

Fossil evidence of Archaean life

J. William Schopf*

*Department of Earth and Space Sciences, Institute of Geophysics and Planetary Physics
(Center for the Study of Evolution and the Origin of Life), and Molecular Biology Institute,
University of California, Los Angeles, CA 90095, USA*

Evidence for the existence of life during the Archaean segment of Earth history (more than 2500 Myr ago) is summarized. Data are presented for 48 Archaean deposits reported to contain biogenic stromatolites, for 14 such units reported to contain 40 morphotypes of putative microfossils, and for 13 especially ancient, 3200–3500 Myr old geologic units for which available organic geochemical data are also summarized. These compilations support the view that life's existence dates from more than or equal to 3500 Myr ago.

Keywords: Archaean; stromatolites; microfossils; oldest life

1. PREFACE

At the request of Thomas Cavalier-Smith, the lead organizer of the Discussion Meeting on which this volume is based, I agreed in December 2002 to address in this contribution the known fossil evidence for the timing of the origin of various prokaryotic lineages. In the interim between then and now, however, questions have been raised regarding the previously widely accepted lines of evidence on which any such discussion would be based—(i) stromatolites; (ii) microfossils; (iii) molecular biomarkers; and (iv) carbon and sulphur isotopic data—for the most part dating from rocks as old as *ca* 3500 Myr. Recently, for example, Stephen Moorbath, in the pages of *Nature* and citing Knoll (2003a) as his authority (perhaps in error?), suggested that ‘true consensus for life’s existence’ dates only from ‘the bacterial fossils of 1.9-billion-year-old Gunflint Formation of Ontario’ (Moorbath 2005). Evidently, all supposed evidences of earlier life, ‘the many claims of life in the first 2.0–2.5 billion years of Earth’s history’, are in doubt (Moorbath 2005). Yet it is precisely during this period of Earth history, prior to 2000 Myr ago (Ma), that most workers have assumed that the major varieties of prokaryotes originated. If the fossil record is to make any contribution to defining the timing of origin of the major prokaryotic lineages, such doubts must be resolved. Clearly, here it would be awkward to address the timing early in Earth history of the origin of various prokaryotic lineages when the evidence supporting such suppositions—and, indeed, of the very existence of life itself—has been called into question. I have therefore elected to recast this contribution to address a more fundamental, first-order question: what evidence exists for life’s existence during the Archaean Eon of Earth history, prior to 2500 Ma?

This discussion will not be exhaustive. Elsewhere in this volume, Roger Summons and his colleagues

consider the molecular biomarker data available from Archaean deposits, and John M. Hayes and Jacob R. Waldbauer address the relevant evidence from carbon isotopes. Thus, I need to address only two of the four generally accepted evidences of early life: stromatolites and microfossils. But given the amount of data reported from even these two categories of evidence, and the space constraints imposed by this journal, my discussion will necessarily be perfunctory. This article is not the place for a full-blown description of each of the 48 occurrences of Archaean stromatolites listed in table 1, nor of the 40 morphotypes of objects described as microfossils known from Archaean-age rocks (table 2). Rather, my aim is to summarize and illustrate representative examples of such occurrences, so that others may have a better understanding of why it is that most workers worldwide are of the opinion that the ‘true consensus for life’s existence’ dates from more than 3500 Myr ago.

2. PRESERVATION OF THE ARCHAEOAN ROCK RECORD

Relatively few workers have considered, even in broad-brush outline, the temporal distribution of the known sedimentary rock record. One of the best such syntheses is provided by Garrels & Mackenzie (1971). According to these authors, the average lifetime of such geologic units is about 200 Myr old and, thus, as a result of geological recycling, about 50% of such sediments that have survived to the present date from the Phanerozoic (less than 550 Myr in age), the remainder from the earlier, *ca* 4000 Myr long Precambrian (Garrels & Mackenzie 1971, pp. 255–276). As estimated by Garrels & Mackenzie (1971, p. 275), ‘about 90 percent of the Precambrian once deposited is gone’, surviving rocks petering out rapidly with increasing geologic age to yield a severely depleted Archaean rock record. Hence, the oldest surviving igneous rocks, from the Acasta Gneiss Complex of Northwest Territories, Canada, are but *ca* 4000 Myr in age (Stern & Bleeker 1998), hundreds of millions of years younger than the age of the planet itself. The oldest known sedimentary

*schopf@ess.ucla.edu

One contribution of 14 to a Discussion Meeting Issue ‘Major steps in cell evolution’.

Table 1. Archaean stromatolites/microbial mats.

age (Myr)	geologic unit	principal stromatolite/ mat type	country	references
ca 3496	Dresser Formation, Warrawoona Group, Pilbara Supergroup	domical	Australia	Walter <i>et al.</i> (1980), Buick <i>et al.</i> (1981, 1995), Groves <i>et al.</i> (1981), Walter (1983), Schopf & Walter (1983), Buick (2001), Van Kranendonk <i>et al.</i> (2003)
ca 3470	Mount Ada Basalt ^a , Warrawoona Group, Pilbara Supergroup	stratiform	Australia	Awramik <i>et al.</i> (1983)
ca 3460	Hooggenoeg Formation, Onverwacht Group, Swaziland Supergroup	stratiform?	South Africa	Hofmann (2000)
ca 3440	Panorama Formation, Warrawoona Group, Pilbara Supergroup	conical	Australia	Hofmann (2000)
ca 3400	Witkop Formation, Nondweni Group	domical	South Africa	Hofmann (2000)
ca 3388	Strelley Pool Chert ^b , Kelly Group, Pilbara Supergroup	conical	Australia	Lowe (1980, 1983), Hofmann <i>et al.</i> (1999), Van Kranendonk <i>et al.</i> (2003), Allwood <i>et al.</i> (2004)
ca 3320	Kromberg Formation, Onverwacht Group, Swaziland Supergroup	stratiform	South Africa	Muir & Grant (1976), Walsh & Lowe (1985) and Walsh (1992)
ca 3316	Buck Reef Chert, Onverwacht Group, Swaziland Supergroup	stratiform	South Africa	Tice & Lowe (2004)
ca 3245	Sheba Formation, Fig Tree Group, Swaziland Supergroup	columnar	South Africa	Byerly <i>et al.</i> (1986) and Byerly & Palmer (1991)
ca 3200	Dixon Island Formation	stratiform	Australia	Kiyokawa <i>et al.</i> (2006)
> 3048	Cattle Well Formation, De Grey Group	domical	Australia	Williams (2000)
ca 2985	Insuzi Group, Pongola Supergroup	diverse	South Africa	Mason & von Brunn (1977), von Brunn & Mason (1977), Walter (1983), Beukes & Lowe (1989)
ca 2925	Ball Assemblage, Red Lake Metasediments	domical	Canada	Hofmann <i>et al.</i> (1985)
ca 2850	Mushandike Formation	domical	Zimbabwe	Hofmann (2000)
ca 2850	Woman Lake Marble	domical	Canada	Walter (1983), Hofmann <i>et al.</i> (1985)
ca 2850	Keeyask Metasediments, Eyapamikama Lake	domical	Canada	Arias <i>et al.</i> (1986)
ca 2800	Steepprock Group	diverse	Canada	Joliffe (1955), Hofmann (1971), Walter (1983), Wilks & Nisbet (1985, 1988), Thurston <i>et al.</i> (1987), Sumner (2000)
ca 2800	Sebakwian Group	domical	Zimbabwe	Opren & Wilson (1981)
ca 2800	Vanivilas Formation, Chidradurga Group, Dharwar Supergroup	diverse	India	Hofmann (2000)
ca 2772	Mount Roe Basalt, Fortescue Group, Mount Bruce Supergroup	columnar	Australia	K. Grey (2005, personal communication)
ca 2759	Hardey Formation, Fortescue Group, Mount Bruce Supergroup	columnar	Australia	K. Grey (2005, personal communication)
ca 2750	Muskkrat Dam Greenstone Belt	pseudocolumnar	Canada	Hofmann (2000)
ca 2742	Kylena Formation, Fortescue Group, Mount Bruce Supergroup	columnar	Australia	K. Grey (2005, personal communication)
> 2730	Leonora area, Eastern Goldfields, Yilgarn Block	columnar	Australia	K. Grey (2005, personal communication)
ca 2725	Joutel Volcanic Complex	conical	Canada	Hofmann & Masson (1994)
ca 2725	Helen Iron Formation, Michipicoten Group	conical	Canada	Hofmann <i>et al.</i> (1991)
ca 2723	Tumbiana Formation, Fortescue Group, Mount Bruce Supergroup	diverse	Australia	Walter (1972), Grey (1979), Walter (1983)
ca 2715	Madina Formation, Fortescue Group, Mount Bruce Supergroup	columnar	Australia	K. Grey (2005, personal communication)
ca 2715	Klippan Formation, Platberg Group, Ventersdorp Supergroup	pseudocolumnar	South Africa	de la Winter (1963), Grobler & Emslie (1976), Buck (1980)
ca 2715	Rietgat Formation, Platberg Group, Ventersdorp Supergroup	domical	South Africa	de la Winter (1963), Grobler & Emslie (1976), Buck (1980), Walter (1983)
ca 2710	Bothaville Formation, Platberg Group, Ventersdorp Supergroup	conical	South Africa	de la Winter (1963), Grobler & Emslie (1976), Buck (1980), Walter (1983)

(Continued.)

