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Evidence of Archean life: Stromatolites and microfossils

J. William Schopf [a,*], Anatoliy B. Kudryavtsev [b], Andrew D. Czaja [c], Abhishek B. Tripathi [c]

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

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Abstract

Fossil evidence of the existence of life during the Archean Eon of Earth history (>2500 Ma) is summarized. Data are outlined for 48 Archean deposits reported to contain biogenic stromatolites and for 14 such units that contain a total of 40 morphotypes of described microfossils. Among the oldest of these putatively microfossiliferous units is a brecciated chert of the ~3465 Ma Apex Basalt of Western Australia. The paleoenvironment, carbonaceous composition, mode of preservation, and morphology of the Apex microbe-like filaments, backed by new evidence of their cellular structure provided by two- and three-dimensional Raman imagery, support their biogenic interpretation. Such data, together with the presence of stromatolites, microfossils, and carbon isotopic evidence of biological activity in similarly aged deposits, indicate that the antiquity of life on Earth extends to at least ~3500 Ma.

Keywords: Archean; Stromatolites; Microfossils; Oldest life; Raman imagery; Apex Basalt; Apex chert

1. Introduction

It has recently been 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," have been cast in doubt (Moorbath, 2005). Yet it is precisely during this period of Earth history, prior to 2000 Ma, that most workers have assumed that prokaryotic microbes originated and diversified to comprise Earth's earliest biosphere. If the fossil record is to make any contribution to defining life's early history, doubts such as those raised by Moorbath (2005) must be laid to rest. This prompts the fundamental first-order question addressed here: What fossil evidence exists for life's presence during the Archean Eon of Earth history, prior to 2500 Ma?

This discussion need not be exhaustive. Elsewhere in this issue of *Precambrian Research*, Sugitani and his colleagues (p. 228) report new finds of Archean microfossils and Allwood et al. summarize their recent in-depth studies of the stratigraphic setting and morphology, paleoecology, and biogenicity of ~3400 Ma stromatolites (p. 198). Moreover, carbon isotopic evidence of Archean biologic activity and the known fossil records, both of Archean stromatolites and of microbial microscopic fos-

* Corresponding author. Tel.: +1 310 825 1170; fax: +1 310 825 0097.
E-mail address: schopf@ess.ucla.edu (J.W. Schopf).

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sils, have recently been reviewed (Schopf, 2006a,b). Thus, the aims of this contribution need only be two-fold: (1) to summarize in broad-brush outline and to illustrate selected examples of the 48 occurrences of Archean stromatolites and 40 morphotypes of putative microfossils described from Archean deposits and (2) to provide new Raman-based evidence that demonstrates the cellularity of microbe-like filaments reported from brecciated chert of the ~3465 Ma Apex Basalt (hereafter referred to informally as the "Apex chert"), one of the oldest putatively fossiliferous deposits yet reported and the subject of recent controversy (Brasier et al., 2002, 2005; Schopf, 2004; Altermann, 2005; Altermann et al., 2006). Taken together, the data presented support the view that the "true consensus for life's existence" dates from ≥3500 Ma, not from some 1500 Ma later.

2. Preservation of the Archean rock record

As shown by Lowe (p. 177) in this issue of *Precambrian Research*, vanishingly few rock units have survived from the Archean to the present. Similarly, as Garrels and Mackenzie suggested some years ago (1971, p. 275), "about 90% of the Precambrian once deposited is gone," surviving rocks petering out rapidly with increasing geologic age to produce a severely depleted Archean rock record. As currently known, only two relatively thick especially ancient Archean sedimentary sequences have survived to the present, those of the Pilbara Craton of Western Australia and the Barberton Greenstone Belt of South Africa and Swaziland. Both of these sequences span the period between ~3500 and 3000 Ma and both have been regionally metamorphosed to lower greenschist facies (~250 to 300 °C, ~2 to 5 kb; Klein and Hurlbut, 1985, p. 505).

Given the markedly depleted Archean rock record and the fossil-destroying effects of metamorphism typical of such terrains, it is not surprising that "in comparison with the fossil record of the Proterozoic (<2500 Ma) Precambrian, that of the Archean is minuscule" (Schopf et al., 2005, p. 338). Nevertheless, it is notable that both of the particularly old relatively thick Archean sedimentary sequences contain structures interpreted to be microbially deposited stromatolites (Figs. 1 and 2), and both contain putative microscopic fossils (Figs. 3 through 5).

3. Archean stromatolites

As used here, the term "stromatolite" refers to accretionary sedimentary structures, commonly thinly layered, megascopic and calcareous, produced by the activities of mat-building communities of mucilage-secreting microorganisms, mainly photoautotrophic prokaryotes. Other definitions have been proposed, some similarly emphasizing the biogenic, organosedimentary nature of such structures (e.g., Awramik and Margulis, in Walter, 1976; Awramik, in Semikhatov et al., 1979; Buick et al., 1981), others focusing solely on the sedimentologi-

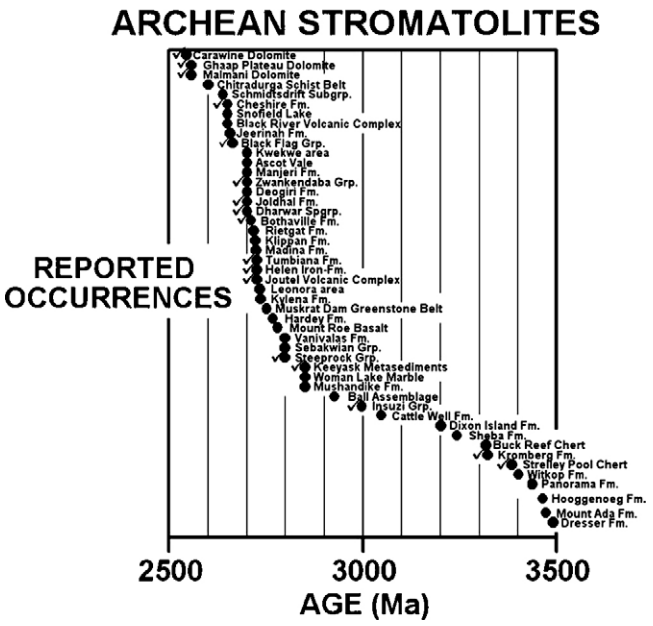


Fig. 1. Stromatolite-containing Archean geologic units; check marks denote occurrences of conical stromatolites (data from Hofmann, 2000; Schopf, 2006a).

