate-replicated endolithic algae from Emei, Sichuan, SW China. Bulletin of the National Museum of Natural Science (Taichung, China) 10:193–216.

Li, Jinhua, Karim Benzerara, Sylvain Bernard, & Oliver Beyssac. 2013. The link between biomineralization and fossilization of bacteria: Insights from field and experimental studies. Chemical Geology 359:49–69 [doi:10.1016/j.chemgeo.2013.09.013].

Li, Jinhua, Nicolas Menguy, A. P. Roberts, Lin Gu, Eric Leroy, Julie Bourgon, Xin'an Yang, Xiang Zhao, Peiyu Liu, H. G. Changela, & Yongxin Pan. 2020. Bullet-shaped magnetite biomineralization within a magnetotactic deltaproteobacterium: Implications for magnetofossil identification. Journal of Geophysical Research: Biogeosciences 125:e2020JG005680 [doi:10.1029/2020JG005680].

Lin,Yitian, Dongjie Tang, Xiaoying Shi, Xiqiang Zhou, & Kangjun Huang. 2019. Shallow-marine ironstones formed by microaerophilic iron-oxidizing bacteria in terminal Paleoproterozoic. Gondwana Research 76:1–18 [doi:10.1016/j.gr.2019.06.004].

Little, C. T. S., K. C. Johannessen, Stefan Bengtson, C. S. Chan, Magnus Ivarsson, J. F. Slack, Curt Broman, I. H. Thorseth, Tor Grenne, O. J. Rouxel, & Andrey Bekker. 2021. A late Paleoproterozoic (1.74 Ga) deep-sea, low-temperature, iron-oxidizing microbial hydrothermal vent community from Arizona, USA. Geobiology [doi:10.1111/gbi.12434].

Locey, K. J., & J. T. Lennon. 2019. Scaling laws predict global microbial diversity. Proceedings of the National Academy of Sciences, USA 113:5970–5975 [doi:10.1073/pnas.152191113].

LoDuca, S. T., Natalia Bykova, Mengying Wu, Shuhai Xiao, & Yuanlong Zhao. 2017. Seaweed morphology and ecology during the great animal diversification events of the early Paleozoic: A tale of two floras. Geobiology 15:588–616 [doi:10.1111/gbi.12244].

Lovley, D. R. 2013. Dissimilatory Fe(III)- and Mn(IV)-reducing prokaryotes. *In* Eugene Rosenberg, E. F. DeLong, S. Lory, E. Stackebrandt, & F. Thompson, eds., The Prokaryotes: Prokaryotic Physiology and Biochemistry (4th edition). Springer-Verlag. Berlin Heidelberg. p. 287–308 [doi:10.1007/978-3-642-30141-4_69].

Lovley, D. R., S. J. Giovannoni, D. C. White, J. E. Champine, E. J. P. Phillips, Y. A. Gorby, & Steve Goodwin. 1993. *Geobacter metallireducens* gen. nov. sp. nov., a microorganism capable of coupling the complete oxidation of organic compounds to the reduction of iron and other metals. Archives of Microbiology 159:336–344 [doi:10.1007/BF00290916].

Luo, Genming, Shuhei Ono, N. J. Beukes, D. T. Wang, Shucheng Xie, & R. E. Summons. 2016. Rapid oxygenation of Earth's atmosphere 2.33 billion years ago. Science Advances 2:e1600134 [doi:10.1126/sciadv.1600134].

Lyons, T. W., C. T. Reinhard, & N. J. Planavsky. 2014. The rise of oxygen in Earth's early ocean and atmosphere. Nature 506:307–315.

Lyu, Zhe, & Yuchen Liu. 2018. Diversity and taxonomy of methanogens. *In* A. J. M. Stams, & D. Z. Sousa, eds., Biogenesis of Hydrocarbons: Handbook of Hydrocarbon and Lipid Microbiology. Springer.

New York. p. 19–77 [doi:/10.1007/978-3-319-78108-2_5].

MacDonell, Michael, & Rita Colwell. 1985. Phylogeny of the Vibrionaceae, and recommendation for two new genera, *Listonella* and *Shewanella*. Systematic and Applied Microbiology 6:171–182 [doi:10.1016/s0723-2020(85)80051-5].

Maliva, R. G., A. H. Knoll, & B. M. Simonson. 2005. Secular change in the Precambrian silica cycle: Insights from chert petrology. Geological Society of America Bulletin 117:835–845.

Martin, Derek, D. E. G. Briggs, & R. J. Parkes. 2003. Experimental mineralization of invertebrate eggs and the preservation of Neoproterozoic embryos. Geology 31:39–42.

Martindale, R. C., J. V. Strauss, E. A. Sperling, J. E. Johnson, M. J. Van Kranendonk, David Flannery, Katherine French, Kevin Lepot, Rajat Mazumder, M. S. Rice, D. P. Schrag, Roger Summons, Malcolm Walter, John Abelson, & A. H. Knoll. 2015. Sedimentology, chemostratigraphy, and stromatolites of lower Paleoproterozoic carbonates, Turee Creek Group, Western Australia. Precambrian Research 266:194–211 [doi:10.1016/j.precamres.2015.05.021].