Table 1. (Continued.)

age (Myr)	geologic unit	principal stromatolite/ mat type	country	references
ca 2700	Dharwar Supergroup, Kalche area	diverse	India	Hofmann (2000)
ca 2700	Joldhal Formation, Chidradurga Group, Dharwar Supergroup	diverse	India	Hofmann (2000)
ca 2700	Deogiri Formation, Dharwar Supergroup, Sandur Belt	domical	India	Grobler & Emslie (1976)
ca 2700	Zwankendaba Group, Bulawayan Supergroup	domical	Zimbabwe	MacGregor (1941), Cloud & Semikhatov (1969), Schopf <i>et al.</i> (1971), Bond <i>et al.</i> (1973), Bickle <i>et al.</i> (1975), Martin <i>et al.</i> (1980), Walter (1983)
ca 2700	Manjeri Formation, Ngesi Group, Bulawayan Supergroup	pseudocolumnar	Zimbabwe	Bickle <i>et al.</i> (1975), Martin <i>et al.</i> (1980)
ca 2700	Ascot Vale, Mount Hampdon area, Bulawayan Supergroup	columnar	Zimbabwe	Bickle <i>et al.</i> (1975), Martin <i>et al.</i> (1980)
ca 2700	Kwekwe (Que Que) area, Bulawayan Supergroup	stratiform?	Zimbabwe	Bickle <i>et al.</i> (1975), Martin <i>et al.</i> (1980)
ca 2668	Black Flag Group, Kanowna area, Eastern Goldfields	conical	Australia	Grey (1981)
ca 2660	Jeerinah Formation, Fortescue Group, Mount Bruce Supergroup	columnar	Australia	K. Grey (2005, personal communication)
ca 2650	Back River Volcanic Complex, Yellowknife Supergroup	stratiform	Canada	Burbridge & Lambert (1990), Lambert <i>et al.</i> (1990)
ca 2650	Snofield Lake, Yellowknife Supergroup	diverse	Canada	Henderson (1975), Walter (1983), Lambert <i>et al.</i> (1990), Lambert (1996, 1998)
ca 2650	Cheshire Formation, Ngesi Group, Bulawayan Supergroup	diverse	Zimbabwe	Bickle <i>et al.</i> (1975), Martin <i>et al.</i> (1980)
ca 2642	Schmidtsdrif Subgroup, Transvaal Supergroup	columnar	South Africa	Bertrand-Sarfati & Eriksson (1977)
ca 2600	Chitradurga Schist Belt	domical	India	Srinivasan <i>et al.</i> (1989)
ca 2560	Malmari Dolomite, Chuniespoort Group, Transvaal Supergroup	diverse	South Africa	Young (1932), Truswell & Eriksson (1972, 1973, 1975), Lanier (1986), Sumner (1997)
ca 2560	Ghaap Plateau Dolomite, Ghaap Group, Transvaal Supergroup	diverse	South Africa	Young (1932), Truswell & Eriksson (1972, 1973, 1975), Lanier (1986), Sumner (1997)
ca 2548	Carawine Dolomite, Hamersley Group, Mount Bruce Supergroup	diverse	Australia	Walter (1983)

^a An occurrence that maps within the Mount Ada Basalt (Van Kranendonk *et al.* 2003), the exact stratigraphic position of the stromatolitic fossil-bearing cherts reported from this locality (Awramik *et al.* 1983) has not been confirmed by subsequent sampling (Schopf 1999, pp. 83–84). If not from the ca 3470 Myr old Mount Ada Basalt, these assuredly stromatolitic microfossiliferous cherts are from the overlying ca 2700 Myr old Fortescue Group.

^b The biogenicity of the putative stromatolites reported from the Strelley Pool Chert prior to 1994 has been questioned (Lowe 1994).

rocks, amphibolite facies (ca 450–700 °C, ca 3–10 kb; Klein & Hurlbut 1985, p. 505) metasediments of the Isua Supracrustal Group of southwestern Greenland, date from ca 3800 Ma (Nutman *et al.* 1984; Moorbath 2005). And only two relatively thick ancient sedimentary sequences, those of the Pilbara Craton of Western Australia and the Barberton Greenstone Belt of South Africa and Swaziland, have survived to the present—both spanning the period between ca 3500 and 3000 Ma and both regionally metamorphosed to lower greenschist facies (ca 250–300 °C, ca 2–5 kb; Klein & Hurlbut 1985, p. 505).

Given the markedly depleted Archaean rock record and the fossil-destroying effects of metamorphism typical of such ancient terrains, it is not surprising that ‘in comparison with the fossil record of the Proterozoic (less than 2500 Myr old) Precambrian, that of the Archaean is minuscule’ (Schopf *et al.* 2005). Nevertheless, it is notable that both of the two

relatively thick Archaean sedimentary sequences that have survived to the present contain what has been widely regarded as firm evidence of life, each containing layered megascopic structures interpreted to be microbially deposited stromatolites (table 1; figures 1 and 2), each containing microscopic objects regarded as prokaryotic microfossils (tables 2 and 3; figures 3–5).

3. ARCHAEOAN STROMATOLITES

As used here, the term ‘stromatolite’ refers to accretionary sedimentary structures, commonly thinly layered, megascopic and calcareous, interpreted to have been produced by the activities of mat-building communities of mucilage-secreting micro-organisms, mainly photoautotrophic prokaryotes. Other definitions have been proposed, some similarly emphasizing the inferred biogenic, organosedimentary nature of such

Table 2. Morphotypes of microscopic fossils described from Archaean geologic units.

<p>ca 3496 Myr, Dresser Formation, Warrawoona Group, Pilbara Supergroup (Pilbara Craton, Western Australia, Australia)</p> <p>(1) narrow unbranched prokaryotic filaments cf. bacteria (unnamed, ca 0.5–2 µm in diameter; Ueno <i>et al.</i> 2001a,b, 2004)</p> <p>(2) broad unbranched septate prokaryotic filaments cf. bacteria or oscillatoriacean cyanobacteria (<i>Archaeosclerotrioposis</i> sp., ca 4–16 µm in diameter; Ueno <i>et al.</i> 2001b)</p> <p>(3) broad unbranched tubular prokaryotic filaments cf. bacteria or oscillatoriacean cyanobacteria (<i>Siphonophycus antiquus</i>, ca 7–20 µm in diameter; Ueno <i>et al.</i> 2001b)</p> <p>ca 3470 Myr, Mount Ada Basalt^a, Warrawoona Group, Pilbara Supergroup (Pilbara Craton, Western Australia, Australia)</p> <p>(4) narrow unbranched prokaryotic filaments cf. bacteria (<i>Archaeotrichion contortum</i>, ca 0.5 µm in diameter; Awramik <i>et al.</i> 1983; Schopf & Walter 1983)</p> <p>(5) narrow unbranched septate(?) prokaryotic filaments cf. bacteria (<i>Eoleptonema australicum</i>, ca 1.0 µm in diameter; Awramik <i>et al.</i> 1983; Schopf & Walter 1983)</p> <p>(6) broad unbranched septate prokaryotic filaments cf. oscillatoriacean cyanobacteria (<i>Primaevifilum septatum</i>, ca 4–6 µm in diameter; Awramik <i>et al.</i> 1983; Schopf & Walter 1983)</p> <p>(7) broad unbranched tubular prokaryotic sheaths cf. oscillatoriacean cyanobacteria (<i>Siphonophycus antiquus</i>, ca 3–10 µm in diameter; Awramik <i>et al.</i> 1983; Schopf & Walter 1983)</p> <p>ca 3465 Myr, Apex chert^b, Apex Basalt, Warrawoona Group, Pilbara Supergroup (Pilbara Craton, Western Australia, Australia)</p> <p>(8) narrow unbranched septate prokaryotic filaments <i>Incertae Sedis</i> cf. bacteria? (<i>Archaeotrichion septatum</i>, ca 0.5 µm in diameter; Schopf 1992, 1993)</p> <p>(9) narrow unbranched septate prokaryotic filaments <i>Incertae Sedis</i> cf. bacteria? (<i>Eoleptonema apex</i>, ca 1 µm in diameter; Schopf 1992, 1993)</p> <p>(10) narrow unbranched septate prokaryotic filaments <i>Incertae Sedis</i> cf. bacteria? or cyanobacteria? (<i>Primaevifilum minutum</i>, ca 1–2 µm in diameter; Schopf 1993)</p> <p>(11) narrow unbranched septate prokaryotic filaments <i>Incertae Sedis</i> cf. bacteria? or cyanobacteria? (<i>Primaevifilum delicatulum</i>, ca 1–3 µm in diameter; Schopf & Packer 1987; Schopf 1992, 1993)</p> <p>(12) intermediate-diameter unbranched septate prokaryotic filaments <i>Incertae Sedis</i> cf. cyanobacteria? (<i>Primaevifilum amoenum</i>, ca 2–5 µm in diameter; Schopf & Packer 1987; Schopf 1992, 1993)</p> <p>(13) intermediate-diameter unbranched septate prokaryotic filaments having disc-shaped medial cells <i>Incertae Sedis</i> cf. cyanobacteria? (<i>Archaeosclerotrioposis disciformis</i>, ca 3–5 µm in diameter; Schopf 1993)</p> <p>(14) broad unbranched septate prokaryotic filaments having conical end cells <i>Incertae Sedis</i> cf. cyanobacteria? (<i>Primaevifilum conicoterminatum</i>, ca 4–6 µm in diameter; Schopf 1992, 1993)</p> <p>(15) broad unbranched septate prokaryotic filaments having equant medial cells <i>Incertae Sedis</i> cf. cyanobacteria? (<i>Primaevifilum laticellulosum</i>, ca 6–8.5 µm in diameter; Schopf 1992, 1993)</p> <p>(16) broad unbranched septate prokaryotic filaments <i>Incertae Sedis</i> cf. cyanobacteria? (<i>Archaeosclerotrioposis grandis</i>, ca 8–11.5 µm in diameter; Schopf 1993)</p> <p>(17) broad unbranched markedly tapering septate prokaryotic filaments <i>Incertae Sedis</i> cf. cyanobacteria? (<i>Primaevifilum attenuatum</i>, ca 4–12 µm in diameter; Schopf 1993)</p> <p>(18) broad unbranched septate prokaryotic filaments having hemispheroidal end cells <i>Incertae Sedis</i> cf. cyanobacteria? (<i>Archaeosclerotrioposis maxima</i>, ca 15–19.5 µm in diameter; Schopf 1993)</p> <p>ca 3460 Myr, Hooggenoeg Formation, Onverwacht Group, Swaziland Supergroup (Barberton Greenstone Belt, Transvaal Province, South Africa)</p> <p>(19) narrow unbranched prokaryotic filaments cf. bacteria or cyanobacteria (unnamed, ca 0.2–2.5 µm in diameter; Walsh & Lowe 1985; Walsh 1992)</p> <p>ca 3388 Myr, Strelley Pool Chert, Kelly Group, Pilbara Supergroup (Pilbara Craton, Western Australia, Australia)</p> <p>(20) colonial ensheathed prokaryotic coccids ellipsoids cf. chroococcacean cyanobacteria (unnamed, ca 5–10 µm in diameter; Schopf & Packer 1987; Schopf 1992)</p> <p>ca 3320 Myr, Kromberg Formation (and Buck Reef Chert Member), Onverwacht Group, Swaziland Supergroup (Barberton Greenstone Belt, Transvaal Province, South Africa)</p> <p>(21) solitary, paired and clustered prokaryotic coccoidal unicells cf. bacteria or cyanobacteria (unnamed, ca 2.0–5 µm in diameter; Muir & Grant 1976; Schopf & Walter 1983)</p> <p>(22) narrow unbranched prokaryotic filaments cf. bacteria (unnamed, ca 0.5 µm in diameter; Walsh & Lowe 1985)</p> <p>(23) narrow unbranched prokaryotic filaments cf. bacteria (unnamed, ca 1.0–1.5 µm in diameter; Tice & Lowe 2004)</p> <p>(24) broader unbranched prokaryotic filaments cf. bacteria or cyanobacteria (unnamed, ca 1.5–2.5 µm in diameter; Walsh & Lowe 1985; Walsh 1992; Schopf <i>et al.</i> 2002)</p> <p>(25) broad unbranched tubular prokaryotic sheath cf. oscillatoriacean cyanobacteria (unnamed, ca 5 µm in diameter; Walsh 1992; Schopf <i>et al.</i> 2002)</p> <p>ca 3260 Myr, Swartkoppie Formation, Onverwacht Group, Swaziland Supergroup (Barberton Greenstone Belt, Transvaal Province, South Africa)</p> <p>(26) solitary, paired and ‘dividing’ prokaryotic coccoidal unicells cf. bacteria or cyanobacteria (unnamed, ca 1–4 µm in diameter; Knoll & Barghoorn 1977)</p> <p>ca 3245 Myr, Sheba Formation, Fig Tree Group, Swaziland Supergroup (Barberton Greenstone Belt, Transvaal Province, South Africa)</p> <p>(27) solitary prokaryotic coccoids cf. chroococcacean cyanobacteria (<i>Archaeosphaeroides barbertonensis</i>, ca 16–23 µm in diameter; Schopf & Barghoorn 1967)</p> <p>ca 3240 Myr, Kangaroo Caves Formation (Marker chert), Sulphur Springs Group, Pilbara Supergroup (Pilbara Craton, Western Australia, Australia)</p>
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(Continued.)