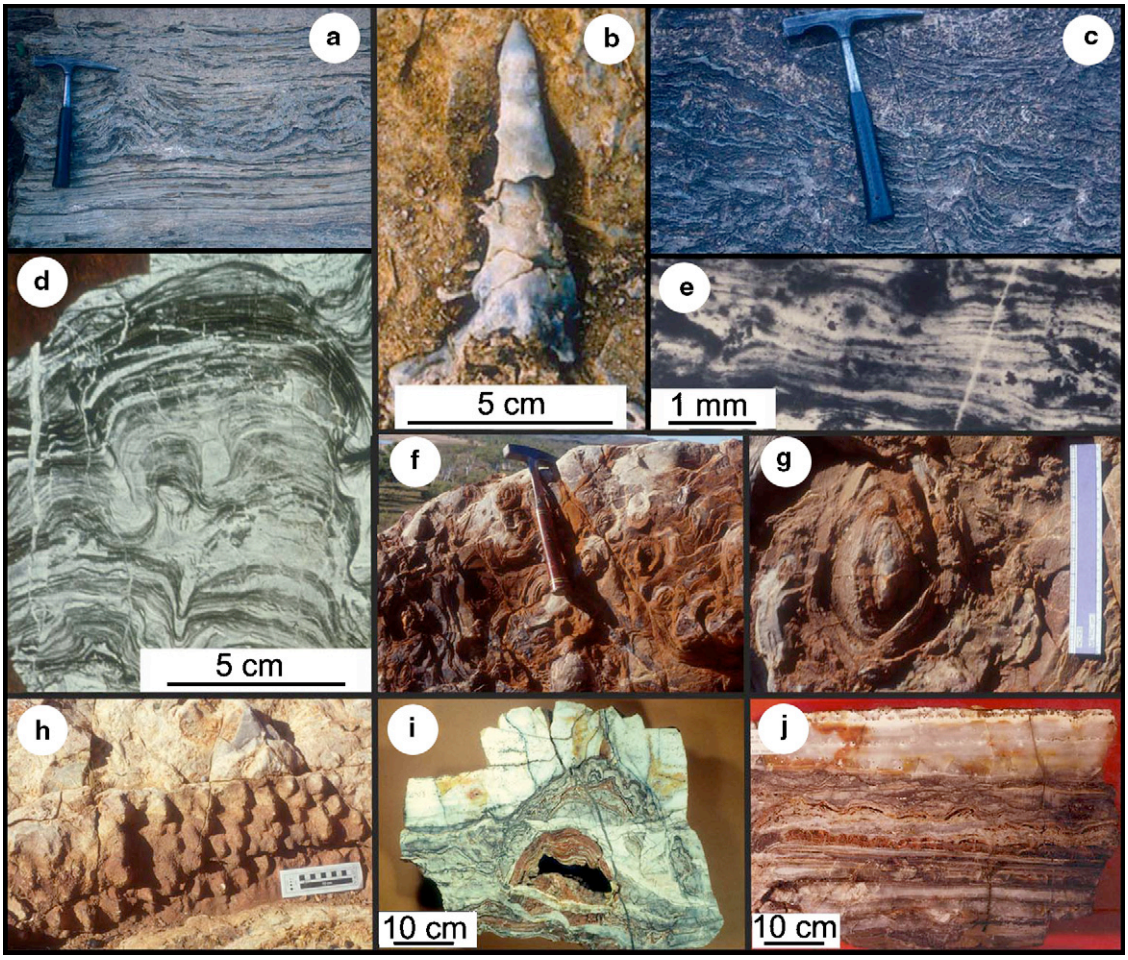


Fig. 2. Representative Archean stromatolites: (a–c) Stratiform and conical stromatolites from the ~2985 Ma Insuzi Group, South Africa (Beukes and Lowe, 1989); photo in (b) courtesy of N.J. Beukes. (d) Laterally linked, low relief stratiform to domical stromatolitic mats from the ~3245 Ma Fig Tree Group of South Africa (Byerly et al., 1986); photo courtesy of D.R. Lowe. (e) Stratiform microbial mats from the ~3320 Ma Kromberg Formation of South Africa (Walsh and Lowe, 1985). (f–h) Conical stromatolites from the ~3388 Ma Strelley Pool Chert of Western Australia (Hofmann et al., 1999; see also Allwood et al. 2007 of *Precambrian Research*, p. 198); scale in (g) = 20 cm; scale in (h) = 10 cm. (i) Domical and (j) stratiform stromatolites from the 3496 Ma Dresser Formation, Western Australia (Walter et al., 1980; Buick et al., 1981).

cal morphology of such structures (e.g., Semikhatov et al., 1979, excluding Awramik; Grotzinger and Knoll, 1999), and still others searching for a middle ground (Hofmann, 1971, 1973, 2000). Such divergence reflects the difficulties in differentiating unambiguously between assuredly biogenic stromatolites and abiotic look-alikes (e.g., geyserites, stalagmites and similar cave deposits, tectonically or otherwise deformed sediments, and finely layered duricrusts such as calcretes, silcretes and the like). Criteria for such differentiation have been enumerated by Buick et al. (1981, pp. 165–167) and by Walter (1983, pp. 189–190) in which establishment of biogenicity centers on detection within such structures of cellularly preserved microfossils or trace fossils ("palimpsest microstructures") of the microscopic organisms responsible for their formation. This criterion can fall short if injudiciously applied, since the mere presence of remnants of fossilized microorganisms within an ancient stromatolite-like structure cannot demonstrate that the structure accreted as a direct result of microbial mat-building activities. Nevertheless, it can be used with confidence in numerous stromatolites: the preservation of huge numbers of microbial fossils comprising the laminae of a stromatolite-like structure would be exceedingly difficult to understand were such microbes not the formative agents of the structures in which they occur.

Unfortunately, however, cellularly preserved fossils and palimpsest microstructures are present only rarely in ancient stromatolites. Because almost all such structures are or were originally calcareous, presumably com-