McLoughlin, Nicola, David Wacey, Siyolise Phungu-phungu, Martin Saunders, & E. G. Grosch. 2020. Deconstructing Earth's oldest ichnofossil record from the Pilbara Craton, West Australia: Implications for seeking life in the Archean subseafloor. Geobiology 18:525–543 [doi:10.1111/gbi.12399].

McMahon, Sean. 2019. Earth's earliest and deepest purported fossils may be iron-mineralized chemical gardens. Proceedings of the Royal Socity B (Biological Sciences) 286:20192410 [doi:10.1098/rspb.2019.2410].

Mendelson, C. V., & J. W. Schopf. 1992. Proterozoic and selected early Cambrian microfossils and microfossil-like objects. *In* J. W. Schopf, & Cornelis Klein, eds., The Proterozoic biosphere: A multidisciplinary study. Cambridge University Press. Cambridge, UK. p. 865–952.

Moczydłowska, Malgorzata, J. W. Schopf, & Sebastian Willman. 2010. Micro- and nano-scale ultrastructure of cell walls in Cryogenian microfossils: revealing their biological affinity. Lethaia 43:129–136.

Moore, E. S. 1918. The iron-formation on Belcher Islands, Hudson Bay, with special reference to its origin and its associated algal limestones. Journal of Geology 26:412–438.

Moore, K. R., Tanja Bosak, Francis Macdonald, Kimberly Du, S. A. Newman, D. J. G. Lahr, & S. B. Pruss. 2017. Pyritized Cryogenian cyanobacterial fossils from Arctic Alaska. Palaios 32:769–778 [doi:10.2110/palo.2017.063].

Moore, K. R., Mihkel Pajusalu, Jian Gong, Victor Sojo, Thomas Matreux, Dieter Braun, & Tanja Bosak. 2020. Biologically mediated silicification of marine cyanobacteria and implications for the Proterozoic fossil record. Geology 48:862–866 [doi:10.1130/G47394.1].

Moyer, A. E., Wenxia Zheng, E. A. Johnson, M. C. Lamanna, D.-q. Li, K. J. Lacovara, & M. H. Schweitzer. 2014. Melanosomes or microbes: Testing an alternative hypothesis for the origin of microbodies in fossil feathers. Scientific Reports 4:4233 [doi:10.1038/srep04233].

Muscente, A. D., A. D. Hawkins, & Shuhai Xiao. 2015. Fossil preservation through phosphatization and silicification in the Ediacaran Doushantuo Formation (South China): A comparative synthesis. Palaeogeography Palaeoclimatology Palaeoecology 434:46–62 [doi:10.1016/j.palaeo.2014.10.013].

Muscente, A. D., J. D. Schiffbauer, Jesse Broce, Marc Laflamme, Kenneth O'Donnell, T. H. Boag, Michael Meyer, A. D. Hawkins, J. W. Huntley, Maria McNamara, L. A. MacKenzie, G. D. Stanley Jr., N. W. Hinman, M. H. Hofmann, & Shuhai Xiao. 2017. Exceptionally preserved fossil assemblages through geologic time and space. Gondwana Research 48:164–188 [doi:10.1016/j.gr.2017.04.020].

Nägeli, Carl. 1849. Gattungen einzelliger Algen, physiologisch und systematisch bearbeitet. Neue Denkschriften der Allg. Schweizerischen Gesellschaft für die Gesammten Naturwissenschaften 10: i-viii, 1–139, pl. I-VIII.

Newman, S. A., Vanja Klepac-Ceraj, Giulio Mariotti, S. B. Pruss, Nicki Watson, & Tanja Bosak. 2017. Experimental fossilization of mat-forming cyanobacteria in coarse-grained siliciclastic sediments. Geobiology 15:484–498 [doi:10.1111/gbi.12229].

Nicholson, H. A., & Robert Etheridge. 1878. A monograph of the Silurian fossils of the Girvan district in Ayrshire, with special reference to those contained in the 'Gray collection' (Fasciculus I). W. Blackwood and Sons. London. 135 p.

Noffke, Nora. 2010. Microbial Mats in Sandy Deposits from the Archean Era to Today. Springer. Heidelberg. 194 p.

Normington, V. J., E. E. Beyer, J. A. Whelan, C. J. Edgoose, & J. D. Woodhead. 2019. Summary of results. NTGS LA-ICP-MS Hf program: Amadeus Basin, July 2013–June 2015. Northern Territory Geological Survey Record 2019–005:1–34.

Oehler, J. H., & J. W. Schopf. 1971. Artificial microfossils: Experimental studies of permineralization of blue-green algae in silica. Science 174:1229–1231.

Pang, Ke, Qing Tang, Lei Chen, Bin Wan, Changtai Niu, Xunlai Yuan, & Shuhai Xiao. 2018. Nitrogen-fixing heterocystous cyanobacteria in the Tonian Period. Current Biology 28:616–622 [doi:10.1016/j.cub.2018.01.008].