Table 2. (Continued.)

- (28) narrow unbranched prokaryotic filaments cf. bacteria (unnamed, *ca* 0.5–2 µm in diameter; Rasmussen 2000)
ca 3200 Myr, Dixon Island Formation, Cleaverville Group, Pilbara Supergroup (Pilbara Craton, Western Australia, Australia)
- (29) narrow unbranched septate prokaryotic filaments cf. bacteria (unnamed, *ca* 0.5–2 µm in diameter; Kiyokawa *et al.* 2006)
ca 2723 Myr, Tumbiana Formation (Meentheena Carbonate Member), Fortescue Group, Mount Bruce Supergroup (Hamersley Basin, Western Australia, Australia)
- (30) narrow unbranched septate prokaryotic filament cf. bacteria or cyanobacteria (unnamed, *ca* 2 µm in diameter; Schopf & Walter 1983)
- (31) broad unbranched sheath-enclosed septate prokaryotic filament with hemispheroidal end cell cf. oscillatoriacean (*Lyngbya* sp.) cyanobacteria (unnamed, *ca* 7–12 µm in diameter; Schopf & Walter 1983)
ca 2600 Myr, Monte Cristo Formation, Chuniespoort Group, Transvaal Supergroup (Kaarvaal Craton, Transvaal Basin, Transvaal Province, South Africa)
- (32) solitary, paired and clustered prokaryotic rod-shaped (ellipsoidal) unicells cf. bacteria (unnamed, *ca* 0.75 broad, *ca* 1.5 µm long; Lanier 1986; Buick 2001)
- (33) solitary, paired and clustered prokaryotic coccoidal unicells cf. bacteria or cyanobacteria (unnamed, *ca* 1.5–5.0 µm in diameter; Lanier 1986; Buick 2001)
- (34) narrow unbranched septate prokaryotic filaments cf. bacteria (unnamed, *ca* 1–2 µm in diameter; Lanier 1986)
ca 2560 Myr, Ghaap Plateau Dolomite (Lime Acres Member), Campbell Group, Transvaal Supergroup (Kaarvaal Craton, Griqualand West Basin, Cape Province, South Africa)
- (35) colonial prokaryotic coccids and ellipsoids cf. entophysalidacean cyanobacteria (*Eoentophysalis* sp., *ca* 5–15 µm in diameter; Altermann & Schopf 1995)
- (36) colonial prokaryotic coccids cf. chroococcacean cyanobacteria (unnamed, *ca* 10–20 µm in diameter; Altermann & Schopf 1995)
- (37) narrow unbranched septate(?) prokaryotic filaments cf. bacteria (*Archaeotrichion* sp., up to 1 µm in diameter; Altermann & Schopf 1995)
- (38) narrow unbranched tubular prokaryotic sheaths cf. oscillatoriacean cyanobacteria (*Eomycetopsis* cf. *filiformis*, *ca* 1.5–3.0 µm in diameter; Altermann & Schopf 1995)
- (39) broad unbranched tubular prokaryotic sheaths cf. oscillatoriacean cyanobacteria (*Siphonophycus transvaalense*, *ca* 10–28 µm in diameter; Altermann & Schopf 1995)
- ca* 2516 Myr, Gamohaam Formation (Tsineng Member), Ghaap Group, Transvaal Supergroup (Kaarvaal Craton, Griqualand West Basin, Cape Province, South Africa)
- (40) broad unbranched tubular prokaryotic sheaths cf. oscillatoriacean cyanobacteria (*Siphonophycus transvaalense*, *ca* 15–27 µm in diameter; Klein *et al.* 1987; Buick 2001)

^a Although this occurrence maps within the Mount Ada Basalt (Van Kranendonk *et al.* 2003), the exact stratigraphic position of the fossil-bearing carbonaceous cherts reported from this locality (Awramik *et al.* 1983; Schopf & Walter 1983) has not been confirmed by subsequent sampling (Schopf 1999, pp. 83–84). If not from the *ca* 3470 Myr old Mount Ada Basalt, these assuredly stromatolitic microfossiliferous cherts are from the overlying *ca* 2700 Myr old Fortescue Group.

^b The biogenicity of these filamentous putative fossils has been questioned (Brasier *et al.* 2002, 2004).

structures (e.g. Walter 1976; Awramik, in Semikhatov *et al.* 1979; Buick *et al.* 1981), others focusing solely on the sedimentological morphology of such structures (e.g. Semikhatov *et al.* 1979, excluding Awramik; Grotzinger & Knoll 1999), and still others searching for a middle ground (Hofmann 1973, pp. 348–350; 2000). Such divergence reflects the difficulties inherent in consistently differentiating unambiguously between assuredly biogenic stromatolites and accretionary abiotic look-alikes (e.g. geysers, stalagmites and similar cave deposits, tectonically or otherwise deformed sediments, and duricrusts such as calcretes, silcretes and the like). Criteria for such differentiation have been enumerated by Buick *et al.* (1981, pp. 165–167) and Walter (1983, pp. 189–190), in which firm establishment of biogenicity revolves chiefly around detection within such structures of cellularly preserved microfossils or trace fossils ('palimpsest microstructures') of the microscopic organisms responsible for their formation. Unfortunately, even this criterion falls short, since the mere presence of fossilized micro-organisms within an ancient stromatolite-like structure cannot demonstrate that the structure accreted as a direct result of microbial mat-building activities. Moreover, because almost all known ancient stromatolites are or were

originally of calcareous composition, presumably composed initially of metastable aragonite or high-Mg calcite (Grotzinger & Knoll 1999), growth of carbonate grains (aggrading neomorphism) during early diagenesis as well as changes occurring during subsequent diagenetic alteration have in all but a relatively few instances served to obliterate morphologically identifiable evidence of the formative mat-building microbes. For this reason, cellularly preserved fossil microbes are known almost without exception only from those stromatolitic deposits in which the initial carbonate matrix was replaced by silica very early during diagenesis, prior to the onset of widespread cellular decay and microbial disintegration and before the development of carbonate neomorphic alteration. Thus, 'it is probably conservative to estimate that less than 1 percent of all stromatolites ever described have a fossilized microbiota associated with them' (Grotzinger & Knoll 1999, p. 316).