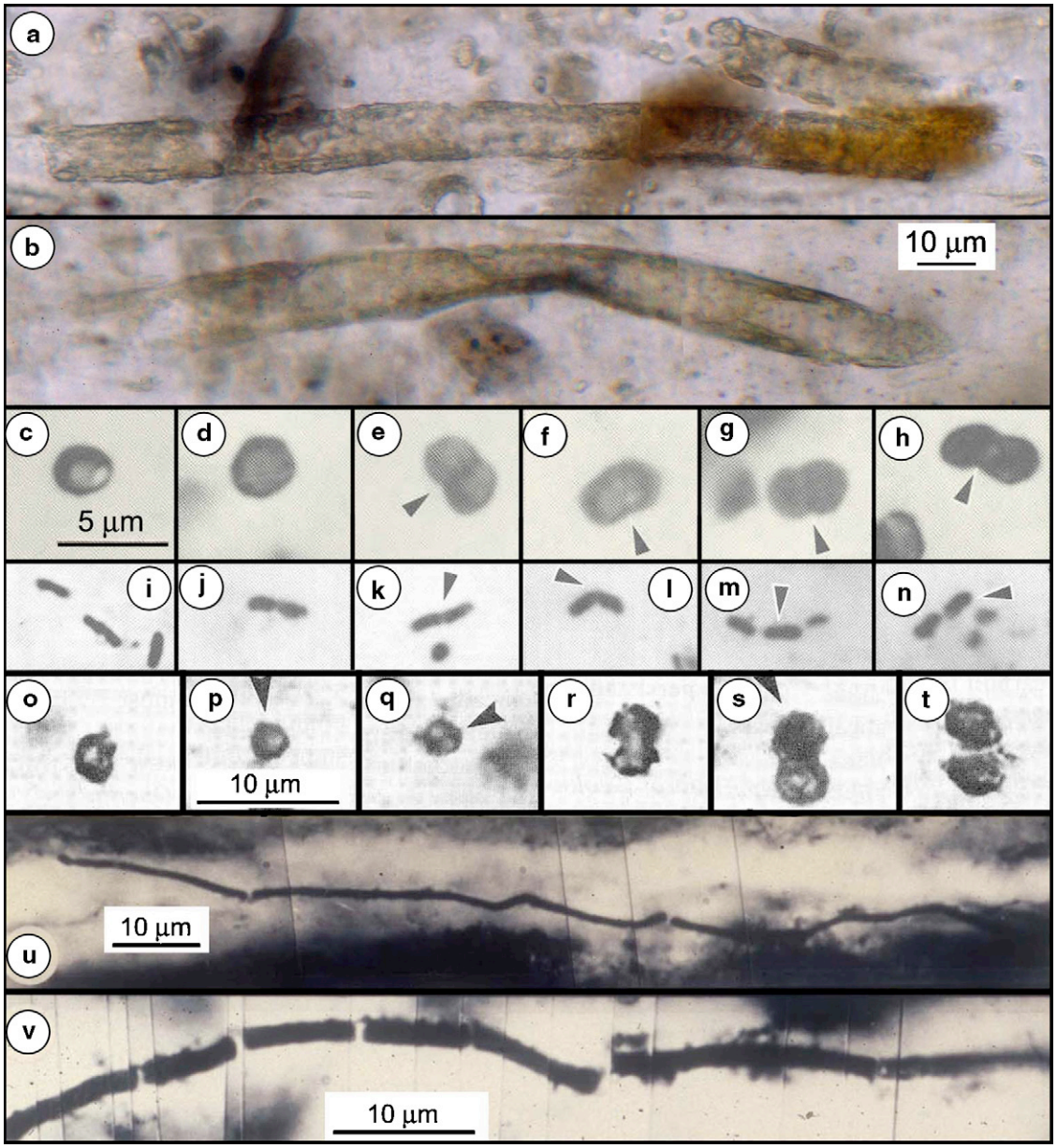


Fig. 3. Representative Archean microfossils in petrographic thin sections: (a and b) Broad prokaryotic (oscillatoriacean cyanobacterium-like) tubular sheaths (*Siphonophycus transvaalense*) from the ~2516 Ma Gamohaan Formation of South Africa (Klein et al., 1987; Buick, 2001); scale shown in (b). (c–h) Solitary or paired (denoted by arrows) microbial coccoidal unicells, and (i–n) solitary or paired (denoted by arrows) bacterium-like rod-shaped unicells from the ~2600 Ma Monte Cristo Formation of South Africa (Lanier, 1986; Buick, 2001); scale for parts (c–n) shown in (c) (modified after Lanier, 1986). (o–t) Solitary and paired microbial coccoidal unicells from the ~3260 Ma Swartkoppie Formation of South Africa, in (p–s) ordered in a sequence inferred to represent stages of cell division (Knoll and Barghoorn, 1977); arrows point to dark organic contents within cells; scale shown in (p); (modified after Knoll and Barghoorn, 1977). (u) Narrow bacterium-like filament and (v) broader microbial filament from the ~3320 Ma Kromberg Formation of South Africa (Walsh and Lowe, 1985; Walsh, 1992; Schopf et al., 2002).

posed initially of metastable aragonite or high-Mg calcite (Grotzinger and Knoll, 1999), growth of carbonate grains (aggrading neomorphism) during early diagenesis, as well as changes during lithification, have in all but a relatively few instances obliterated morphologically identifiable evidence of the formative mat-building microbes. For this reason, cellularly preserved fossil microbes are known almost without exception from 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# of all stromatolites ever described have a fossilized microbiota associated with them" (Grotzinger and 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, are assuredly biogenic. Yet in the Proterozoic, stromatolites are so widespread and abundant, and their biological interpretation is so firmly backed by studies of microbial communities cellularly preserved in Proterozoic cherty stromatolites (e.g., Mendelson and 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 Archean, the problem of proving the biogenicity of such structures presents a greater challenge, due chiefly to the paucity of Archean sediments and the correspondingly small number of known occurrences of stromatolites and preserved microbial assemblages. Nevertheless, Archean stromatolites are now established to have been more abundant and decidedly more diverse than was appreciated even a few years ago (Hofmann, 2000; Schopf, 2006a). Virtually all of the workers who have reported such structures have also studied in detail stromatolites of the Proterozoic. Their interpretation of the biogenicity of the Archean forms, and the differentiation of such structures from abiotic 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; Hofmann, 2000). All of the occurrences of Archean stromatolites listed in Fig. 1, and the representative examples shown in Fig. 2, are regarded by those who reported them as meeting the biology-centered definition of stromatolite used here.

Fig. 1 lists 48 occurrences of Archean stromatolites reported to date, based largely on the compilation of Hofmann (2000). Occurrences regarded by Hofmann as being of possibly younger geologic age or of questionable biogenicity are not included. These data support three principal generalizations (cf. Schopf, 2006a):

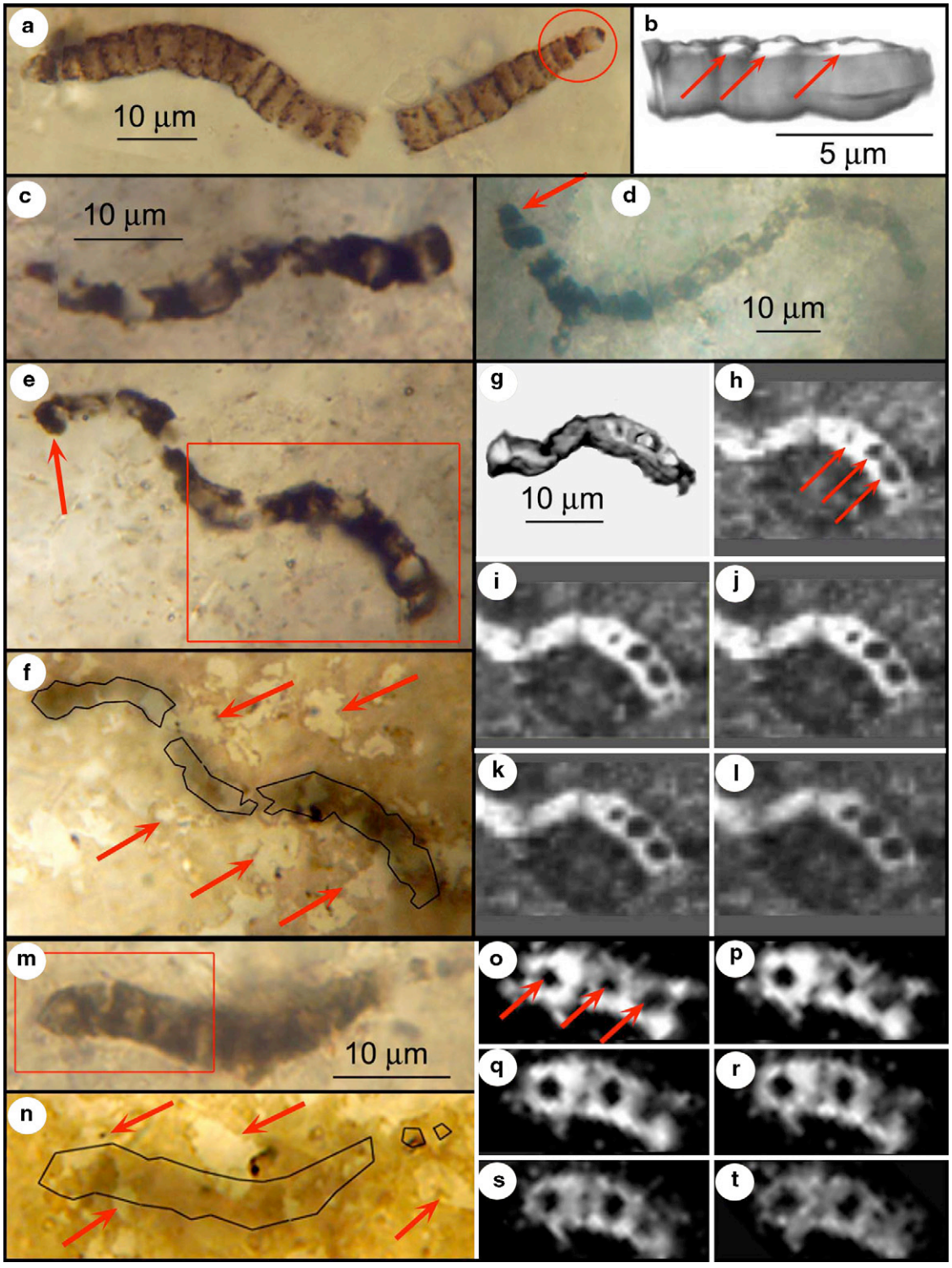
(1) Despite the scarcity of Archean geologic units relative to those of the Proterozoic, the temporal distribution of stromatolites is more or less continuous from 2500 to 3500 Ma. This distribution rather faithfully parallels the estimated temporal distribution of Archean sediments that have survived to the present, with most Archean stromatolites reported from rocks 2500 to 3000 Ma, where sedimentary rocks are relatively plentiful, and somewhat fewer from the older, 3000 to 3500 Ma interval (Fig. 1).