Peng, Xiaotong, & Brian Jones. 2012. Rapid precipitation of silica (opal-A) disguises evidence of biogenicity in high-temperature geothermal deposits: Case study from Dagunguo hot spring, China. Sedimentary Geology 257–260:45–62.

Perfilev, B. V., & D. R. Gabe. 1961. Capillary methods of investigating micro-organisms (English translation 1969). Oliver and Boyd. Edinburgh.

Pesquero, M. D., Virginia Souza-Egipsy, Luis Alcalá, Carmen Ascaso, & Yolanda Fernández-Jalvo. 2014. Calcium phosphate preservation of faecal bacterial negative moulds in hyaena coprolites. Acta Palaeontologica Polonica 59:997–1005 [doi:10.4202/app.2012.0067].

Pia, Julius. 1927. Thallophyta. *In* M. J. Hirmer, ed., Handbuch der Paläobotanik, Band 1: Thallophyta, Bryophyta, Pteridophyta. Oldenbourg. Munich. p. 31–136

Poinar, G. O., Jr., B. M. Waggoner, & U.-C. Bauer. 1993. Terrestrial soft-bodied protists and other microorganisms in triassic amber. Science 259:222–224 [doi:10.1126/science.259.5092.222].

Qu, Yuangao, Anders Engdahl, Shixing Zhu, Vivi Vajda, & Nicola McLoughlin. 2015. Ultrastructural heterogeneity of carbonaceous material in ancient cherts: Investigating biosignature origin and preservation. Astrobiology 15:825–842.

Qu, Yuangao, Shixing Zhu, Martin Whitehouse, Anders Engdahl, & Nicola McLoughlin. 2018. Carbonaceous biosignatures of the earliest putative macroscopic multicellular eukaryotes from 1630 Ma Tuanshanzi Formation, north China. Precambrian Research 304:99–109 [doi:10.1016/j.precamres.2017.11.004].

Raff, E. C., M. E. Andrews, F. R. Turner, Evelyn Toh, D. E. Nelson, & R. A. Raff. 2013. Contingent interactions among biofilm-forming bacteria determine preservation or decay in the first steps toward fossilization of marine embryos. Evolution & Development doi:10.1111/ede.12028.

Raff, E. C., K. L. Schollaert, D. E. Nelson, P. C. J. Donoghue, C.-W. Thomas, F. R. Turner, B. D. Stein, Xiping Dong, Stefan Bengtson, Therese Huldtgren, Marco Stampanoni, Chongyu Yin, & R. A. Raff. 2008. Embryo fossilization is a biological process mediated by microbial biofilms. Proceedings of the National Academy of Sciences, USA 105:19360–19365.

Rashby, S. E., A. L. Sessions, R. E. Summons, & D. K. Newman. 2007. Biosynthesis of 2-methylbacteriohopanepolyols by an anoxygenic phototroph. Proceedings of the National Academy of Sciences, USA 104:15099–15104 [doi:10.1073/pnas.0704912104].

Rasmussen, Birger. 2000. Filamentousmicrofossils in a 3,235-million-year-old volcanogenicmassive sulphide deposit. Nature 405:676–679.

Rasmussen, Birger, I. R. Fletcher, J. J. Brocks, & M. R. Kilburn. 2008. Reassessing the first appearance of eukaryotes and cyanobacteria. Nature 455:1101–1104.

Reitlinger, E. A. 1948. Kembriiskie foraminiferi Yakutii (Cambrian Foraminifera of Yakutia). Byulletin' Moskovskogo Obshchestva Ispytatelej Prirody, Otdelenie Geologii 23:77–81.

Renault, B. 1896. Recherches sur les Bactériacées fossils. Annales des Sciences Naturelles Série 8 (Botanique) 2:275–349.

Renaut, R. W., Brian Jones, & J. J. Tiercelin. 1998. Rapid *in situ* silicification of microbes at Loburu hot springs, Lake Bogoria, Kenya Rift Valley. Sedimentology 45:1083–1103.

Riding, Robert. 1991. Calcified cyanobacteria. *In* R. Riding, ed., Calcareous Algae and Stromatolites. Springer-Verlag. Berlin. p. 55–87

Riding, Robert. 2006. Cyanobacterial calcification, carbon dioxide concentrating mechanisms, and Proterozoic-Cambrian changes in atmospheric composition. Geobiology 4:299–316 [doi:10.1111/j.1472-4669.2006.00087.x].

Roberts, A. P., Fabio Florindo, Giuliana Villa, Liao Chang, Luigi Jovane, S. M. Bohaty, J. C. Larrasoaña, David Heslop, & J. D. F. Gerald. 2011. Magnetotactic bacterial abundance in pelagic marine environments is limited by organic carbon flux and availability of dissolved iron. Earth and Planetary Science Letters 310:441–452 [doi:10.1016/j.epsl.2011.08.011].

Rosing, M. T. 1999. ^{13}C-depleted carbon microparticles in >3700-Ma sea-floor sedimentary rocks from West Greenland. Science 283:674–676.

Rouillard, Joti, J. M. García-Ruiz, Jian Gong, & M. A. van Zuilen. 2018. A morphogram for silica-witherite biomorphs and its application to microfossil identification in the early earth rock record. Geobiology 16:279–296 [doi:10.1111/gbi.12278].