Given the general absence of microscopic fossils in stromatolitic structures, it clearly is difficult, and is perhaps impossible, to *prove beyond question* that the vast majority of reported stromatolites, even those of the Proterozoic Precambrian, are assuredly biogenic. Yet in the Proterozoic, stromatolites are so widespread

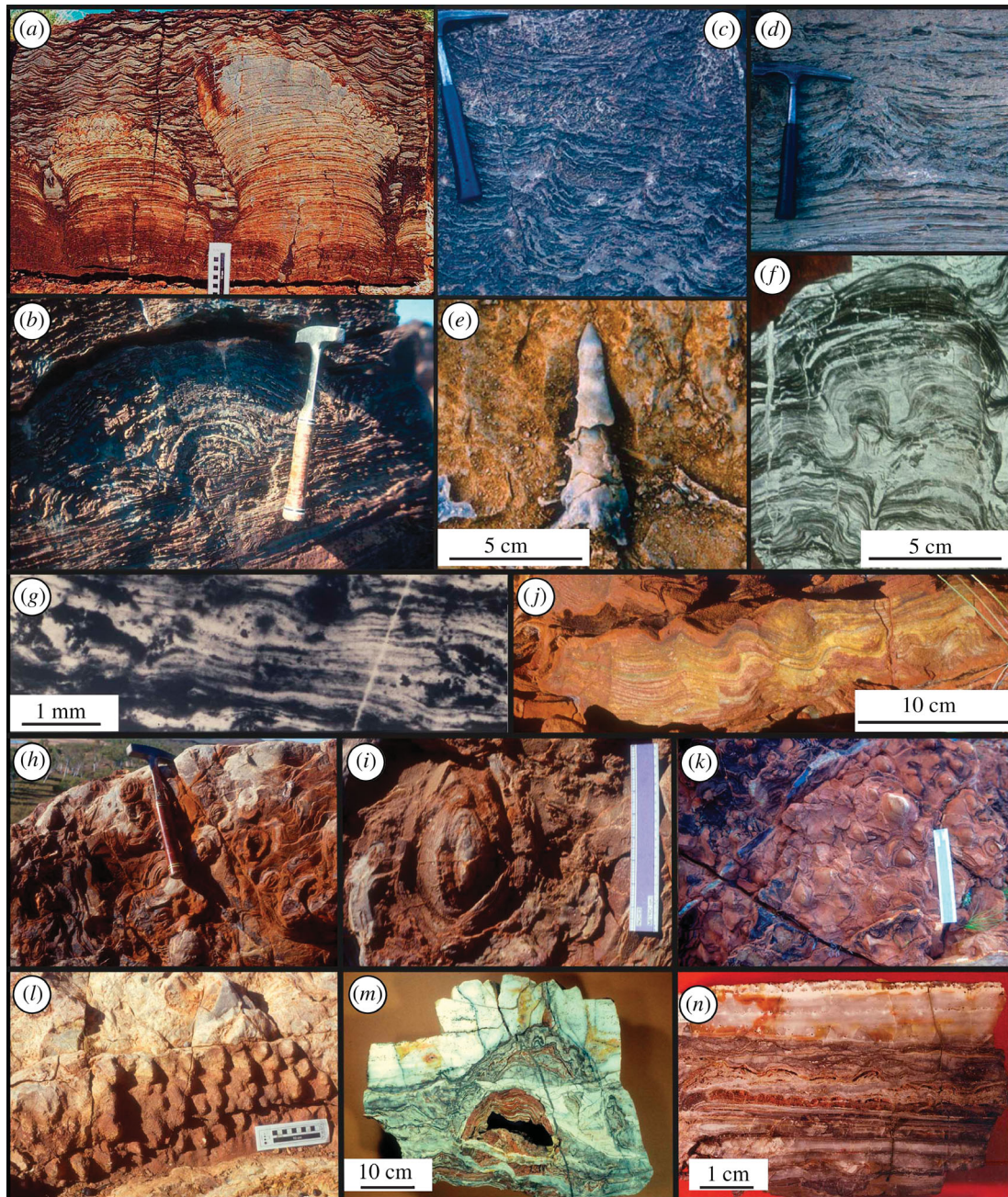


Figure 1. Archaean stromatolites/microbial mats. (a) Domical, pseudocolumnar and branching columnar stromatolites, overlain by rippled sediments and (b) domical stromatolite, from the *ca* 2723 Myr old Tumbiana Formation, Western Australia (Walter 1972, 1983; Grey 1979); photo in (a) courtesy of I. R. Williams; scale, 10 cm. (c–e) Stratiform and conical stromatolites from the *ca* 2985 Myr old Insuzi Group, South Africa (Mason & von Brunn 1977; von Brunn & Mason 1977; Walter 1983; Beukes & Lowe 1989); photo in (e) courtesy of N. J. Beukes. (f) Laterally linked, low relief stratiform to domical stromatolitic mats from the *ca* 3245 Myr old Fig Tree Group of South Africa (Byerly *et al.* 1986; Byerly & Palmer 1991); photo courtesy of D. R. Lowe. (g) Stratiform microbial mats from the *ca* 3320 Myr old Kromberg Formation of South Africa (Walsh & Lowe 1985; Walsh 1992). (h–l) Laterally linked (j) conical stromatolites from the *ca* 3388 Myr old Strelley Pool Chert of Western Australia (Hofmann *et al.* 1999; Hofmann 2000; Van Kranendonk *et al.* 2003; Allwood *et al.* 2004); (i) and (k) scale, 20 cm; (l) scale, 10 cm. (m) Domical and (n) stratiform stromatolites from the 3496 Myr old Dresser Formation, Western Australia (Walter *et al.* 1980; Buick *et al.* 1981; Groves *et al.* 1981; Walter 1983; Schopf & Walter 1983; Buick *et al.* 1995; Buick 2001).

and abundant, and their biological interpretation is so firmly backed by studies of microbial communities cellularly preserved in Proterozoic cherty stromatolites (e.g. Mendelson & Schopf 1992; Schopf 1999; Knoll 2003a; Schopf *et al.* 2005), that there can be no doubt that nearly all are products of biological activity.

In the Archaean, the problem of proving the biogenicity of such structures presents a greater problem, due chiefly to the paucity of Archaean sediments (for reasons such as those discussed above)

and the correspondingly small number of known occurrences of stromatolites and preserved microbial assemblages. Still, it is important to recognize that reports of Archaean stromatolites have increased markedly over the past decade, with such structures now known to be decidedly more abundant and more diverse than was previously appreciated (table 1). Virtually all of the workers who have recorded Archaean stromatolites have also studied in detail stromatolites of the Proterozoic; interpretation of the

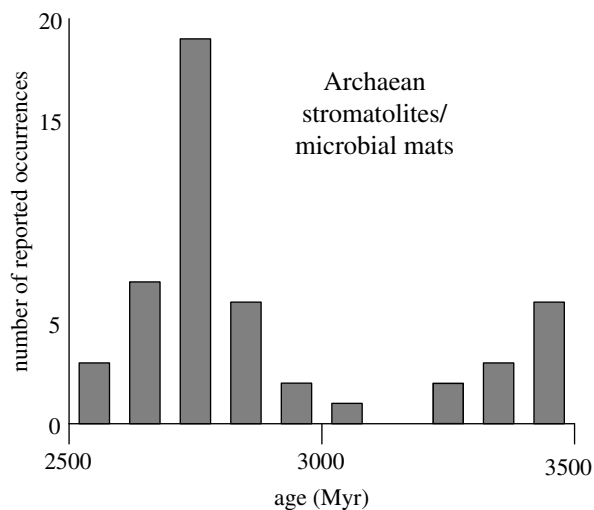


Figure 2. Temporal distribution of the reported occurrences of stromatolites/microbial mats listed in table 1.

biogenicity of the Archaean forms and the differentiation of such structures from abiotic accretionary look-alikes are based on the same criteria as those applied to stromatolites of unquestioned biogenicity in the younger Precambrian (including analyses of their laminar microstructure, morphogenesis, mineralogy, diagenetic alteration and so forth; e.g. Buick *et al.* 1981; Walter 1983). All of the Archaean stromatolites listed in table 1, and the representative examples shown in figure 1, are regarded by those who have reported them as meeting the definition of stromatolite used here, ‘accretionary sedimentary structures, commonly thinly layered, megascopic and calcareous, interpreted to have been produced by the activities of mat-building communities of mucilage-secreting micro-organisms, mainly photoautotrophic prokaryotes’.

Table 1 lists 48 occurrences of Archaean stromatolites reported to date. Occurrences regarded as being of questionable biogenicity and/or Archaean age are not included. Three principal observations are suggested by this compilation.

- (i) Despite the scarcity of Archaean geologic units relative to those of the younger Proterozoic, the temporal distribution of such reported occurrences is more or less continuous throughout much of the Archaean, ranging from *ca* 2500 to 3500 Ma (table 1; figure 2).
- (ii) An impressive array of morphological diversity has been recorded in numerous Archaean units: sediments of the Transvaal Supergroup (*ca* 2560 Myr old) and of the Insuzi (*ca* 2985 Myr old), Steeprock (*ca* 2800 Myr old) and Fortescue (*ca* 2723 Myr old) Groups are all reported to contain stratiform (e.g. figure 1*c,d,f,g,n*), pseudocolumnar (e.g. figure 1*a,f*), domical (figure 1*a,b,m*), conical (figure 1*e,j-l*), columnar (figure 1*a*) and branching stromatolites (figure 1*a,f*), whereas those of the Yellowknife Supergroup (*ca* 2650 Myr old) are reported to contain all of these stromatolite/microbial mat types with the exception of conical forms (Hofmann 2000). Such diversity in stromatolite morphology in a

given geologic unit, not uncommonly in the same sedimentary facies, suggests that such forms are not a product of a single set of non-biogenic accretionary processes.

- (iii) Conical stromatolites have been recorded in 17 of the 48 units listed in table 1 (Hofmann 2000). Present in fully one-third of these deposits—notably including the more than 3300 Myr old Strelley Pool Chert (Hofmann *et al.* 1999; Allwood *et al.* 2004) and Kromberg and Panorama Formations (Hofmann 2000)—such ‘conoform stromatolites appear to constitute a special case’, distinctive structures evidently requiring for their formation ‘both highly motile [microbial] mat builders and penecontemporaneous mineral precipitation’ (Grotzinger & Knoll 1999, pp. 342–343). Thus, Archaean conoform stromatolites, ‘especially the conical structures found in 3.45 Gyr rocks of the Warrawoona Group [*viz.*, the Strelley Pool Chert]’, have been regarded as having their accretion most probably ‘facilitated by micro-organisms’ (Knoll 2003*b*, p. 6).