(2) An impressively broad array of stromatolitic morphologies has been recorded in numerous Archean units: sediments of the Transvaal Supergroup (∼2560 Ma) and of the Fortescue (∼2723 Ma), Steeprock (∼2800 Ma) and Insuzi (∼2985 Ma) Groups are all reported to contain stratiform (e.g., Fig. 2a, c through e and j), pseudocolumnar (e.g., Fig. 2d), domical (Fig. 2i), conical (Fig. 2b and f through h), branching (Fig. 2d) and columnar stromatolites, whereas those of the Yellowknife Supergroup (∼2650 Ma) are reported to contain all of these stromatolite types with the exception of conical forms (Hofmann, 2000). Despite the absence in these stromatolites of cellularly preserved microscopic fossils or of palimpsest microstructures, such morphological diversity in a given geologic unit, not uncommonly in a single sedimentary facies, indicates that they are not a product of a single set of nonbiologic accretionary processes.

(3) Conical stromatolites have been recorded in 17 of the 48 units listed in Fig. 1 (Hofmann, 2000; Schopf, 2006a). Present in more than one-third of these deposits – notably including the >3300 Ma Strelley Pool Chert (Hofmann et al., 1999; Allwood et al., 2004, 2006a) and Kromberg Formation (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 and Knoll, 1999, pp. 342–343). Thus, Archean conical stromatolites, "especially the conical structures found in [the ∼3388 Ma Strelley Pool Chert] . . . may have been facilitated by microorganisms" (Knoll, 2003b, p. 6).

4. Archean microfossils

Over recent 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 and Walter, 1983; Schopf, 2004). Of these criteria, the most difficult to satisfy has been that of biogenicity (Hofmann and Schopf,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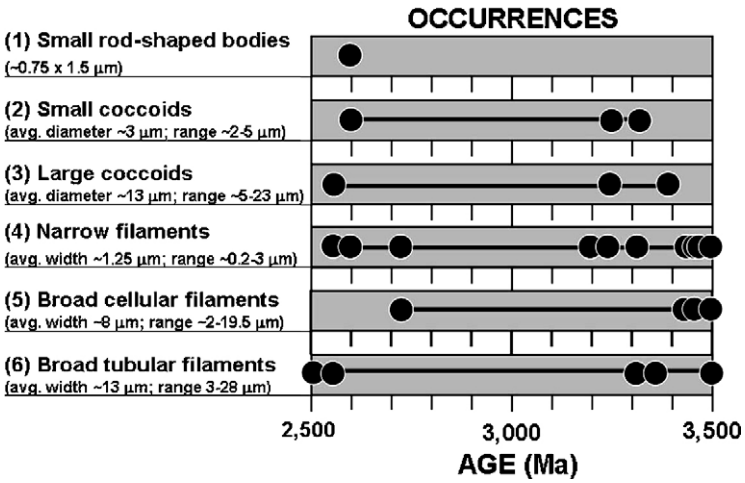

Fig. 5. Temporal distribution of the six classes of 40 morphotypes of microfossils reported from 14 Archean units: data from Schopf (2006a).

1983; Schopf and Walter, 1983; Mendelson and Schopf, 1992). A nested suite of seven traits for establishment of such biogenicity has been proposed (Buick, 1990); 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); 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).

As such analyses demonstrate, a prime indicator of the biological origin of fossil-like objects is the micron-scale co-occurrence of identifiable biological morphology and geochemically altered remnants of biological chemistry. Thus, evidence consistent with and seemingly supportive of a biogenic interpretation would be provided were chemical data to show that populations of objects characterized morphologically as "cellular microfossils" were composed of carbonaceous matter, as would be expected of organically preserved microorganisms (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 exposed at the surface of samples studied, by use of ion microprobe (House et al., 2000; Ueno et al., 2001), electron microprobe (Boyce et al., 2001) and Raman spectroscopy (Arouri et al., 2000); and for rock-embedded specimens, by Raman point spectra or two-dimensional (Kudryavtsev et al., 2001; Schopf et al., 2002, 2005) or three-dimensional Raman imaging (Schopf and Kudryavtsev, 2005), as well as by confocal laser scanning microscopy, in which the kerogen-emitted fluorescence of the specimens analyzed can demonstrate their carbonaceous composition (Schopf et al., 2006).

The co-occurrence of biological morphology and carbonaceous chemistry in ancient microfossil-like objects is strongly suggestive of biogenicity. It is therefore notable that each of the many morphotypes of Archean microfossil-like objects now known, representative

Fig. 4. Permineralized carbonaceous filaments in petrographic thin sections of cherts from the ~750 Ma Bitter Springs Formation (a and b, *Cephalophytarion laticellulosum*: Harvard University Paleobotanical Collections 58571; Schopf and Kudryavtsev, 2005) and the ~3465 Ma Apex chert (c–l, *Primaevifilum amoenum*: c, Natural History Museum, London V.63164 [5]; d, V.63166 [1]; E-L, V.63164 [6]; and m–t, *P. conicoterminatum*: V.63164 [9]; Schopf, 1993). Magnification of (c, e, and f) denoted in (c), (g–l) in (g), and (m–t) in (m); (a, c–e and m) show photomontages. (a) Photomicrograph of *C. laticellulosum*; the circle denotes the region in (b). (b) Three-dimensional Raman image; arrows point to quartz-filled cell lumina (white) defined by carbonaceous walls (gray). (c and d) Photomicrographs of specimens of *P. amoenum*; arrow in (d) points to a rounded terminus. (e and f) Photomicrographs of *P. amoenum*, in (e) 3–9 μm below the section surface with the rectangle outlining the part in (g–l), and in (f) showing that the specimen (black outline) is embedded in irregularly shaped quartz grains (arrows). (g) Three-dimensional Raman image; the carbonaceous filament (gray) is cylindrical and quartz-filled (white). (h–l) Two-dimensional Raman images at sequential depths below the filament surface (h, at 0.75 μm; i, 1.5 μm; j, 2.25 μm; k, 3.0 μm; l, 3.75 μm); arrows in (h) point to cell-like quartz-filled compartments (black) defined by carbonaceous walls (white), evident also in (i–l). (m and n) Photomicrographs of *P. conicoterminatum*; the rectangle in (m) denotes the part of the filament shown in (o–t); (n) shows the section surface and the position of the embedded filament (black outline) with arrows pointing to irregularly shaped quartz grains. (o–t) Two-dimensional Raman images at sequential depths below the filament surface (o, at 1.5 μm; p, 2.25 μm; q, 3.0 μm; r, 3.75 μm; s, 4.5 μm; t, 5.25 μm); arrows in (o) point to cell-like quartz-filled compartments (black) defined by carbonaceous walls (white), evident also in (p–t).

examples of which are illustrated here (Figs. 3 and 4), meet both of these criteria, and that all such putative fossils, whether spheroidal or filamentous, satisfy the enumerated sets of criteria required for establishment of biogenicity (Schopf, 2004). Many of the rod-shaped to spheroidal morphotypes are juxtaposed in adpressed pairs (Fig. 3e through h, k through n and s), presumptive evidence of biologic cell division. Similarly, numerous filamentous specimens exhibit uniseriate sequences of discoidal to boxlike chert-filled cavities defined in three dimensions by transverse and lateral carbonaceous walls (Fig. 4c through e, g through m, and o through t), presumptive cell lumina and a definitive feature of *bona fide* cellular filamentous microbes, both modern and Proterozoic (e.g., Fig. 4a and b, a microbial filament from the ∼750 Ma Bitter Springs Formation of Australia; Schopf and Kudryavtsev, 2005).