Rouillard, Joti, M. A. van Zuilen, Celine Pisapia, & J.-M. Garcia-Ruiz. 2021. An alternative approach for assessing biogenicity. Astrobiology 21(2):151–164 [doi:10.1089/ast.2020.2282].

Rozanov, A. Yu, & M. M. Astafieva. 2009. The evolution of the early precambrian geobiological systems. Paleontological Journal 43:911–927.

Runnegar, Bruce. 1985. Early Cambrian endolithic algae. Alcheringa 9:179–182.

Sánchez-Baracaldo, Patricia. 2015. Origin of marine planktonic cyanobacteria. Scientific Reports 5:17418 [doi:10.1038/srep17418].

Schiffbauer, J. D., A. F. Wallace, Jesse Broce, & Shuhai Xiao. 2014a. Exceptional fossil conservation through phosphatization. *In* Marc Laflamme, J. D. Schiffbauer, & S. A. F. Darroch, eds., Reading and Writing of the Fossil Record: Preservational Pathways to Exceptional Fossilization. The Paleontological Society Papers, Volume 20. p. 59–82.

Schiffbauer, J. D., Shuhai Xiao, Yaoping Cai, A. F. Wallace, Hong Hua, Jerry Hunter, Huifang Xu, Yongbo Peng, & A. J. Kaufman. 2014b. A unifying model for Neoproterozoic–Palaeozoic exceptional fossil preservation through pyritization and carbonaceous compression. Nature Communications 5:5754 [doi:10.1038/ncomms6754].

Schiffbauer, J. D., Leiming Yin, R. J. Bodnar, A. J. Kaufman, Fanwei Meng, Jie Hu, Bing Shen, Xunlai Yuan, Huiming Bao, & Shuhai Xiao. 2007. Ultrastructural and geochemical characterization of Archean-Paleoproterozoic graphite particles: Implications for recognizing traces of life in highly metamorphosed rocks. Astrobiology 7:684–704.

Schirrmeister, B. E., Muriel Gugger, & P. C. J. Donoghue. 2015. Cyanobacteria and the Great Oxidation Event: evidence from genes and fossils. Palaeontology 58:769–785 [doi:10.1111/pala.12178].

Schirrmeister, B. E., Patricia Sánchez-Baracaldo, & David Wacey. 2016. Cyanobacterial evolution during the Precambrian. International Journal of Astrobiology 15:187–204. [doi:10.1017/S1473550415000579].

Schloss, P. D., R. A. Girard, Thomas Martin, Joshua Edwards, J. C. Thrash, & E. F. Delong. 2016. Status of the archaeal and bacterial census: An update. mBio 7:e00201-00216 [doi:10.1128/mBio.00201-16].

Schmidt, A. R., & Ursula Schäfer. 2005. *Leptotrichites resinatus* new genus and species: A fossil sheathed

bacterium in Alpine Cretaceous amber. Journal of Paleontology 79:175–184 [doi:10.1666/0022-3360(2005)079<0175:LRNGAS>2.0.CO;2].

Schopf, J. M., E. G. Ehlers, D. V. Stiles, & J. D. Birle. 1965. Fossil iron bacteria preserved in pyrite. Proceedings of the American Philosophical Society 109:288–308.

Schopf, J. W. 1968. Microflora of the Bitter Springs Formation, Late Precambrian, central Australia. Journal of Paleontology 42:651–688.

Schopf, J. W. 1983. Earth's Earliest Biosphere: Its Origin and Evolution. Princeton University Press. Princeton. 543 p.

Schopf, J. W. 1992a. Historical development of Proterozoic micropaleontology. *In* J. W. Schopf, & Cornelis Klein, eds., The Proterozoic Biosphere: A Multidisciplinary Study. Cambridge University Press. New York. p. 179–183.

Schopf, J. W. 1992b. Proterozoic prokaryotes: Affinities, geologic distribution, and evolutionary trends. *In* J. W. Schopf, & Cornelis Klein, eds., The Proterozoic Biosphere: A Multidisciplinary Study. Cambridge University Press. New York. p. 195–218.

Schopf, J. W. 1993. Microfossils of the Early Archean Apex Chert: New evidence of the antiquity of life. Science 260:640–646.

Schopf, J. W. 1994. Disparate rates, differing fates: Tempo and mode of evolution changed from the Precambrian to the Phanerozoic. Proceedings of the National Academy of Sciences, USA 91:6735–6742.

Schopf, J. W. 2006a. The first billion years: When did life emerge? Elements 2:229–233.

Schopf, J. W. 2006b. Fossil evidence of Archaean life. Philosophical Transactions of the Royal Society of London B (Biological Sciences) 361:869–885.

Schopf, J. W. 2012. The fossil record of cyanobacteria. *In* B. A. Whitton, ed., Ecology of Cyanobacteria II: Their Diversity in Space and Time. Springer. Dordrecht. p. 15–36 [doi:10.1007/978-94-007-3855-3_2].

Schopf, J. W., & E. S. Barghoorn. 1967. Alga-like fossils from the early Precambrian of South Africa. Science 156:508–512 [doi:10.1126/science.156.3774.508].

