



Microfossils of the Early Archean Apex Chert: New Evidence of the Antiquity of Life

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REFERENCES AND NOTES

1. H. Takayama, *News Letter No. 1* (Research Group on a new project, "Computational Physics as a New Frontier in Condensed Matter Research" under the support of the Grant-in-Aid for Scientific Research on Priority Areas from the Ministry of Education, Science, and Culture of Japan, Tokyo, 1991).
2. N. Metropolis, A. Rosenbluth, M. Rosenbluth, A. Teller, E. Teller, *J. Chem. Phys.* **21**, 1087 (1953).
3. F. Yonezawa, Ed., *Molecular Dynamics Simulations*, vol. 103 of the *Springer Series in Solid State Sciences* (Springer-Verlag, Heidelberg, 1992).
4. S. Nosé, Ed., *Prog. Theor. Phys. Suppl.* **103**, 1 (1991).
5. F. Yonezawa, in *Solid State Physics*, H. Ehrenreich and D. Turnbull, Eds. (Academic Press, New York, 1990), vol. 45, p. 179.
6. _____, S. Nosé, S. Sakamoto, *Neue Folge* **156**, 77 (1988).
7. F. C. Frank, *Proc. R. Soc. London Ser. A* **215**, 43 (1952).
8. J.-L. Barrat, J.-N. Roux, J.-P. Hansen, *Chem. Phys.* **149**, 198 (1990); J.-L. Barrat and M. L. Klein, *Annu. Rev. Phys. Chem.* **42**, 23 (1991).
9. Y. Hiwatari, in *Molecular Dynamics Simulations*, F. Yonezawa, Ed., vol. 113 of *Springer Series in Solid State Sciences* (Springer-Verlag, Heidelberg, 1992), p. 32.
10. S. Fujiwara and F. Yonezawa, in preparation.
11. S. Chandrasekhar, *Contemp. Phys.* **29**, 527 (1988).
12. K. M. Aoki and F. Yonezawa, *Phys. Rev. A* **46**, 6541 (1992).
13. K. Omata, K. M. Aoki, F. Yonezawa, in preparation.
14. M. Cheng, J. T. Hsi, R. Pindak, *Phys. Rev. Lett.* **61**, 550 (1988).
15. B. I. Halperin and D. R. Nelson, *ibid.* **41**, 121 (1978).
16. R. J. Birgeneau and J. D. Lister, *J. Phys. Paris* **39**, L399 (1978).
17. R. Pindak, D. E. Moncton, S. C. Davey, J. S. Goodby, *Phys. Rev. Lett.* **46**, 1135 (1981).
18. R. Geer *et al.*, *Nature* **355**, 152 (1992).
19. W. E. Spear and P. G. LeComber, *Solid State Commun.* **17**, 1193 (1975).
20. D. L. Staebler and C. R. Wronski, *Appl. Phys. Lett.* **31**, 292 (1977).
21. K. Morigaki, *Jpn. J. Appl. Phys.* **27**, 163 (1988).
22. W. B. Jackson and J. Kakalios, in *Amorphous Silicon and Related Materials*, H. Fritzsche, Ed. (World Scientific, Singapore, 1988), vol. 1, p. 247.
23. F. Yonezawa, S. Sakamoto, M. Hori, *J. Non-Cryst. Solids* **137**, 135 (1991).
24. F. Yonezawa and S. Sakamoto, *Optoelectronics-Devices Technol.* **7**, 117 (1992).
25. R. Car and M. Parrinello, *Phys. Rev. Lett.* **55**, 2471 (1985).
26. _____, *ibid.* **60**, 204 (1988); G. Galli, R. M. Martin, R. Car, M. Parrinello, *ibid.* **62**, 555 (1989); *ibid.* **63**, 988 (1989); I. Stich, R. Car, M. Parrinello, *ibid.*, p. 2243; G. Seifert, G. Pastore, R. Car, *J. Phys. Condens. Matter* **4**, L179 (1992); P. Ballone, W. Andreoni, R. Car, M. Parrinello, *Phys. Rev. Lett.* **60**, 271 (1988).
27. T. Oguchi and T. Sasaki, *Prog. Theor. Phys. Suppl.* **103**, 93 (1991).
28. Y. Morikawa, K. Kobayashi, K. Terakura, S. Bluger, *Phys. Rev. B* **44**, 3459 (1991).
29. M. Tsukada, K. Kobayashi, N. Isshiki, H. Kageshima, *Surf. Sci. Rep.* **13**, 265 (1991).
30. W. Kohn and L. J. Sham, *Phys. Rev.* **140**, 1133 (1965).
31. G. B. Bachelet, D. R. Hamann, M. Schlüter, *Phys. Rev. B* **26**, 4199 (1982).
32. I thank my students S. Sakamoto, K. M. Aoki, S. Fujiwara, and K. Omata for collaboration.