As has been documented in some detail (Schopf, 2006a), all of the 40 morphotypes of microfossil-like objects now known from 14 Archean geologic units are morphologically simple – small rod-shaped bodies, unornamented coccoids, or sinuous tubular or uniseriate filaments – microbe-like morphologies typical of unquestionable Proterozoic microscopic fossils (e.g., Hofmann and Schopf, 1983; Mendelson and Schopf, 1992; Schopf, 1999; Knoll, 2003a) and a simplicity consistent with their interpretation as early-evolved Archean members of the microbial evolutionary continuum now well established in the younger Precambrian. The known temporal distribution of the six classes of such morphotypes (Schopf, 2006a) is summarized in Fig. 5. All of the classes are composed of microfossil-like structures that are of the size and shape of well-accepted Proterozoic fossil microbes. Members of all but one of the classes (that composed of small rod-shaped bodies) have been reported from several or many Archean geologic units of markedly differing geologic age, age-ranges consistent with their interpretation as members of exceedingly slowly evolving Precambrian microbial lineages (Schopf, 1994). Notably, such putative microfossils are well represented in 3200–3500 Ma geologic units (Fig. 5), the oldest segment of the currently known Archean rock record in which identifiable fossil microbes might plausibly be expected to be preserved (Schopf, 2006b).

4.1. The problem of biogenicity

Despite the evidence summarized above, in recent years some geoscientists have questioned the existence of Archean life. The reasons for such doubts are easy to understand. Though the Archean fossil record is appreciably more abundant than has been generally assumed – as is documented above – evidence of early life remains limited, and it is markedly so in comparison with that of the Proterozoic with which it typically is compared. All data suggest that this relative paucity of fossil evidence from the Archean is a result of normal geological processes, the recycling of such especially ancient sediments coupled with the fossil-destroying metamorphism of Archean rock units that have survived to the present. Nevertheless, to some the problem posed by this limited ancient fossil record has yet to be resolved, a view stimulated by the report of Brasier et al. (2002) that questioned the biogenicity of the particularly ancient fossil-like microstructures of the ∼3465 Ma Apex chert of northwestern Australia (Schopf, 1992, 1993). Geoscientists unfamiliar with the known Archean fossil record could easily have surmised that such questioning cast doubt on all evidence of early life.

In a general sense, the answer to the question of biogenicity is straightforward, as was shown in the 1960s when early workers in the field first demonstrated that "Precambrian microfossils" are, indeed, true fossils (Barghoorn and Tyler, 1965; Cloud, 1965; Barghoorn and Schopf, 1965; Schopf, 1968). In answer to skeptics who conjectured about what sorts of nonfossils such objects seemingly "could be" or "might be" (Schopf, 1999, p. 62), it was recognized early that the critical problem was to establish what the "fossils" *actually* are. The solution was to establish their biological origin by showing that they possess a suite of traits that, taken together, are unique to life—a suite shared by such fossils and living microorganisms, but not by inanimate matter (a formulation, it may be noted, that is essentially identical to that promulgated in the early 1800s by Baron Georges Cuvier, a founder of paleontology, as he sought to establish that megascopic fossils were not merely "sports of nature").

The early proposed multi-trait solution to the biogenicity problem, augmented today by lines of evidence unavailable years ago (such as analyses of the molecular-structural characteristics, isotopic composition, and three-dimensional morphology of the kerogen that comprises individual microscopic fossils), is decidedly more powerful now than it was when it was first applied. Thus, though neither morphology (Hofmann and Schopf, 1983; Schopf and Walter, 1983; Mendelson and Schopf, 1992), nor carbonaceous makeup (Schopf and Walter, 1983; Schopf et al., 2002; Pasteris and Wopenka, 2003), nor carbon isotopic composition (van Zuilen et al., 2002) – *if considered alone* – has proven consistently reliable as an indicator of biogenicity, the biologic origin of putative microscopic fossils can be established if multiple factors

are considered together. For example, because (1) only living systems are known to be capable of producing biologic-like populations of three-dimensionally cellular, morphologically diverse, microfossil-like objects composed of carbonaceous matter that exhibits a biological isotopic composition; (2) fossil-like objects that meet this suite of tests – such as the microorganisms permineralized in cherts of the Proterozoic Bitter Springs and Gunflint Formations (Barghoorn and Tyler, 1965; Schopf, 1968; Schopf and Blacic, 1971; House et al., 2000; Schopf et al., 2002), two particularly well-studied Precambrian fossiliferous units – can be accepted as being assuredly biogenic.

Such traits, each typically composed of a series of factors and subfactors, constitute a cascade of evidence in which differing traits are used in differing situations, depending on the data available. Assuming that an appropriately biological set of traits is so used, this solution to the biogenicity problem could be shown to be in error only were it to be demonstrated that an identical suite of "biogenic" indicators is mimicked by assemblages of assuredly nonbiologic microscopic objects—for instance, by showing for the Bitter Springs and Gunflint examples that biologic-like populations of diverse, cellular, carbonaceous, microfossil-like objects that exhibit a biological isotopic signature can be produced by solely abiotic processes.

5. Fossil-like filaments of the Apex chert

In the discussion below, we apply this multi-trait strategy to the putative fossils of the ~3465 Ma Apex chert of the Pilbara Block of northwestern Western Australia (Schopf, 1992, 1993). Questions have been raised about the paleoenvironment of the 11 taxa of microbe-like structures described from this deposit (Schopf, 1993), as well as about their chemical composition, mode of preservation, and putative biological morphology (Brasier et al., 2002, 2005). These questions are addressed in turn below. The evidence presented here, in part provided by techniques newly introduced to paleobiology – two-dimensional (Kudryavtsev et al., 2001; Schopf et al., 2002, 2005) and three-dimensional (Schopf and Kudryavtsev, 2005) Raman spectroscopic imagery – supports interpretation of the Apex filaments as *bona fide* microbial fossils.

5.1. Paleoenvironment

Although initially mapped as a marine shallow-water facies (Hickman and Lipple, 1978; Hickman, 1983), the fossiliferous locality of the Apex chert (Schopf, 1993) has recently been reinterpreted to be a hydrothermal vein deposit (Van Kranendonk, 2006), a setting suggested to be unlikely for preservation of delicate fossil microbes (Brasier et al., 2002, 2005). However, microorganisms morphologically comparable to the Apex filaments are common in modern hydrothermal environments (Pentecost, 2003); tapered "cyanobacterium-like" microbes similar to *Primaevifilum amoenum*, the most abundant of the described Apex taxa (Schopf, 1993), have long been known to occur at deep-sea thermal vents (Jannasch and Wirsen, 1981); and fossil filaments, including specimens so similar to those of the Apex chert that they have been referred to two of the Apex taxa (Ueno et al., 2004), are present in three other hydrothermal cherts of the Pilbara Craton (Ueno et al., 2004; Schopf, 2006a). Like some microfossils preserved in other Archean hydrothermal units, the Apex filaments may represent remnants of thermophilic microbes preserved *in situ*, but it seems more likely that the specimens illustrated here, embedded in rounded chert granules (as shown in Schopf, 1993), represent mesophiles emplaced in the unit in reworked detrital clasts.