Schopf, J. W., & E. S. Barghoorn. 1969. Microorganisms from the late Precambrian of South Australia. Journal of Paleontology 43:111–118.

Schopf, J. W., & J. M. Blacic. 1971. New microorganisms from the Bitter Springs Formation (Late Precambrian) of the north-central Amadeus Basin, Australia. Journal of Paleontology 45:925–960.

Schopf, J. W., J. D. Farmer, I. S. Foster, A. B. Kudryavtsev, V. A. Gallardo, & Carola Espinoza. 2012. Gypsum-permineralized microfossils and their relevance to the search for life on Mars. Astrobiology 7:619–633 [doi:10.1089/ast.2012.0827].

Schopf, J. W., K. Kitajima, M. J. Spicuzza, A. B. Kudryavtsev, & J. W. Valley. 2018. SIMS analyses of the oldest known assemblage of microfossils document their taxon-correlated carbon isotope compositions. Proceedings of the National Academy of Sciences, USA 115:53–58 [doi:10.1073/pnas.1718063115].

Schopf, J. W., & Cornelis Klein. 1992. The Proterozoic Biosphere: A Multidisciplinary Study. Cambridge University Press. Cambridge, UK. 1348 p.

Schopf, J. W., A. B. Kudryavtsev, D. G. Agresti, A. D. Czaja, & T. J. Wdowiak. 2005. Raman imagery: a new approach to assess the geochemical maturity and biogenicity of permineralized Precambrian fossils. Astrobiology 5:333–371.

Schopf, J. W., A. B. Kudryavtsev, D. G. Agresti, T. J. Wdowiak, & A. D. Czaja. 2002. Laser-Raman imagery of Earth's earliest fossils. Nature 416:73–76.

Schopf, J. W., A. B. Kudryavtsev, K. Sugitani, & M. R. Walter. 2010. Precambrian microbe-like pseudofossils: A promising solution to the problem. Precambrian Research 179:191–205 [doi:10.1016/j.precamres.2010.03.003].

Schopf, J. W., A. B. Kudryavtsev, M. R. Walter, M. J. Van Kranendonk, K. H. Williford, R. Kozdon, J. W. Valley, V. A. Gallardo, Carola Espinoza, & D. T. Flannery. 2015. Sulfur-cycling fossil bacteria from the 1.8-Ga Duck Creek Formation provide promising evidence of evolution's null hypothesis. Proceedings of the National Academy of Sciences, USA 112:2087–2092 [doi:10.1073/pnas.1419241112].

Schopf, J. W., & B. M. Packer. 1987. Ealry Archean (3.3-billion to 3.5-billion-year-old) microfossils from Warrawoona group, Australia. Science 237:70–73.

Schubert, J. K., D. L. Kidder, & D. H. Erwin. 1997. Silica-replaced fossils through the Phanerozoic. Geology 25:1031–1034 [doi:10.1130/0091-7613(1997)025<1031:SRFTTP>2.3.CO;2].

Schulz, H. N., Thorsten Brinkhoff, T. G. Ferdelman, M. H. Mariné, Andreas Teske, & B. B. Jørgensen. 1999. Dense populations of a giant sulfur bacterium in Namibian shelf sediments. Science 284:493–495 [doi:10.1126/science.284.5413.493].

Sergeev, V. N. 1994. Microfossils in cherts from the Middle Riphean (Mesoproterozoic) Avzyan Formation, southern Ural Mountains, Russian Federation. Precambrian Research 65:231–254.

Sergeev, V. N., A. H. Knoll, & J. P. Grotzinger. 1995. Paleobiology of the Mesoproterozoic Billyakh Group, Anabar Uplift, northern Siberia. The Paleontological Society Memoir 39:1–37.

Sergeev, V. N., J. W. Schopf, & A. B. Kudryavtsev. 2020. Global microfossil changes through the Precambrian-Cambrian phosphogenic event: The Shabakta Formation of the phosphorite-bearing Maly Karatau Range, South Kazakhstan. Precambrian Research 349:105386 [doi:10.1016/j.precamres.2019.105386].

Sergeev, V. N., Mukund Sharma, &Yogmaya Shukla. 2012. Proterozoic fossil cyanobacteria. The Palaeobotanist 61:189–358.

She, Zhenbing, Yantao Zhang, Wei Liu, Jingjing Song, Yaguan Zhang, Chao Li, Paul Strother, & Dominic Papineau. 2016. New observations of Ambient Inclusion Trails (AITs) and pyrite framboids in the Ediacaran Doushantuo Formation, South China. Palaeogeography, Palaeoclimatology, Palaeoecology 461:374–388 [doi:10.1016/j.palaeo.2016.08.035].

Shen, Yanan, & Roger Buick. 2004. The antiquity of microbial sulfate reduction. Earth-Science Reviews 64:243–272.

Shi, Min, Qinglai Feng, M. Z. Khan, & Shixing Zhu. 2017. An eukaryote-bearing microbiota from the early Mesoproterozoic Gaoyuzhuang Forma-

tion, Tianjin, China and its significance. Precambrian Research 303:709–726 [doi:10.1016/j.precamres.2017.09.013].