4. ARCHAEOAN MICROFOSSILS

Over the past decades, the rules for accepting Precambrian microfossil-like objects as *bona fide* have come to be well established; namely, that such objects be demonstrably biogenic, and indigenous to and syngenetic with the formation of rocks of known provenance and well-defined Precambrian age (Schopf & Walter 1983; Schopf 2004). Of these criteria, the most difficult to satisfy has been that of biogenicity (Hofmann & Schopf 1983; Schopf & Walter 1983; Mendelson & Schopf 1992). A nested suite of seven traits for establishment of such biogenicity has been proposed (Buick 1990, pp. 443–446); sets of traits, six for spheroidal microfossils and nine for filamentous forms, that can be used to demonstrate a biological origin of these two particularly common Precambrian morphotypes, have been enumerated (Schopf 2004, pp. 521–523); and the use of this multi-trait strategy to establish the biogenicity of members of Proterozoic microbial communities has been documented (Schopf *et al.* 2005, pp. 362–365).

Such analyses have shown that a prime indicator of the biological origin of such objects is the micron-scale co-occurrence of identifiable biological morphology and geochemically altered remnants of biological chemistry. Thus, evidence consistent with a biogenic interpretation would be provided were chemical data to show that populations of objects well characterized morphologically as ‘cellular microfossils’ were composed of carbonaceous matter, as would be expected of organically preserved micro-organisms, and would seem especially strong were the data to demonstrate that such carbonaceous matter was unquestionably of biological origin (Schopf *et al.* 2005). Analytical techniques now available permit a one-to-one correlation, at micron-scale spatial resolution, of cellular morphology and carbonaceous chemistry in objects claimed to be microscopic fossils—for specimens

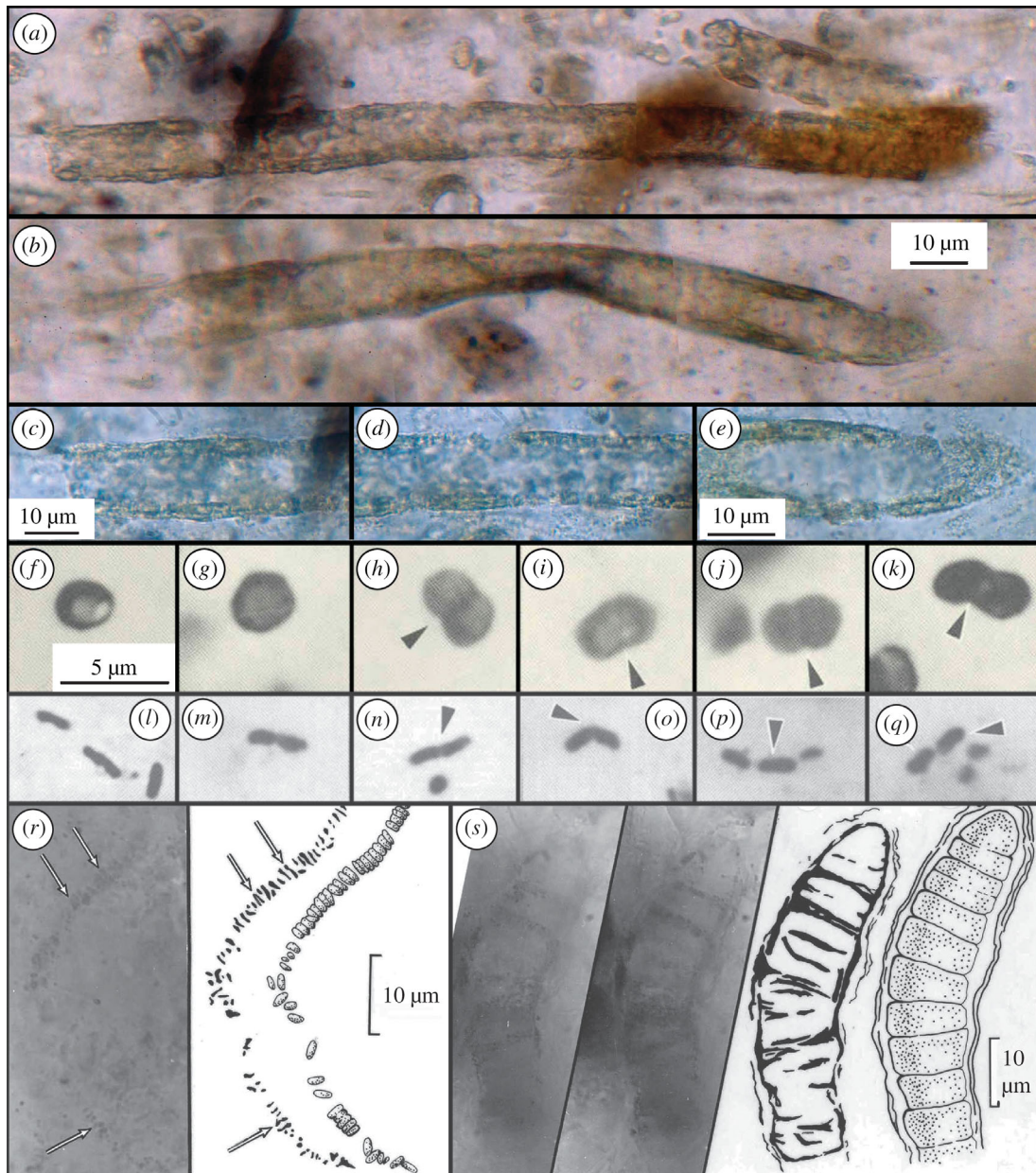


Figure 3. *ca* 2500–2700 Myr old Archaean microfossils photographed in petrographic thin sections. (a–e) Broad prokaryotic (oscillatoriacean cyanobacterium-like) tubular sheaths (*Siphonophycus transvaalense*) from the *ca* 2516 Myr old Gamohaam Formation of South Africa (Klein *et al.* 1987; Buick 2001); scale for parts (a) and (b) shown in (b); scale for parts (c) and (d) shown in (c). (f–k) Solitary and paired (denoted by arrows) prokaryotic (bacterial or cyanobacterial) coccoidal unicells and (l–q) solitary and paired (denoted by arrows) bacterium-like rod-shaped unicells from the *ca* 2600 Myr old Monte Cristo Formation of South Africa (Lanier 1986; Buick 2001); scale for parts (f–q) shown in (f) (modified after Lanier 1986). (r) Narrow prokaryotic (bacterial or cyanobacterial) septate filament and (s) broad sheath-enclosed prokaryotic (oscillatoriacean cyanobacterium-like) septate filament from the *ca* 2723 Myr old Tumbiana Formation of Western Australia (Schopf & Walter 1983).

exposed at the surface of samples studied, by use of ion microprobe (House *et al.* 2000; Ueno *et al.* 2001a), electron microprobe (Boyce *et al.* 2001) and Raman spectroscopy (Arouri *et al.* 2000); and for rock-embedded specimens, by Raman point spectra and by both two-dimensional and three-dimensional Raman imaging (Kudryavtsev *et al.* 2001; Schopf *et al.* 2002, 2005; Schopf & Kudryavtsev 2005).

Given that the co-occurrence of biological morphology and carbonaceous chemistry in ancient microfossil-like objects is a presumptive indicator of biogenicity, recent reports of sinuous microscopic tubular structures reported from Archaean pillow lavas (Furnes *et al.* 2004) are not regarded here as

bona fide evidence of ancient life: such tubes exhibit neither distinctively biological morphology nor are they of demonstrable carbonaceous composition. In contrast, each of the many morphotypes of Archaean microfossil-like objects listed in table 2 meets both of these traits, and all of the spheroidal and filamentous morphotypes satisfy the enumerated sets of criteria required for establishment of biogenicity of forms of such morphology (Schopf 2004). Many of the rod-shaped to spheroidal morphotypes are juxtaposed in addressed pairs (figures 3h–k, n–q and 4c–f, h–j), presumptive evidence of biologic cell division. Similarly, numerous filamentous specimens exhibit uniseriate sequences of discoidal to boxlike chert-filled