5.2. Carbonaceous composition

On the basis of their optical characteristics, the Apex filaments were initially interpreted to be composed of carbonaceous kerogen (Schopf, 1992, 1993). Though this interpretation is backed by Raman analyses of numerous specimens (Schopf et al., 2002), others have claimed them to be composed of abiotic graphite produced by Fischer-Tropsch-Type (FTT) reactions under hydrothermal conditions (Brasier et al., 2002, 2005). Recently, Raman analyses of assured fossil microorganisms permineralized in 21 Precambrian cherts of diverse low grade metamorphic histories have documented the range of spectra exhibited by their kerogenous cell walls and introduced the Raman Index of Preservation ("RIP"), a quantitative measure of the geochemical maturity of the preserved organic matter (Schopf et al., 2005). As shown in Fig. 6 (fourth spectrum from top), the RIP value of the carbonaceous Apex filaments lies near the middle of this documented range of geochemical maturation (Schopf et al., 2005), a state of alteration consistent with the reported lower greenschist facies regional metamorphism of the Apex rocks to temperatures of ~250 °C (Hickman, 1983). Indeed, such Raman spectra establish that rather than being crystalline graphite, the end-product of such maturation, the Apex filaments are composed of geochemically moderately altered amorphous carbonaceous matter

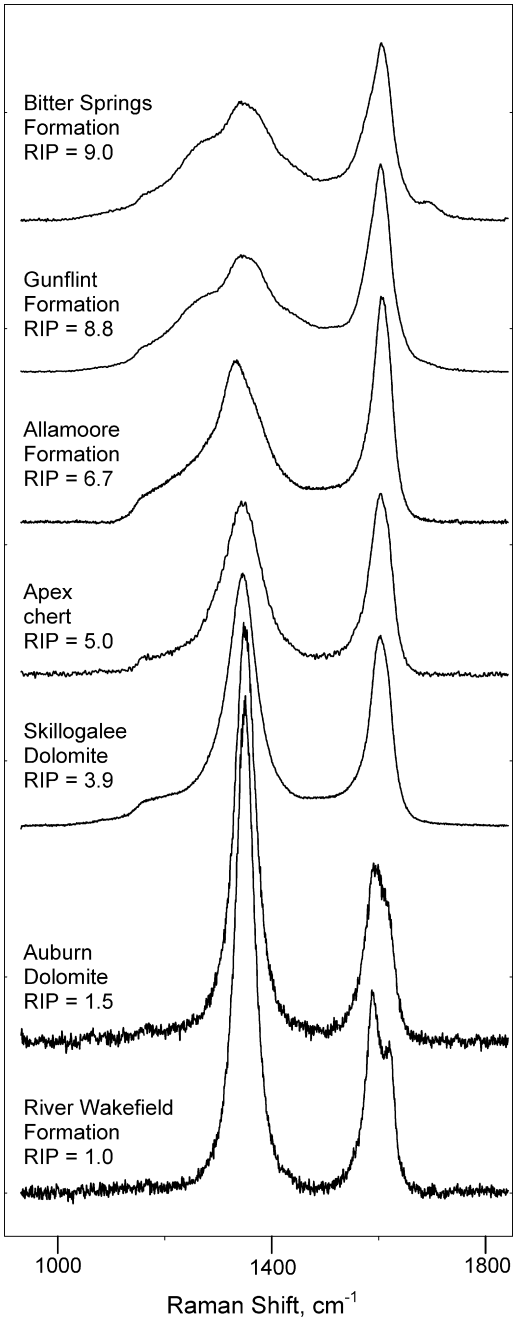

Fig. 6. Raman spectra of assured carbonaceous microfossils permineralized in cherts of the ~750 Ma Bitter Springs, ~1900 Ma Gunflint, and ~1050 Ma Allamoore Formations, the ~760 Ma Skillogalee and ~720 Ma Auburn Dolomites, and the ~775 Ma River Wakefield Formation (Schopf et al., 2005) compared with that of *P. amoenum* from the ~3465 Ma Apex chert (Figs. 4e and 7a; Schopf, 1993), ordered by their RIP values (Schopf et al., 2005) from less (top) to more (bottom) geochemically mature.

(interlinked polycyclic aromatic hydrocarbons) like the kerogen comprising *bona fide* fossils (Schopf et al., 2002, 2005).

Raman data, if taken alone (in the absence of their combination with morphological evidence of biogenicity), cannot "prove" the biological origin of the geochemically altered kerogen-like carbonaceous matter that comprises the organic-walled fossils, fossil-like objects and associated organic detritus analyzed to date in any of numerous Proterozoic or Archean geologic units (e.g., Schopf et al., 2002, 2005). Such is not true of the kerogen of unmetamorphosed, relatively little altered organic-walled fossils and associated carbonaceous debris in which evidence of biogenicity, the presence of various non-hydrocarbon functional groups, can be preserved (e.g., in the permineralized fossils and organic matter of the Eocene-age Clarno and Allenby Formations; Czaja, 2006). Such clear-cut chemical evidence of biogenicity is lost during geochemical maturation, all such functional groups being geochemically labile, and is thus no longer detectable in Precambrian organic matter except for that comprising exceptionally well preserved microbes and associated organics (e.g., those of the ~750 Ma Bitter Springs Formation in which carbonyl, C=O, groups are readily identifiable; Schopf et al., 2005, Fig. 9i, pp. 254–356). Nevertheless, Raman spectra can demonstrate unequivocally the state of maturation of such carbonaceous matter and whether it is amorphous or composed of crystalline graphite, spectra that should be essentially the same for the fossils and organic debris in any given deposit (if both are syngenetic with deposition of the unit analyzed), since both the fossils and the detrital organic matter associated with them will have experienced the same geochemical history (Schopf et al., 2005).

In this regard, Raman data, showing the amorphous, non-graphitic nature of the carbonaceous matter of the Apex microbe-like objects and associated detritus, have been confirmed by use of other geochemical techniques (De Gregorio and Sharp, 2003, 2006; De Gregorio et al., 2005), results consistent with those obtained from analyses of carbonaceous matter similarly preserved in other ancient cherts of the Pilbara Block (Marshall et al., 2004; Derenne et al., 2004; Tice et al., 2004; Allwood et al., 2006b; Duck et al., in press). Moreover, such studies have rendered implausible an FTT origin for the ancient organic matter preserved in such deposits (Ueno et al., 2004) and have shown that the kerogen-like Apex organic matter is "consistent with the interpretation that the microbial-like features in the Apex chert are *bona fide* microfossils" (De Gregorio et al., 2005). The carbon

isotopic composition of the Apex organic matter, having an average $\delta^{13}C_{PDB}$ value of −27.7‰ ($n = 10$; Schopf, 2006a), like that of kerogens preserved in eight other >3200 Ma deposits from which microfossils have been reported (average $\delta^{13}C_{PDB} = -28.8‰$, $n = 192$; Schopf, 2006a), is similarly consistent with a biological origin (Schopf, 1993, 2004, 2006a,b; Schidlowski, 2001; Brasier et al., 2005).