RESEARCH ARTICLE

Microfossils of the Early Archean Apex Chert: New Evidence of the Antiquity of Life

J. William Schopf

Eleven taxa (including eight heretofore undescribed species) of cellularly preserved filamentous microbes, among the oldest fossils known, have been discovered in a bedded chert unit of the Early Archean Apex Basalt of northwestern Western Australia. This prokaryotic assemblage establishes that trichomic cyanobacterium-like microorganisms were extant and morphologically diverse at least as early as ~3465 million years ago and suggests that oxygen-producing photoautotrophy may have already evolved by this early stage in biotic history.

When life originated and the rate of evolution and diversification of the early biota continue to be fascinating questions. Similarly, it is unclear when a physiologically modern ecosystem based on oxygen-producing photosynthesis became established. The sole source of direct evidence relevant to such questions is the paleobiologic record contained in rocks deposited during the Archean Eon of Earth history [>2500 million years ago (Ma)]. The search for Archean fossils, however, is fraught with difficulty: Few Archean sedimentary rocks have survived to the present, and paleobiologic evidence in most such units has been

severely altered by metamorphism (1). The most promising terrain for such studies is that of the Pilbara Block of northwestern Western Australia, a region underlain by a 30-km-thick sequence of relatively well-preserved sedimentary and volcanic rocks that are ~3000 to ~3500 million years old (Fig. 1). From this region, I describe a diverse assemblage of filamentous microbial fossils detected in the Early Archean (~3465 million years old) Apex chert, cellular prokaryotes more than 1300 million years older than any comparable suite of fossils previously reported from the geologic record. Microfossils were first discovered in this deposit in 1986 (2); in a preliminary account, three taxa were identified (3). The eight additional species described here demonstrate that the Early Archean biota was more diverse than previously known (3, 4), provide new

understanding of the evolutionary status of early evolving microorganisms, and suggest that cyanobacterial oxygen-producing photosynthesizers may have already been extant this early in Earth history.

The Archean fossil record. Unlike that of the later Precambrian Proterozoic (5), the fossil record of the Archean is minuscule; few fossils have been detected and their study has been plagued by misinterpretation and questionable results (4). In order to establish the authenticity of Archean microfossils, five principal criteria must be satisfied (3). The putative microfossils must (i) occur in rocks of known provenance and (ii) established Archean age; (iii) be demonstrably indigenous to and (iv) syngenetic with the primary deposition of the enclosing rock; and (v) be of assured biological origin. All but a few of the microfossil-like objects reported from Archean sediments have failed to meet one or more of these requirements (3, 4). Among recent such examples was the discovery of authentic microfossils in rocks evidently belonging to the Early Archean Warrawoona Group of Australia (6), a report unconfirmed because it has not proved possible to relocate the geologic source of the fossiliferous samples (3). Similarly, because of their simple morphology, solitary unicell-like spheroids reported from several Archean units (7, 8) are best considered to be possibly rather than assuredly biogenic (3, 4). Other than the filamentous Apex fossils discussed below, the relatively well-established Archean microfossil record consists of two types of cyanobacterium-like filaments from the ~2750-million-year-old Tumbiana Formation of Western Australia (4); sheath-enclosed colonial unicells occurring in ~3465-million-year-old sedimentary rocks of the Towers Formation, also of Western Australia (2); and narrow

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nonseptate bacterium-like filaments from ~3450-million-year-old units of the Swaziland Supergroup of South Africa (3, 8, 9). Although stromatolites (finely layered mound-shaped sedimentary structures produced by microbial communities) have been reported from more than 20 Archean geologic units (10), including the Tumbiana, Towers, and Swaziland deposits (11), their putative biological origin has been questioned (12).