Shih, P. M., James Hemp, L. M. Ward, N. J. Matzke, & W. W. Fischer. 2017. Crown group Oxyphotobacteria postdate the rise of oxygen. Geobiology 15:19–29 [doi:10.1111/gbi.12200].

Sohm, J. A., E. A. Webb, & D. G. Capone. 2011. Emerging patterns of marine nitrogen fixation. Nature Reviews Microbiology 9:499–508 [doi:10.1038/nrmicro2594].

Stal, L. J. 2012. Cyanobacterial mats and stromatolites. *In* B. A. Whitton, ed., Ecology of Cyanobacteria II: Their Diversity in Space and Time. Springer. London. p. 65–125

Stasiuk, L. D., & K. G. Osadetz. 1990. The life cycle and phyletic affinity of *Gloeocapsomorpha prisca* Zalessky 1917 from Ordovician rocks in the Canadian Williston Basin. Geological Survey of Canada Paper 89–1D:123–137.

Staudigel, Hubert, Harald Furnes, N. R. Banerjee, Yildirim Dilek, & Karlis Muehlenbachs. 2006. Microbes and volcanoes: A tale from the oceans, ophiolites, and greenstone belts. GSA Today 16(10):4–10 [doi:10.1130/GSAT01610A.1].

Staudigel, Hubert, Harald Furnes, Nicola McLoughlin, N. R. Banerjee, L. B. Connell, & Alexis Templeton. 2008. 3.5 billion years of glass bioalteration: Volcanic rocks as a basis for microbial life? Earth-Science Reviews 89:156–176 [doi:10.1016/j.earscirev.2008.04.005].

Steiner, Michael, & Oldrich Fatka. 1996. Lower Cambrian tubular micro- to macrofossils from the Paseky Shale of the Barrandian area (Czech Republic). Paläontologische Zeitschrift 70(3/4):275–299 [doi:10.1007/BF02988075].

Stueken, E. E., Roger Buick, R. E. Anderson, J. A. Baross, N. J. Planavsky, & T. W. Lyons. 2017. Environmental niches and metabolic diversity in Neoarchean lakes. Geobiology 15:767–783 [doi:10.1111/15 gbi.12251].

Sugitania, Kenichiro, Koichi Mimura, Tsutomu Nagaoka, Kevin Lepot, & Makoto Takeuchi. 2013. Microfossil assemblage from the 3400 Ma Strelley Pool Formation in the Pilbara Craton, Western Australia: Results form a new locality. Precambrian Research 226:59–74 [doi:10.1016/j.precamres.2012.11.005].

Summons, R. E., L. L. Jahnke, J. M. Hope, & G. A. Logan. 1999. 2-Methylhopanoids as biomarkers for cyanobacterial oxygenic photosynthesis. Nature 400:554–557.

Sun, Funing, Wenxuan Hu, Xiaolin Wang, Jia Cao, Bin Fu, Haiguang Wu, & Shengchao Yang. 2020. Methanogen microfossils and methanogenesis in Permian lake deposits. Geology 49:13–18 [doi:10.1130/G47857.1].

Tang, Qing, Ke Pang, Shuhai Xiao, X. Yuan, Z. Ou, & B. Wan. 2013. Organic-walled microfossils from the early Neoproterozoic Liulaobei Formation in the Huainan region of North China and their biostratigraphic significance. Precambrian Research 236:157–181 [doi:10.1016/j.precamres.2013.07.019].

Tang, Qing, Ke Pang, Xunlai Yuan, Bin Wan, & Shuhai Xiao. 2015. Organic-walled microfossils from the Tonian Gouhou Formation, Huaibei region, North China Craton, and their biostratigraphic implications. Precambrian Research 266:296–318 [doi:10.1016/j.precamres.2015.05.025].

Tang, Ruikang, G. H. Nancollas, & C. A. Orme. 2001. Mechanism of dissolution of sparingly soluble electrolytes. Journal of Americal Chemical Society 123:5437–5443 [doi:10.1021/ja010064p].

Taylor, T. N., & Michael Krings. 2005. Fossil microorganisms and land plants: Associations and interactions. Symbiosis 40:119–135.

Taylor, T. N., E. L. Taylor, & Michael Krings. 2009. Paleobotany: The Biology and Evolution of Fossil Plants (Second Edition). Academic Press. Amsterdam. 1252 p.

Timofeev, B. V., T. N. Hermann, & N. S. Mikhailova. 1976. Microphytofossils of the Precambrian, Cambrian and Ordovician. Nauka. Leningrad. 106 p.

Tomitani, Akiko, A. H. Knoll, C. M. Cavanaugh, & Terufumi Ohno. 2006. The evolutionary diversification of cyanobacteria: Molecular–phylogenetic and paleontological perspectives. Proceedings of the National Academy of Sciences, USA 103:5442–5447 [doi:10.1073/pnas.0600999103].

Toporski, J. K. W., Andrew Steele, Frances Westall, K. L. Thomas-Keprta, & D. S. McKay. 2002. The simulated silicification of bacteria: New clues to the modes and timing of bacterial preservation and implications for the search for extraterrestrial microfossils. Astrobiology 2:1–26.