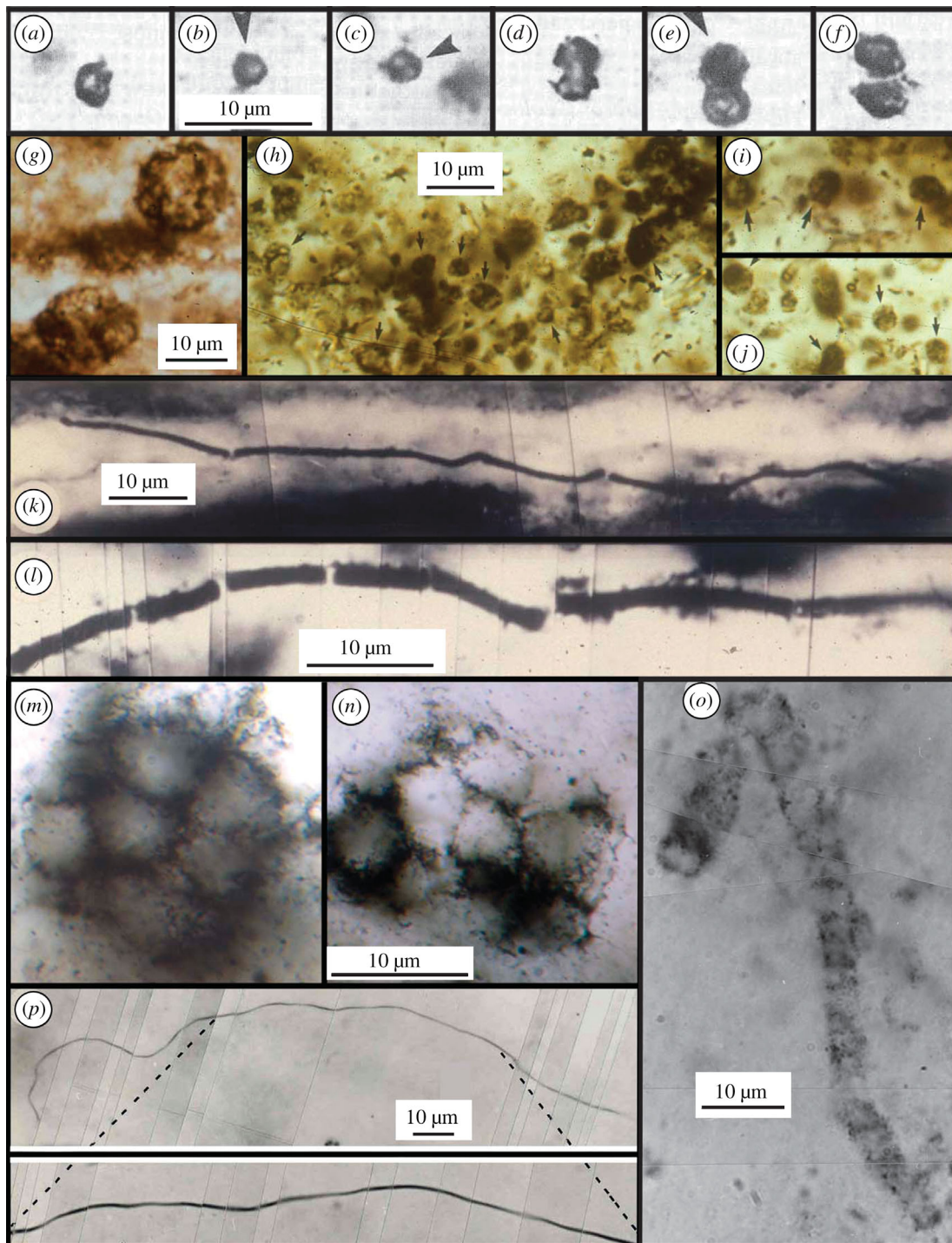


Figure 4. More than 3200 Myr old Archaean microfossils photographed in petrographic thin sections. (a–f) Solitary and paired prokaryotic (bacterial or cyanobacterial) coccoidal unicells from the *ca* 3260 Myr old Swartkoppie Formation of South Africa, in (b–f) ordered in a sequence inferred to represent stages of cell division (Knoll & Barghoorn 1977); arrows point to dark organic contents within cells; scale for parts (a–f) shown in (b) (modified after Knoll & Barghoorn 1977). (g) Solitary prokaryotic (chroococcacean cyanobacterium-like) coccoidal unicells (*Archaeosphaeroides barbertonensis*) from the *ca* 3245 Myr old Sheba Formation of South Africa (Schopf & Barghoorn 1967); photo courtesy of A. H. Knoll. (h–j) Solitary, paired (denoted by arrows) and clustered prokaryotic (bacterial or cyanobacterial) coccoidal unicells from the *ca* 3320 Kromberg Formation of South Africa (Muir & Grant 1976; Schopf & Walter 1983); scale for parts (h–j) shown in (h). (k) Narrow prokaryotic (bacterium-like) filament and (l) broader prokaryotic (bacterial or cyanobacterial) filament from the *ca* 3320 Kromberg Formation of South Africa (Walsh & Lowe 1985; Walsh 1992; Schopf *et al.* 2002). (m, n) Colonial ensheathed prokaryotic (chroococcacean cyanobacterium-like) coccoidal unicells from the *ca* 3388 Myr old Strelley Pool Chert of Western Australia (Schopf & Packer 1987; Schopf 1992); scale for parts (m) and (n) shown in (n). (o) Broad septate prokaryotic (oscillatoriacean cyanobacterium-like) filament (*Primaevifilum septatum*) and (p) narrow prokaryotic (bacterium-like) filament (*Archaeotrichion contortum*), reported by Awramik *et al.* (1983) from stromatolitic cherts collected at a locality that maps within the *ca* 3470 Myr old Mount Ada Basalt (Van Kranendonk *et al.* 2003). Of unconfirmed stratigraphic provenance (Schopf 1999, pp. 83–84), these fossiliferous samples may be from a chert unit of the overlying *ca* 2700 Myr old Fortescue Group.

Table 3. Palaeoarchean (range 3200–3600 Myr old) evidence of life.

geology		palaeontology		stromatolites/microbial mats		microfossils		organic geochemistry		
age (Myr)	unit	locality	shape	environment	morphology	environment	bulk	fossils	laser-Raman	images
ca 3496	Dresser Formation (Warrawoona Group, Pilbara Supergroup)	Western Australia	domical (Walter <i>et al.</i> 1980; Buick <i>et al.</i> 1981, 1995; Groves <i>et al.</i> 1981; Walter 1983; Schopf & Walter 1983; Buick 2001; Van Kranendonk <i>et al.</i> 2003)	hydrothermal (Van Kranendonk <i>et al.</i> 2003)	diverse filaments (Ueno <i>et al.</i> 2001a,b, 2004)	hydrothermal (Ueno <i>et al.</i> 2001a,b, 2004; Van Kranendonk <i>et al.</i> 2003)	√(Ueno <i>et al.</i> 2001a,b, 2004; Strauss & Moore 1992)	√(Ueno <i>et al.</i> 2001a,b, 2004)	√(Ueno <i>et al.</i> 2001a)	—
ca 3470	Mount Ada Basalt ^a (Warrawoona Group, Pilbara Supergroup)	Western Australia	stratiform (Schopf & Walter 1983; Awramik <i>et al.</i> 1983)	shallow marine (Schopf & Walter 1983; Awramik <i>et al.</i> 1983; Van Kranendonk <i>et al.</i> 2003)	diverse filaments (Schopf & Walter 1983; Awramik <i>et al.</i> 1983)	shallow marine (Schopf & Walter 1983; Awramik <i>et al.</i> 1983; Van Kranendonk <i>et al.</i> 2003)	√(Strauss & Moore 1992)	—	—	—
ca 3465	Apex chert ^b (Warrawoona Group, Pilbara Supergroup)	Western Australia	—	—	diverse filaments (Schopf & Packer 1987; Schopf 1992, 1993, 1999; Schopf <i>et al.</i> 2002; Altermann 2005)	hydrothermal (Brasier <i>et al.</i> 2002; Van Kranendonk <i>et al.</i> 2003)	√(Strauss & Moore 1992; Brasier <i>et al.</i> 2002)	—	√(Schopf <i>et al.</i> 2002)	√(Schopf <i>et al.</i> 2002)
ca 3460	Hoogenoeg Formation (Onverwacht Group, Swaziland Supergroup)	South Africa	stratiform? (Hofmann 2000)	shallow marine (Walsh & Lowe 1985; Hofmann 2000)	narrow filaments (Walsh & Lowe 1985; Walsh 1992)	shallow marine (Walsh & Lowe 1985; Walsh 1992; Hofmann 2000)	√(Strauss & Moore 1992)	—	—	—
ca 3440	Panorama Formation (Warrawoona Group, Pilbara Supergroup)	Western Australia	conical (Hofmann 2000)	shallow marine (Hofmann 2000; Van Kranendonk <i>et al.</i> 2003)	—	—	—	—	—	—
ca 3400	Witkop Formation (Nondweni Group)	South Africa	domical (Hofmann 2000)	shallow marine (Hofmann 2000)	—	—	—	—	—	—
ca 3388	Strelley Pool Chert ^c (Kelly Group, Pilbara Supergroup)	Western Australia	conical (Lowe 1980, 1983; Hofmann <i>et al.</i> 1999; Hofmann 2000; Van Kranendonk <i>et al.</i> 2003; Allwood <i>et al.</i> 2004)	shallow marine (Lowe 1980, 1983; Hofmann <i>et al.</i> 1999; Hofmann 2000; Van Kranendonk <i>et al.</i> 2003; Allwood <i>et al.</i> 2004)	colonial coccoids (Schopf & Walter 1983; Schopf & Packer 1987; Schopf 1992)	shallow marine (Schopf 1992, 1993; Van Kranendonk <i>et al.</i> 2003)	√(Strauss & Moore 1992)	—	√(Schopf <i>et al.</i> 2002)	√(Schopf <i>et al.</i> 2002)

(Continued.)