Geologic setting. The microfossil assemblage that I describe is found in a sedimentary chert unit of the Apex Basalt, a 1.5- to 2.0-km-thick formation consisting of tholeiitic pillow lava, high-magnesium basalt, and komatiite interbedded with minor chert members that immediately overlies the Towers Formation in the lower third of the Lower Archean Pilbara Supergroup of northwestern Western Australia (Fig. 1) (13). Kerogens isolated from Towers Formation sediments have H/C ratios from 0.30 to 0.16 (Fig. 1) (14), consistent with mineralogic data indicating that these units have been metamorphosed to prehnite-pumpellyite and lower greenschist facies (1, 13). A maximum age for the Apex chert of ~3470 Ma is constrained by U-Pb zircon ages (3465 ± 3 Ma and 3471 ± 5 Ma) from the stratigraphically underlying Duffer Formation (Fig. 1) (15). A minimum age for the fossiliferous rocks of ~3460 Ma is provided by a U-Pb zircon date of 3458 ± 1.9 Ma for the immediately overlying Panorama Formation (Fig. 1) (15). Thus, the age of the fossiliferous Apex chert is evidently about 3465 Ma.

The Apex microfossils occur in bedded chert collected from outcrops near Chinaman Creek and ~12 km west of the town of Marble Bar (Fig. 2) in an area of Western Australia that has been geologically

mapped in detail (13). Studies of petrographic thin sections demonstrate that the three-dimensional fossils are cellularly per-

mineralized in subangular to rounded siliceous sedimentary clasts less than 1 mm to a few millimeters in diameter (Fig. 3, A and

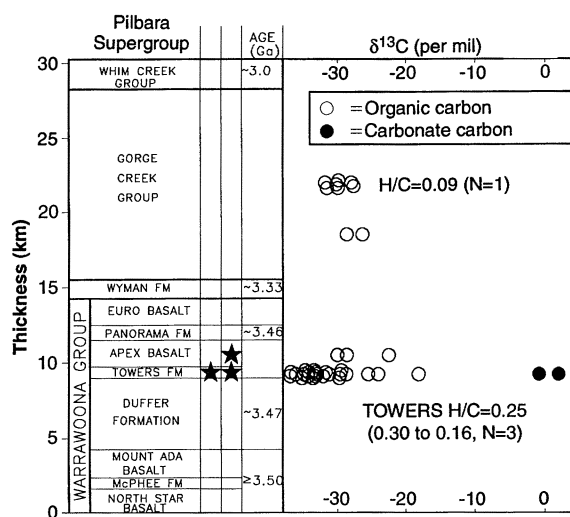


Fig. 1. Stratigraphic column (13, 15), distribution of reported stromatolites and microfossils (3), approximate ages (15, 40), and carbon isotopic data (14) for geologic units of the Pilbara Supergroup of northwestern Western Australia.

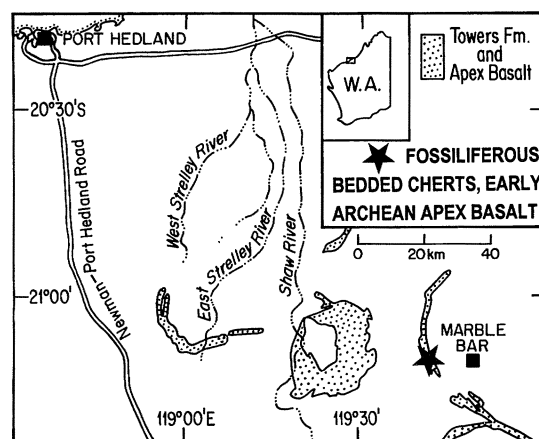


Fig. 2. Location in Western Australia of described fossiliferous locality.

Table 1. Morphological characteristics of microbial taxa from the Early Archean Apex chert. All measurements are in micrometers. *Arch.*, *Archaeotrichon*; *E.*, *Eoлектonema*; *P.*, *Primaevifilum*; *A.*, *Archaeosclatoropsis*. B, blunt-rounded; C, conical; D, disc; FL, flat; FR, flat-rounded; G,

globose; H, hemispheroidal; MAR, markedly; MOD, moderately; N, number measured; NOT, not at all; P, pillow-shaped; Q, quadrate; R, rounded; SC, short-cylinder; SL, slightly; SP, spheroidal; VMAR, very markedly; VSL, very slightly; and Avg., average.