Trevisan, Vittore. 1842. Prospetto della Flora Euganea. Coi Tipi Del Seminario. Padova. 68 p.

Trewin, N. H., S. R. Fayers, & Ruth Kelman. 2003. Subaqueous silicification of the contents of small ponds in an Early Devonian hot-spring complex, Rhynie, Scotland. Canadian Journal of Earth Sciences 40:1697–1712 [doi:10.1139/e03-065].

Turner, E. C., G. M. Narbonne, & N. P. James. 1993. Neoproterozoic reef microstructures from the Little Dal Group, northwestern Canada. Geology 21:259–262 [doi:10.1130/0091–7613(1993)021<0259:NRMFTL>2.3.CO;2].

Tyler, S. A., & E. S. Barghoorn. 1954. Occurrence of structurally preserved plants in pre-Cambrian rocks of the Canadian Shield [Ontario]. Science 119:606–608.

Tyler, S. A., & E. S. Barghoorn. 1963. Ambient pyrite grains in Precambrian cherts. American Journal of Science 261:424–432.

Uyeda, J. C., L. J. Harmon, & C. E. A. Blank. 2016. A comprehensive study of cyanobacterial morphological and ecological evolutionary dynamics through deep geologic time. PLoS One 11:e0162539. [doi:10.1371/journal.pone.0162539].

Vai, G. B., & F. R. Lucchi. 1977. Algal crusts, autochthonous and clastic gypsum in a cannibalistic evaporite basin: a case history from the Messinian of Northern Apennines. Sedimentology 24:211–244 [doi:10.1111/j.1365-3091.1977.tb00255.x].

Vidal, Gonzalo. 1976. Late Precambrian microfossils from the Visingso beds in southern Sweden. Fossils and Strata 9:1–57.

Vidal, Gonzalo. 1981. Micropalaeontology and biostratigraphy of the upper Proterozoic and Lower Cam-

brian sequences in East Finnmark, northern Norway. Norges Geologiske Undersokelse Bulletin 362:1–53.

Vinther, Jakob. 2015. Fossil melanosomes or bacteria? A wealth of findings favours melanosomes. BioEssays 38:220–225 [doi:10.1002/bies.201500168].

Vologdin, A. G. 1932. Arkehotsiaty Sibiri, II [The Archaeocyathinae of Siberia, II]. Moscow-Leningrad. 106 p.

Wacey, David, Kate Eiloart, & Martin Saunders. 2019. Comparative multi-scale analysis of filamentous microfossils from the c. 850 Ma Bitter Springs Group and filaments from the c. 3460 Ma Apex chert. Journal of the Geological Society of London 176:1247–1260 [doi:10.1144/jgs2019-053].

Wacey, David, M. R. Kilburn, Nicola McLoughlin, John Parnell, C. A. Stoakes, C. R. Grovenor, & M. D. Brasier. 2008. Use of NanoSIMS in the search for early life on Earth: ambient inclusion trails in a c. 3400 Ma sandstone. Journal of the Geological Society of London 165:43–53.

Waggoner, B. M. 1994. An aquatic microfossil assemblage from Cenomanian amber of France. Lethaia 27:77–84 [doi:10.1111/j.1502-3931.1994.tb01559.x].

Waksman, S. A., & A. T. Henrici. 1943. The nomenclature and classification of the actinomycetes. Journal of Bacteriology 46:337–341.

Walcott, C. D. 1914. Pre-cambrian Algonkian algal flora. Smithsonian Miscellaneous Collections (Cambrian Geology and Paleontology II) 64 (2):77–156.

Walcott, C. D. 1915. Discovery of Algonkian bacteria. Proceedings of the National Academy of Sciences, USA 1:256–257 [doi:10.1073/pnas.1.4.256].

Walcott, C. D. 1919. Cambrian Geology and Paleontology IV: Middle Cambrian algae. Smithsonian Miscellaneous Collections 67:217–260.

Wang, Jiasheng, Ganqing Jiang, Shuhai Xiao, Qing Li, & Qing Wei. 2008. Carbon isotope evidence for widespread methane seeps in the ~635 Ma Doushantuo cap carbonate in South China. Geology 36:347–350.

Wang, Yangeng, Gongzheng Yin, Shufang Zheng, Shourong Qin, Shuncai Zhu, Yulin Chen, Qiling Luo, Shixing Zhu, Fuxing Wang, Yi Qian. 1984. The Upper Precambrian and Sinian-Cambrian Boundary in Guizhou. The People's Publishing House of Guizhou. Guiyang. 170 p.

Westall, Frances, Laurita Boni, & Elisabetta Guerzoni. 1995. The experimental silicification of microorganisms. Palaeontology 38:495–528.

Westall, Frances, & R. L. Folk. 2003. Exogenous carbonaceous microstructures in Early Archaean cherts and BIFs from the Isua Greenstone Belt: implications for the search for life in ancient rocks. Precambrian Research 126:313–330 [doi:10.1016/S0301-9268(03)00102-5].