Table 3. (Continued.)

geology		palaeontology			microfossils			organic geochemistry										
age (Myr)	unit	locality	stromatolites/microbial mats		environment		morphology		environment		avg. $\delta^{13}\text{C}_{\text{PDB}}$ (‰)		fossils		laser-Raman		images	
			shape	environment	microfossils	environment	microfossils	environment	bulk	fossils	laser-Raman	images						
ca 3320	Kromberg Formation (Onverwacht Group, Swaziland Supergroup)	South Africa	stratiform (Walsh & Lowe 1985; Walsh 1992)	shallow marine (Walsh & Lowe 1985; Walsh 1992)	diverse filaments (Walsh & Lowe 1985; Walsh 1992)	shallow marine (Walsh & Lowe 1985; Walsh 1992)	colonial coccoids (Muir & Grant 1976; Schopf & Walter 1983)	shallow marine (Muir & Grant 1976; Westall <i>et al.</i> 2001)	shallow marine (Walsh & Lowe 1985; Walsh 1992)	shallow marine (Walsh & Lowe 1985; Walsh 1992)	√(Strauss & Moore 1992)	√(Schopf <i>et al.</i> 2002)	√(Schopf <i>et al.</i> 2002)	√(Schopf <i>et al.</i> 2002)	√(Schopf <i>et al.</i> 2002)	√(Schopf <i>et al.</i> 2002)	√(Schopf <i>et al.</i> 2002)	√(Schopf <i>et al.</i> 2002)
ca 3316	Buck Reef Chert (Onverwacht Group, Swaziland Supergroup)	South Africa	stratiform (Tice & Lowe 2004)	shallow marine (Tice & Lowe 2004)	narrow filaments (Tice & Lowe 2004)	shallow marine (Tice & Lowe 2004)		shallow marine (Tice & Lowe 2004)	shallow marine (Tice & Lowe 2004)	shallow marine (Tice & Lowe 2004)	—	—	—	—	—	—	—	—
ca 3260	Swartkoppie Formation (Onverwacht Group, Swaziland Supergroup)	South Africa	—	—	paired coccoids (Knoll & Barghoorn 1977)	shallow marine (Knoll & Barghoorn 1977)		shallow marine (Knoll & Barghoorn 1977)	shallow marine (Knoll & Barghoorn 1977)	shallow marine (Knoll & Barghoorn 1977)	√(Strauss & Moore 1992)	—	—	—	—	—	—	—
ca 3245	Sheba Formation (Fig Tree Group, Swaziland Supergroup)	South Africa	columnar (Byerly <i>et al.</i> 1986)	shallow marine (Byerly <i>et al.</i> 1986)	solitary coccoids (Schopf & Barghoorn 1967)	shallow marine (Byerly <i>et al.</i> 1986)		shallow marine (Byerly <i>et al.</i> 1986)	shallow marine (Schopf & Barghoorn 1967; Byerly <i>et al.</i> 1986)	shallow marine (Schopf & Barghoorn 1967; Byerly <i>et al.</i> 1986)	√(Strauss & Moore 1992)	—	—	—	—	—	—	—
ca 3240	Sulphur Springs Group	Western Australia	—	—	narrow filaments (Rasmussen 2000)	hydrothermal (Rasmussen 2000)		hydrothermal (Rasmussen 2000)	hydrothermal (Rasmussen 2000)	hydrothermal (Rasmussen 2000)	—	—	—	—	—	—	—	—
ca 3200	Dixon Island Formation	Western Australia	stratiform (Kiyokawa <i>et al.</i> 2006)	hydrothermal (Kiyokawa <i>et al.</i> 2006)	diverse filaments (Kiyokawa <i>et al.</i> 2006)	hydrothermal (Kiyokawa <i>et al.</i> 2006)		hydrothermal (Kiyokawa <i>et al.</i> 2006)	hydrothermal (Kiyokawa <i>et al.</i> 2006)	hydrothermal (Kiyokawa <i>et al.</i> 2006)	√(Kiyokawa <i>et al.</i> 2006)	—	—	—	—	—	—	—

^a An occurrence that maps within the Mount Ada Basalt (Van Kranendonk *et al.* 2003); the exact stratigraphic position of the fossil-bearing carbonaceous cherts reported from this locality (Schopf & Walter 1983; Awramik *et al.* 1983) has not been confirmed by subsequent sampling (Schopf 1999, pp. 83–84). If not from the ca 3470 Myr old Mount Ada Basalt, these assuredly stromatolitic microfossiliferous cherts are from the overlying ca 2700 Myr old Fortescue Group (and, thus, of Neoproterozoic age).

^b The biogenicity of the filamentous putative fossils reported from the Apex chert has been questioned (Brasier *et al.* 2002, 2004).

^c The biogenicity of the putative stromatolites reported from the Strelley Pool Chert prior to 1994 has been questioned (Lowe 1994).

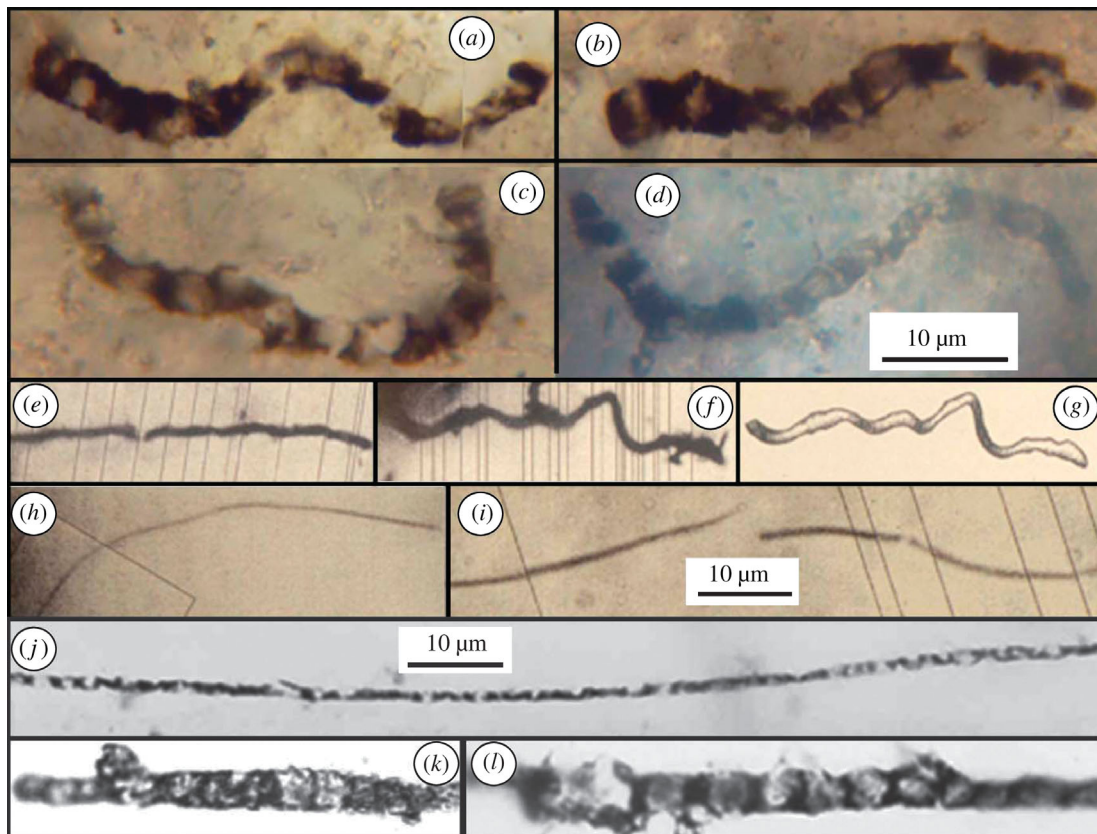


Figure 5. More than 3450 Myr old Archaean putative microfossils and *ca* 2000 Myr old Proterozoic unquestioned microfossils photographed in petrographic thin sections. (a–d) Unbranched carbonaceous filaments (*Primaevifilum amoenum*) described as degraded cellular fossil prokaryotes *Incertae Sedis* and interpreted as exhibiting oscillatoriacean cyanobacterium-like morphology (Schopf 1992, 1993), but regarded by Brasier *et al.* (2002, 2004) as being of questionable biogenicity, from the *ca* 3465 Myr old Apex chert of Western Australia; the faintness of the image of the filament illustrated in part (d) is due to its depth (range *ca* 65–90 µm) within the thin section studied; scale for parts (a–d) shown in (d). (e–i) Narrow carbonaceous filamentous bacterium-like putative fossils from the *ca* 3496 Myr old Dresser Formation of Western Australia (Ueno *et al.* 2001a); parts (e), (f), (h) and (i) show photomontages necessitated by the three-dimensional preservation of the sinuous filaments; part (g) shows an interpretive drawing of the specimen illustrated in (f); scale for parts (e–i) shown in (i) (modified after Ueno *et al.* 2001a). (j) Narrow prokaryotic (bacterium-like) carbonaceous filament (*Gunflintia minuta*) and (k, l) broader degraded septate prokaryotic (oscillatoriacean cyanobacterium-like) filaments (*Gunflintia grandis*) from the *ca* 1900 Myr old Gunflint Formation of southern Ontario, Canada (Hofmann 1971; Hofmann & Schopf 1983); scale for parts (j–l) shown in (j).

cavities defined in three dimensions by transverse and lateral carbonaceous walls (figures 3*r,s*, 4*o* and 5*a–d*), presumptive cell lumina and a definitive feature of *bona fide* cellular filamentous microbes, both modern and Proterozoic (e.g. figure 4*k,l*, unquestioned microbial filaments from the *ca* 2000 Myr old Gunflint Formation of Canada; Hofmann 1971). The combined use of Raman imagery (Schopf & Kudryavtsev 2005) and confocal laser scanning microscopy (Schopf *et al.* 2006) can be expected to more fully demonstrate the three-dimensional cellularity of reported Archaean microbe-like filaments.

Table 2 summarizes salient characteristics of 40 morphotypes of microfossil-like objects reported from 14 Archaean geologic units. Although the biogenicity of such objects in only one of these 14 units has been questioned (those of the Apex chert; Brasier *et al.* 2002, 2004), in deference to Moorbath (2005) such microfossil-like objects are here referred to as ‘putative microfossils.’ Two principal observations are suggested by the compilation presented in table 2. First, all of the 40 morphotypes are morphologically simple—small rod-shaped bodies, unornamented coccoids, or sinuous tubular or uniseriate filaments—microbe-like

morphologies typical of Proterozoic microscopic fossils (e.g. Hofmann & Schopf 1983; Mendelson & Schopf 1992; Schopf 1999; Knoll 2003*a*) and a simplicity of form, thus, consistent with their interpretation as early-evolved Archaean members of the microbial evolutionary continuum well established in the younger Precambrian. Second, of the six distinctive classes of microbe-like morphotypes reported from these Archaean deposits summarized below, all but one are known from several or many geologic units of markedly differing geologic age, a redundancy of occurrence that is similarly consistent with the interpretation of such putative microfossils as members of the Precambrian microbial evolutionary continuum. The six classes of morphotypes now known are as follows.