Taxon	Medial cells					Terminal cells		Trichomes			
	N	Width		Length		Medial shape	Terminal shape	N	Attenuated toward apices	Constricted at septa	Maximum length
		Range	Avg.	Range	Avg.						
<i>Arch. septatum</i> , n. sp.	31	0.5 to 0.6	0.5	0.5 to 0.8	0.6	Q	R	2	NOT	NOT	34
<i>E. apex</i> , n. sp.	24	0.7 to 1.2	1.0	0.8 to 1.4	1.1	SP	FR/H	3	NOT	MOD	31
<i>P. minutum</i> , n. sp.	72	1.2 to 2.1	1.6	0.8 to 2.0	1.5	Q	FR	8	NOT	VSL/NOT	28
<i>P. delicatum</i> Schopf, 1992	673	1.8 to 3.2	2.5	0.7 to 2.2	1.5	D/SC	FL/FR	51	NOT	SL/NOT	46
<i>P. amoenum</i> Schopf, 1992	554	2.0 to 5.0	3.8	1.5 to 4.5	2.8	Q/D	H	47	MOD	MOD/NOT	89
<i>A. disciformis</i> , n. gen., n. sp.	123	3.0 to 5.5	4.2	0.8 to 2.2	1.5	D	H/G	12	SL/MOD	MOD/MAR	39
<i>P. conicoterminatum</i> Schopf, 1992	188	4.0 to 6.0	5.0	1.4 to 3.2	2.2	D/SC	B/C	29	SL/MOD	SL/MOD	72
<i>P. laticellulosum</i> , n. sp.	122	6.0 to 8.5	7.0	2.5 to 5.0	3.5	SC/Q	P	13	SL/NOT	SL/NOT	82
<i>A. grandis</i> , n. gen., n. sp.	26	8.0 to 11.5	9.0	1.0 to 3.5	2.0	D	FR/H	2	NOT	NOT	45
<i>P. attenuatum</i> , n. sp.	49	4.0 to 12.0	7.5	1.0 to 4.0	3.0	D	FR	5	VMAR	SL/MOD	35
<i>A. maxima</i> , n. gen., n. sp.	15	15.0 to 19.5	16.5	3.0 to 6.0	4.5	D	FR/H	2	NOT	NOT	69

B). These small fossiliferous clasts make up ~5 percent of the rock and are distinguishable from other clastic components by their fine-grained relatively homogeneous texture and their grayish brown to dark brown color. The remainder of the bedded chert is composed of similarly rounded unfossiliferous clasts and lithic fragments, less than 1 mm to more than 20 cm in size, and of siliceous matrix. Laterally, over a distance of less than 100 m from the fossiliferous locality, the fossiliferous bed merges into a continuous brecciated gray chert unit, 20 to 30 m thick, that is concordant and interfingering with associated volcanic rocks. The variety and textures of the detrital clasts, the occurrence of cross-bedding in parts of the outcrop, and the stratigraphic relations to adjacent units demonstrate that the fossiliferous chert is a primary sedimentary deposit and not of secondary diagenetic or intrusive origin. The fossils are from samples collected on two occasions: in June 1982 (Fig. 3, A to N; Fig. 4, A to D and F to H; and Fig. 5, A, B, E to G, and K and L) and in August, 1986 (Fig. 3O; Fig. 4, E, I, and J; and Fig. 5, C, D, and H to J).

Paleobiology. The Apex filaments meet all criteria required of bona fide Archean microfossils. (i) Their occurrence in rocks of known provenance has been substantiated by replicate sampling of the fossiliferous locality. (ii) As summarized above, the stratigraphic relations and Early Archean (~3465 Ma) age of the fossiliferous cherts are well documented. (iii) The kerogenous [and iron-stained (Fig. 3L and Fig. 5, D to F)] fossils are encased within and unquestionably indigenous to the Apex chert, as demonstrated by their occurrence in petrographic thin sections (Figs. 3 to 5). (iv) They are localized in organic-rich clasts (Fig. 3B) shown by petrographic relations [for example, cross-cutting veinlets that transect both the clasts and their encompassing matrix; figure 1.5.4A in (3)] to be primary components of the sedimentary chert unit, assuredly syngenetic with its deposition. (v) As discussed below, their evident cellular organization, and their morphological complexity and similarity to younger prokaryotes, both fossil and modern, firmly establish their biogenicity.

The presence of these microfossils in a petrographically distinctive population of clasts and their absence from all other clasts and the surrounding matrix (Fig. 3, A and B) indicate that the filaments predate deposition of the chert unit and were initially preserved in older rocks, some part of which was eroded, transported, and redeposited as a detrital component of the bedded chert. Whether the microfossils are greatly older than or essentially penecontemporaneous with deposition of the Apex chert is unknown.