5.3. Mode of preservation

Like microorganisms permineralized in other Precambrian cherts (Mendelson and Schopf, 1992), the Apex microbe-like filaments have been interpreted to be carbonaceous cellular remnants three-dimensionally embedded in fine-grained quartz (Schopf, 1992, 1993). Such permineralization, characteristic of petrified wood and common for organic-walled microorganisms (Schopf, 1975), results in hollow cell lumina being infilled with silica and bounded by optically distinct kerogenous cell walls that define their three-dimensional form. In contrast, those questioning the biogenicity of the Apex filaments have interpreted them to be "not hollow but composed of solid to discontinuous carbon," their cell-like structure hypothesized to have been "formed from the reorganization of carbonaceous matter . . . during recrystallization" (Brasier et al., 2005, pp. 55, 77). Composed of quartz-filled single cells bounded by carbonaceous walls, unicellular permineralized coccoidal microorganisms can be difficult to distinguish from organic-coated spheroidal mineral grains (Schopf, 2004). But because of their relative complexity, interpretation of similarly preserved many-celled fossil-like filaments, such as those of the Apex chert, is typically less difficult—provided it can be established that they are composed of uniseriate cell-like segments. As shown below, Raman imagery provides a means to determine whether the Apex filaments are "hollow" (i.e., quartz-filled) and cellular, as expected of permineralized microorganisms, or are solid, non-cellular, and potentially abiotic.

5.4. Biological morphology

Like all known *bona fide* microbial fossils, the Apex filaments satisfy well-defined criteria of biogenicity (Schopf, 2004), ranging from the size and shape of individual fossil-like structures and their cell-like compartments – for all of the 11 described taxa, well within the range of living microbes – to such factors as their consistency with the established fossil record, presence in multicomponent "biologic-like" populations, occurrence in a biologically plausible environment, and their carbonaceous composition, mode of preservation, and taphonomy (Schopf, 1992, 1993, 2004, 2006a; Altermann, 2005; Altermann et al., 2006). Like modern (Pentecost, 2003) and fossil (Mendelson and Schopf, 1992) filamentous microbes, the Apex filaments are commonly sinuous (Fig. 4c through t), an indication that they were originally flexible, not rigid like mineralic graphite. If disrupted, they tend to be torn at points of flexure (compare Fig. 4a, c and e), evidence that they were originally rather fragile, and many of the Apex specimens taper to terminate in rounded apices (Fig. 4d; Schopf, 1993), characteristics typical of microbes but not of minerals.

5.5. Cellular fossils or solid pseudofossils?

Despite the evidence outlined above, a prime question remains. Are the Apex filaments demonstrably composed of organic-walled cells? In light of claims that the filaments are solid carbon (Brasier et al., 2005), rather than being composed of permineralized "hollow" cells, or that they resemble laboratory synthesized non-cellular, thread-like, organic-coated crystallites that could have formed abiotically and been preserved in the Apex chert (García-Ruiz et al., 2002, 2003), their cellular structure, or lack thereof, is crucial to assessment of their biogenicity. To address this question we have used two-dimensional (Kudryavtsev et al., 2001; Schopf et al., 2002, 2005) and three-dimensional (Schopf and Kudryavtsev, 2005) Raman imagery, techniques that provide the means to spatially correlate optically discernable morphology and molecular-structural composition at micron-scale resolution. Shown in Fig. 4a and b is an example of the use of such imagery to demonstrate the cellularity of an assured Precambrian microbe ~750 Ma in age (Schopf and Kudryavtsev, 2005). The three-dimensional Raman image of this specimen (Fig. 4b) shows that its "hollow" (quartz-filled) terminal cells are defined by cell walls composed of kerogen, the molecular-structural characteristics of which are documented by the uppermost spectrum in Fig. 6.

By use of well-documented procedures for such imagery (Kudryavtsev et al., 2001; Schopf et al., 2002, 2005; Schopf and Kudryavtsev, 2005), we have investigated 10 of the originally described Apex filaments (Schopf, 1992, 1993), all of which are composed of what we interpret to be quartz-filled organic-walled cells. Results are illustrated here for two such specimens (Fig. 4g through l and o through t). Three Apex filaments assigned to *P. amoenum* (Schopf, 1993) are shown in Fig. 4c through e. The carbonaceous (kerogen-like)