Whitman, W. B., D. C. Coleman, & W. J. Wiebe. 1998. Prokaryotes: The unseen majority. Proceedings of the National Academy of Sciences, USA 95:6578–6583.

Wilby, P. R., & D. E. G. Briggs. 1997. Taxonomic trends in the resolution of detail preserved in fossil phosphatized soft tissues. Geobios, Memoire special No. 20:493–502.

Wood, Alan. 1957. The type-species of the genus *Girvanella* (calcareous algae). Palaeontology 1:22–28.

Xiao, Shuhai, Natalia Bykova, Alex Kovalick, & B. C. Gill. 2017. Stable carbon isotopes of sedimentary kerogens and carbonaceous macrofossils from the Ediacaran Miaohe Member in South China: Implications for stratigraphic correlation and sources of sedimentary organic carbon. Precambrian Research 302:171–179 [doi:10.1016/j.precamres.2017.10.006].

Xiao, Shuhai, & M. F. Hochella, Jr. 2017. Why and how do phosphatic minerals replicate soft tissues at the highest resolution? Geological Society of America Abstracts with Programs 49(6):10.1130/abs/2017AM-299804.

Xiao, Shuhai, & A. H. Knoll. 1999. Fossil preservation in the Neoproterozoic Doushantuo phosphorite Lagerstätte, South China. Lethaia 32:219–240.

Xiao, Shuhai, & J. D. Schiffbauer. 2009. Microfossil phosphatization and its astrobiological implications. *In* J. Seckbach, & M. Walsh, eds., From Fossils to Astrobiology. Springer-Verlag. New York. p. 89–117.

Xiao, S., & Q. Tang. 2018. After the boring billion and before the freezing millions: Evolutionary patterns and innovations in the Tonian Period. Emerging Topics in Life Sciences 2:161–171 [doi:10.1042/ETLS20170165].

Xiao, Shuhai, Xunlai Yuan, Michael Steiner, & A. H. Knoll. 2002. Macroscopic carbonaceous compressions in a terminal Proterozoic shale: A systematic reassessment of the Miaohe biota, South China. Journal of Paleontology 76:347–376.

Xiao, Shuhai, Yun Zhang, & A. H. Knoll. 1998. Three-dimensional preservation of algae and animal embryos in a Neoproterozoic phosphorite. Nature 391:553–558.

Xiao, Shuhai, Chuanming Zhou, & Xunlai Yuan. 2007. Undressing and redressing Ediacaran embryos. Nature 446:E9–10.

Xing, Yusheng, & Zhuizhi Liu. 1973. Sinian micropaleoflora in the Yan-Liao area and its geological significance. Acta Geologica Sinica 1973:1–31.

Yang, X.-g., Jian Han, Xing Wang, J. D. Schiffbauer, Kentaro Uesugi, Osamu Sasaki, & Tsuyoshi Komiya. 2017. Euendoliths versus ambient inclusion trails from Early Cambrian Kuanchuanpu Formation, South China. Palaeogeography Palaeoclimatology Palaeoecology 476:147–157. [doi:10.1016/j.palaeo.2017.03.028].

Yao, Jinxian, Shuhai Xiao, Leiming Yin, Guoxiang Li, & Xunlai Yuan. 2005. Basal Cambrian microfossils from the Yurtus and Xishanblaq formations (Tarim, north-west China): Systematic revision and biostratigraphic correlation of *Micrhystridium*-like acritarchs from China. Palaeontology 48:687–708 [doi:10.1111/j.1475-4983.2005.00484.x].

Yuan, Xunlai, Shuhai Xiao, & T. N. Taylor. 2005. Lichen-like symbiosis 600 million years ago. Science 308:1017–1020.

Zalessky, M. D. 1917. On marine sapropelite of Silurian age, formed by blue-green alga. Izv. imp. akad. nauk (IV) 1:3–18 (in Russian).

Zavarzin, G. A. 1981. The Genus *Metallogenium*. *In* M. P. Starr, H. Stolp, H. G. Truper, A. Balows, &

H. G. Schlegel, eds., The Prokaryotes: A Handbook on Habitats, Isolation, and Identification of Bacteria (Volume 1). Springer-Verlag. Berlin. p. 524–528.

Zhang, Yun, & Stjepko Golubic. 1987. Endolithic microfossils (Cyanophyta) from early Proterozoic stromatolites, Hebei, China. Acta Micropalaeontologica Sinica 4:1–12.

Zhang, Yun, Leiming Yin, Shuhai Xiao, & A. H. Knoll. 1998. Permineralized fossils from the terminal Proterozoic Doushantuo Formation, South China. Journal of Paleontology 72 (supplement to No. 4):1–52.

Zhou, Xiqiang, Daizhao Chen, Dongjie Tang, Shaofeng Dong, Chuan Guo, Zenghui Guo, & Yanqiu Zhang. 2015. Biogenic iron-rich filaments in the quartz veins in the uppermost Ediacaran Qigebulake Formation, Aksu Area, northwestern Tarim Basin, China: Implications for iron oxidizers in subseafloor hydrothermal systems. Astrobiology 15:523–537 [doi:10.1089/ast.2014.1234].