Eleven taxa (Table 1) of filamentous, dark brown to black carbonaceous microfossils, including eight new species (see appendix), have been identified in the deposit. Solitary unicell-like spheroids of possible but uncertain biological origin also occur (Fig. 5, K and L). The assured fossils occur as irregularly distributed and randomly oriented solitary filaments (Fig. 3B) surrounded by more or less homogeneous brown to dark brown kerogen. The kerogen is flocculent and composed of very fine (<0.3 μm) particles, which might originally have been mucilaginous. Single taxa (especially, *Primaevifilum minutum*, n. sp.; *P. laticellulosum*, n. sp.; and *P. attenuatum*, n. sp.) or particular pairs or groups of taxa (for example, *P. delicatulum* and *Archaeosclatorioropsis disciformis*, n. gen., n. sp.; or *P. delicatulum*, *P. amoenum*, and *P. conicoterminatum*) tend to predominate in individual clasts. Although possibly representing a benthic microbial community that was loosely orga-

nized and embedded in mucilage, the filaments exhibit neither the subparallel orientation nor the laminar organization typical of most stromatolitic microbiotas (16). Microfossils have not been detected in stromatolite-like laminated clasts that also occur in the unit (Fig. 3C).

In comparison with permineralized microbiotas from the later Precambrian (16), the Apex assemblage is highly carbonized and poorly preserved. Of the thousands of fragments of cellular filaments detected in the deposit (by examination of a total area of ~450 cm^2 of 150- μm -thick petrographic thin sections), less than 1 percent are sufficiently preserved to warrant detailed study and formal description. Such alteration makes taxonomic delineation difficult. However, like modern filamentous microbes (17, 18), members of discrete size classes of relatively well-preserved Apex filaments exhibit taxonomically useful limited ranges of consistently co-occurring ter-