- (i) Very small solitary, paired or clustered rods (*ca* 0.75 µm broad, *ca* 1.5 µm long), inferred to be prokaryotic (bacterial) unicells: one unit (*ca* 2600 Myr old), one morphotype (figure 3*l–q*).
- (ii) Small, solitary, paired or clustered coccoids (average diameter *ca* 3 µm, range *ca* 2–5 µm), inferred to be prokaryotic (bacterial, perhaps

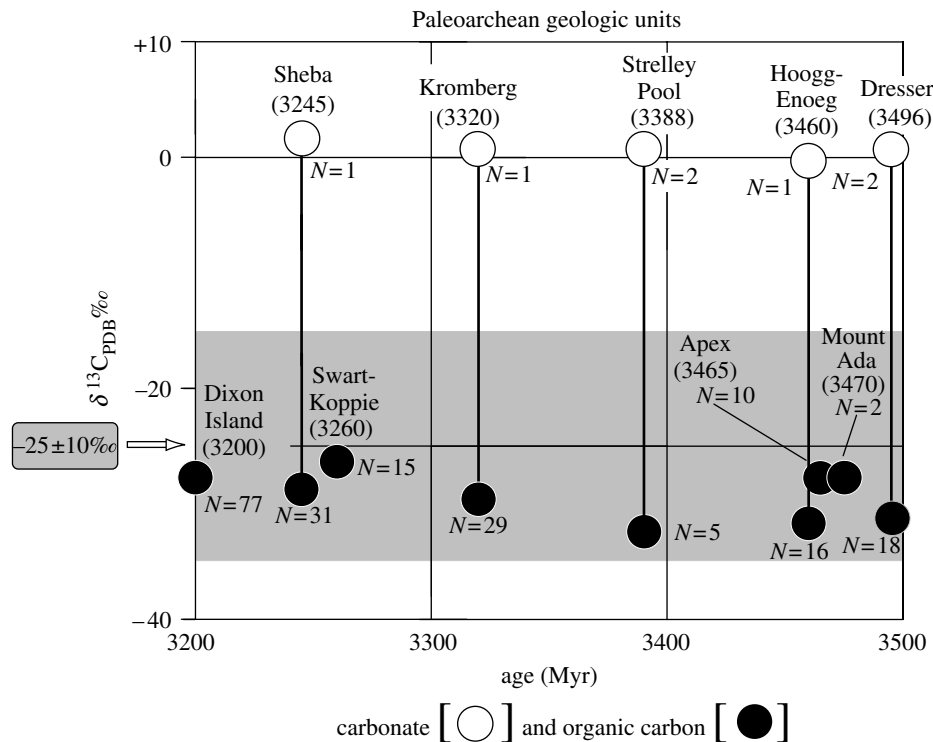


Figure 6. Carbon isotopic values of carbonate and organic carbon measured in bulk samples of the nine Palaeoarchean units reported to contain putative microfossils (Strauss & Moore 1992; Ueno *et al.* 2001a,b; Brasier *et al.* 2002).

- cyanobacterial) unicells: three units (range 3320–2600 Myr old), three morphotypes (e.g. figures 3f–k and 4a–f).
- (iii) Large solitary or colonial coccoids (average diameter *ca* 13 μm , range *ca* 5–23 μm), inferred to be prokaryotic (bacterial, perhaps cyanobacterial) unicells: three units (range 3388–2560 Myr old), four morphotypes (e.g. figure 4g,m,n).
- (iv) Narrow unbranched sinuous filaments (average diameter *ca* 1.25 μm , range *ca* 0.2–3 μm), with or without discernable septations, inferred to be prokaryotic (bacterial, perhaps cyanobacterial) cellular trichomes and/or trichome-encompassing sheaths: 10 units (range 3496–2560 Myr old), 17 morphotypes (e.g. figures 4k,p and 5e–i).
- (v) Broad unbranched septate filaments (average diameter *ca* 8 μm , range *ca* 2–19.5 μm), inferred to be prokaryotic (perhaps cyanobacterial) cellular trichomes: four units (range 3496–2723 Myr old), 10 morphotypes (figures 3s, 4o and 5a–d).
- (vi) Broad unbranched tubular or partially flattened cylinders (average diameter *ca* 13 μm , range *ca* 3–28 μm), inferred to be prokaryotic (perhaps cyanobacterial) trichome-encompassing sheaths: five units (range 3496–2516 Myr old), five morphotypes (e.g. figures 3a–e and 4l).

5. EVIDENCE OF PALAEOARCHEAN LIFE

Table 3 summarizes palaeontologic and organic geochemical data currently available from 13 Palaeoarchean (range 3200–3600 Myr old) geologic units of the two relatively thick ancient sedimentary sequences that have survived to the present, those of

the Pilbara Craton of Western Australia and the Barberton Greenstone Belt of South Africa and Swaziland. As is there tabulated, 10 of these particularly ancient units are reported to contain stromatolites/microbial mats; 11 contain putative microfossils; and carbon isotopic data are available from nine of the units, including data from analyses of individual microfossil-like objects in the oldest such unit, the Dresser Formation, as well as Raman spectra and/or two-dimensional Raman images of the carbonaceous components of putative microfossils from five of the units. As shown in figure 6, bulk analyses of the particulate carbonaceous kerogen in these deposits yield average $\delta^{13}\text{C}_{\text{PDB}}$ values that range from -27 to -32‰ , whereas such values for carbonate carbon measured in five of the units centre at *ca* 0‰, values consistent with carbon isotopic fractionation by autotrophic micro-organisms ($-25 \pm 10\text{‰}$) and, thus, with a biologic origin of the reduced carbon (e.g. Hayes *et al.* 2002).

Although most of the 13 units listed in table 3 are interpreted to have been deposited under shallow marine conditions, four units—the Apex chert, Dresser and Dixon Island Formations, and the Sulphur Springs Group—are regarded as representing hydrothermal settings. Chert units of each of these four deposits contain carbonaceous microfossil-like filaments, those from the two oldest deposits (the *ca* 3496 Myr old Dresser Formation and the *ca* 3465 Myr old Apex chert), including specimens composed of cell-like segments as broad as *ca* 20 μm in diameter. Owing to their preservation in ancient hydrothermal springs, some such putative fossils have been suggested to be chemotrophs (e.g. Rasmussen 2000). Based on morphology, the broad filaments of the Dresser Formation cherts have been compared both with chemotrophic

beggiatocean gliding bacteria and with photoautotrophic oscillatoriacean cyanobacteria (Ueno *et al.* 2001b). In contrast, the Apex filaments were formally described as 'prokaryotes *Incertae Sedis*' (Schopf 1993, p. 643), microbes of uncertain systematic position that because of their 'undetermined phylogenetic relations' were specifically 'not referred to previously described' fossil microbial taxa.

Nevertheless, the fact that about two-thirds of the named Apex taxa exhibit 'cyanobacterium-like' morphology (Schopf 1993, 1999) has presented a puzzle. Cyanobacteria comprise the evolutionarily most advanced lineage of the Bacterial Domain (e.g. Blankenship 1992), all members of the group being capable both of photosynthetic oxygen production and respiratory oxygen consumption. Thus, the presence early in Earth history of these morphologically cyanobacterium-like putative fossils has been widely assumed to suggest that oxygenic photosynthesis and aerobic respiration, both highly derived processes of microbial biochemistry, had already evolved by *ca* 3500 Myr ago.

Such, however, may not have been the case. In particular, as was specifically noted in the paper in which the Apex fossils were formally described and named (Schopf 1993, p. 644): 'it is conceivable that the external similarity of the Apex micro-organisms to younger oxygen-producing [cyanobacteria] masks significant differences of internal biochemical machinery; thus, their morphology may provide a weak basis on which to infer paleophysiology'. Consistent with this contention is the present-day occurrence of non-photosynthetic cyanobacterium-like filaments in microbial mats associated with deep-sea thermal vents (Jannasch & Wirsén 1981). Samples collected at a depth of 2550 m from thermal submarine springs at the Galapagos Rift oceanic spreading centre by use of the research submersible ALVIN (Jannasch & Wirsén 1981) contain short tapered uniseriate filamentous microbes that are morphologically comparable to *Primaevifilum amoenum* (figure 4a–d) of the Apex chert (Schopf 1993). Notably, Jannasch & Wirsén (1981, pp. 528, 537) are impressed by the cyanobacterium-like morphology of these deep-sea microbes, describing them as 'highly differentiated forms [that appear to be] analogues of certain cyanobacteria...tapered trichomes [that] compare strikingly with members of...[the modern cyanobacterial genus] *Homeothrix*'.

Thus, though of cyanobacterium-like morphology, the relatively broad carbonaceous filaments of the Dresser Formation and the Apex chert need not be regarded as being physiologically modern cyanobacteria. Rather, like the modern cyanobacterium *Oscillatoria* and its living chemotrophic apochlorotic analogue *Beggiatoa*, the fossil forms may represent non-photosynthetic cyanobacterium-like microbial mimics.

6. CONCLUSION

Evidence for the existence of life during the Archaean seems strong. Data are presented here from 48 Archaean deposits reported to contain biogenic stromatolites (table 1; figures 1 and 2), from 14 Archaean units reported to contain 40 morphotypes of putative

microfossils (tables 2 and 3; figures 3–5), and from 13 especially ancient, 3200–3500 Myr old, Palaeoarchean units, for which available organic geochemical data are also summarized (table 3; figure 6). These compilations support the view of most workers in the field of Precambrian palaeobiology, worldwide, that the 'true consensus for life's existence' dates from more than or equal to 3500 Myr ago.

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