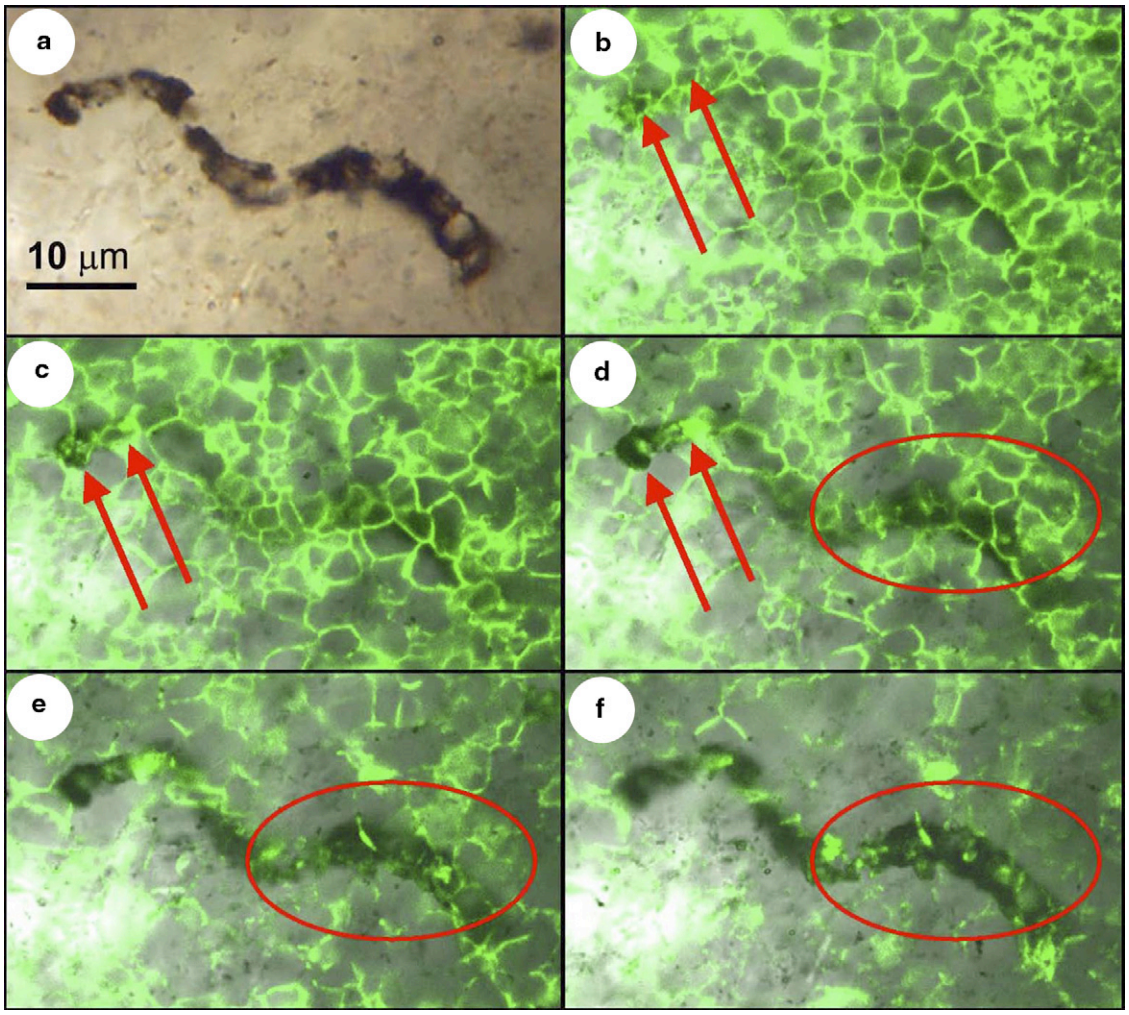

Fig. 7. Permineralized carbonaceous filament (*P. amoenum*) in a thin section of Apex chert (cf. Fig. 4e–l); magnification of all parts denoted in (a), an optical photomontage. (b–f) Confocal laser scanning micrographs (CLSM images, cf. Schopf et al., 2006) at sequential depths below the thin section surface (b, at 3 μm; c, 4 μm; d, 5 μm; e, 6 μm; f, 7 μm). Heating of the specimen-containing ∼150 μm-thick section during its remounting at the Natural History Museum, London (P. Hayes, personal communication to J.W.S., 2005), separated quartz grains at its upper surface that permitted microscopy immersion oil to permeate at grain boundaries to a depth of ∼7 μm within the section. This separation enabled imaging of the outlines of quartz grains at the section surface without the use of polarized optics (Fig. 4f and n), and the fluorescence emission of the permeating oil permitted CLSM imaging of grain margins within the upper few microns of the section. Arrows in (b–d) point to oil-filled grain boundaries that transect the uppermost (3- to 5-μm-deep) part of the filament; ellipses in (d–f) denote deeper parts of the filament (cf. Fig. 4h–l) to which fluorescent oil permeated only partially.

composition of the specimen in Fig. 4e is documented by its Raman spectrum, shown in Fig. 6 (fourth spectrum from the top). The three-dimensional Raman image of a part of this filament (Fig. 4g) demonstrates that it is cylindrical, like *bona fide* Precambrian permineralized microbes (Fig. 4a and b), not flat or platy like mineralic graphite. Fig. 4h through l shows two-dimensional Raman images of the same part of this specimen at sequentially increasing depths, demonstrating that it is composed of uniseriate box-shaped quartz-filled compartments (Fig. 4h, arrows) the walls of which are defined by kerogen-like carbonaceous matter, structures that we interpret to be the "hollow" cell lumina expected of permineralized microorganisms. Comparable results are shown in Fig. 4m through t for a somewhat larger Apex taxon, *P. conicoterminatum*. Two-dimensional Raman images (Fig. 4o through t) demonstrate that this filament is similarly composed of a uniseriate sequence of box-like organic-walled quartz-filled segments that closely resemble the quartz-filled cells of permineralized *bona fide* Precambrian microorganisms (Fig. 4a and b).

That the Apex filaments are partitioned by carbonaceous transverse walls into uniseriate cell-like segments (Fig. 4h through l and o through t) shows that they are not organic-coated, non-cellular, thread-like crystallites (García-Ruiz et al., 2002, 2003). Similarly, such cell-like structures are not a result of carbonaceous matter having been mobilized to envelop quartz grains during recrystallization (Brasier et al., 2005). Such mobilization could occur only were the organic matter to be liquid, like petroleum, rather than being solid carbonaceous particles embedded within or immobilized at the margins of mineral grains. However, as shown in Fig. 7b through g, permeation of organic fluids into the Apex chert results in formation of a three-dimensional chicken wire-like mosaic, not in the production of discrete, cylindrical, microbe-like sinuous filaments composed of regularly aligned uniseriate strands of cell-like segments (Fig. 4e through t). Moreover, the carbonaceous walls that define the box-like compartments of the Apex filaments are relatively thick and continuous (Fig. 4e through t), like the cell walls of modern and fossil microbes, not thin and discontinuous or patchy, like grain boundary-constrained congealed organic matter (compare Figs. 4e through t and 7b through f). Finally, the fine-grained quartz in which the filaments are embedded, like that typical of microfossil-bearing Precambrian cherts (Schopf, 1975; Mendelson and Schopf, 1992), is a mosaic of grains having interlocking variable shapes – some larger, some smaller, all rather irregular, and some transecting putative cells of the fossil-like filaments – grains that in three dimensions differ distinctly from the cylindrical uniform cell-like segments of the Apex filaments (Figs. 4f and n and 7b and d).

Backed by additional factors and subfactors that show the biological origin of such fossil-like structures (Schopf, 2004), demonstration of organic-walled cellularity in putative filamentous microfossils such as these is a strong indicator of biogenicity. Such organic-walled cellular structure is a defining characteristic of *bona fide* microbial filaments, both extant and fossil. Indeed, pseudofossils that exhibit such carbonaceous uniseriate cell-like structure are evidently unknown from the geological record, reported not even from petroleum- or anthraxolite-rich deposits where they might be expected to be abundant. Further, neither FTT-syntheses nor any other abiotic organic synthesis has been shown to produce particulate carbonaceous matter, like that comprising the Apex filaments and, as is documented here (Fig. 7), the formation of discrete cylindrical microbe-like filamentous structures by the permeation of petroleum-like materials is implausible.

5.6. Tests of biogenicity

The fossil-like filaments of the Apex chert meet a multi-trait series of 10 tests of their biogenicity. All exhibit (1) *biological morphology* (a filamentous microbial organismal form), including (2) *structurally distinct carbonaceous cell walls* that define (3) *cell lumina* (originally cytoplasm-filled cell cavities). All occur in (4) a *multi-member population* (if one specimen can be preserved, others should be also) that includes (5) *numerous taxa* (if one member of a biological community can be preserved, others should be also) and that exhibits (6) *variable preservation* (ranging from life-like, to degraded, to markedly decomposed, to biologically nondescript). All are (7) *preserved three-dimensionally by permineralization* (petrifaction) in fine-grained quartz, a common and well understood mode of fossilization (Schopf, 1975) that is characteristic of organic-walled organisms, whether they are microbes (Mendelson and Schopf, 1992) or higher plants (e.g., petrified logs). Detailed morphometric data documenting their (8) *biological size ranges* have been published for several hundred specimens (Schopf, 1992, 1993), and they exhibit a (9) *Raman signal of biogenic kerogen* (Schopf et al., 2005), carbonaceous matter that has an (10) *isotopic composition typical of biologically produced organic matter* (Schopf, 2006a,b).

6. Conclusions

Evidence for the existence of life during the Archean is firm. Consistent with the findings presented in other papers of this special issue of *Precambrian Research*, the data presented here – from diverse Archean stromatolite-bearing (Figs. 1 and 2) and microfossiliferous deposits (Figs. 3 through 5) – show that life was not only extant but was flourishing in the Archean. Further, new findings presented here support the biological interpretation of the microbe-like microstructures of the Apex chert, among the oldest putative fossils known. Taken together, these data show why it is that most workers in the field of Precambrian paleobiology are of the view that the "true consensus for life's existence" dates from $\geq$ 3500 Ma.

Acknowledgements

This discussion of Archean stromatolites and microfossils is in part an abridged version of Schopf (2006a), presented here in order to assure that this special issue of *Precambrian Research* includes fossil data from the entire Archean in addition to those from the more

focused studies of Allwood et al. (p. 198) and Sugitani et al. (p. 228). We thank J. Shen-Miller and an anonymous reviewer for helpful comments on the manuscript, and we are particularly grateful to K. Grey for providing data included in Fig. 1 (cf. Schopf, 2006a) and for her help in clarifying the age relations as currently known among the Australian Precambrian fossiliferous units considered here. A.D.C. and A.B.T. are Fellows in CSEOL, the IGPP Center for Study of the Origin and Evolution of Life at UCLA. This work was supported by NASA Exobiology Grant NAG5-12357 (to J.W.S.) and by CSEOL.

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