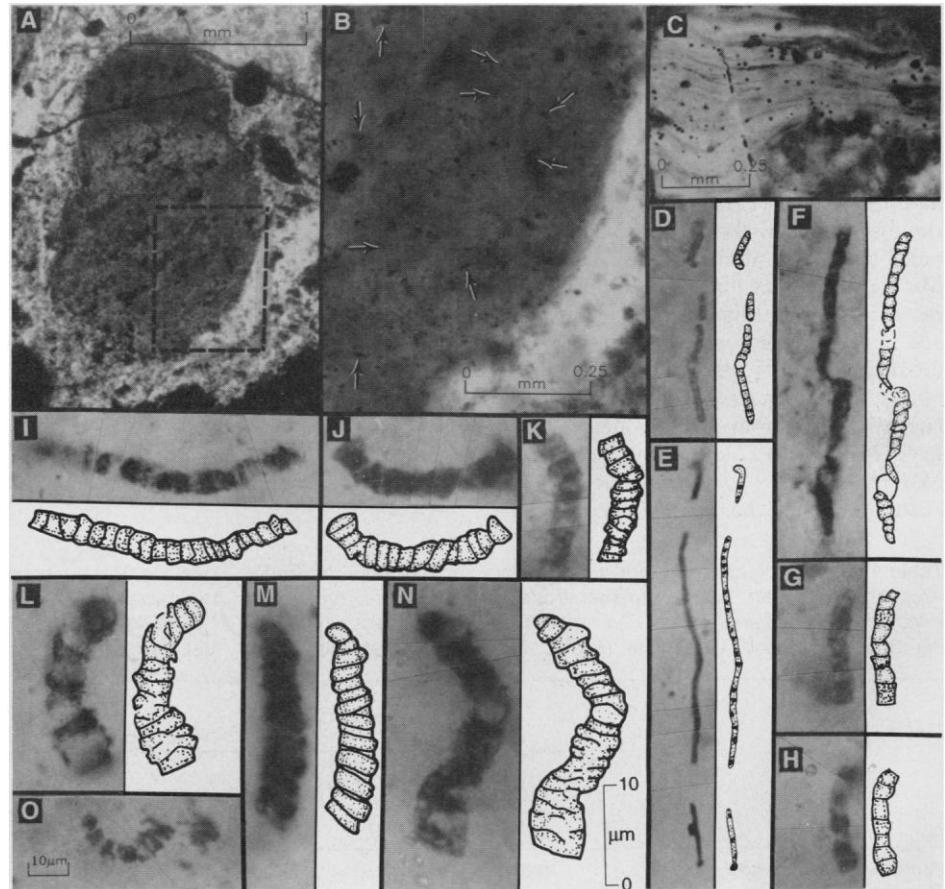


Fig. 3. Microfossiliferous (A and B) and laminated stromatolite-like clasts (C), and carbonaceous and iron-stained (L) microfossils (with interpretive drawings) shown in thin sections of the Early Archean Apex chert of Western Australia. Except as otherwise indicated, magnification of all parts denoted by scale in (N). (D to K) and (N and O) show photomontages of the sinuous three-dimensional microfossils. (A) Microfossiliferous clast; area denoted by dashed lines shown in (B). (B) Arrows point to minute filamentous microfossils, randomly oriented in the clast. (C) Portion of a clast showing stromatolite-like laminae. (D and E) *Archaeotrichion septatum*, n. sp. (D, holotype). (F) *Eoleptonema apex*, n. sp. (holotype). (G and H) *Primaevifilum minutum*, n. sp. (G, holotype). (I, J, and K) *Primaevifilum delicatulum* Schopf, 1992 (I, holotype) (3). (L, M, N, and O) *Archaeosclatorioropsis disciformis*, n. gen., n. sp. (M, holotype).

minimal cell shapes, medial cell shapes and dimensions, and degrees of trichomic attenuation (for example, compare Fig. 3, L to N; Fig. 4, F to H; and Fig. 5, A to C). These characteristics, and the similarity of the delimited size classes (Table 1) to the size ranges of modern microbial taxa (17, 18), make it unlikely that any of the described species represent variants of other members of the assemblage. Indeed, as is documented for younger Precambrian microbiotas (19), the incomplete preservation of the Apex fossils suggests that the original assemblage probably included more taxa than the 11 species identified.

The evolutionary relations of these microfossils to younger fossils and modern microorganisms are of interest. As currently documented, the fossil record is more or less continuous and relatively well known from about 2100 Ma to the present, beginning with the diverse microbiotas of the ~2100-million-year-old Belcher Group (20) and

the ~2080-million-year-old Gunflint Iron Formation (21), both of Canada. But the fossil record from the greater than 1300 million years intervening between these deposits and the Apex chert is essentially undeciphered (5, 22). Although there is thus a profound gap in the record, the morphological similarity of the Apex fossils to septate filamentous prokaryotes, both Proterozoic (16) and modern (17, 18), indicates that they are almost certainly prokaryotes and part of an evolutionary continuum that extends from the Early Archean to the present. This interpretation seems supported by the occurrence in Apex filaments of bifurcated cells and cell pairs [Fig. 5, H to J; figure 1.5.6, F and G, in (3)] that evidently reflect the original presence of partial septations and, thus, of cell division like that occurring in extant prokaryotic filaments (3).

In comparison with modern prokaryotes, most of the Apex microbes particularly

resemble trichomic (nonensheathed or thinly ensheathed) oscillatoriacean cyanobacteria. Cell widths of the Apex taxa range from 0.5 μm (Fig. 3, D and E) to 19.5 μm (Fig. 5F) and average ~5.0 μm (Table 1). Modern filamentous bacteria tend to be quite narrow, predominantly <1.5 μm in diameter, whereas most oscillatoriacean trichomes are notably broader (Fig. 6). On the basis of morphometric analyses of more than 500 taxa of modern filamentous microbes, I have suggested that fossil septate filaments <1.5 μm wide be regarded as "probable bacteria," those 1.5 μm to 3.5 μm wide as (undifferentiated) "prokaryotes," and those >3.5 μm broad as "probable cyanobacteria" (23). Applying these criteria to the Apex fossils, I interpret two taxa (*Archaeotrichion septatum*, n. sp., and *Eoleptonema apex*, n. sp.) as probable bacteria; two taxa (*Primaevifilum minutum*, n. sp., and *P. delicatulum*) as either bacteria or cyanobacteria; and the remaining seven species, nearly two-thirds of the taxa (and ~63 percent of measured specimens) as probable cyanobacteria.

Because the size ranges of filamentous bacteria and cyanobacteria overlap (Fig. 6), the suggested affinities are not absolute. Nevertheless, the pattern of size distribution exhibited by the Apex assemblage is more like that of modern oscillatoriaceans than of noncyanobacterial prokaryotes (Fig. 6). Furthermore, several of the Apex taxa, particularly those with broad trichomes (*Primaevifilum laticellulosum*, n. sp.; *Archaeooscillatoriopsis grandis*, n. gen., n. sp.; and *A. maxima*, n. gen., n. sp.), differ in cell size from almost all bacteria but are essentially indistinguishable from specific oscillatoriaceans, both Proterozoic (*Oscillatoriopsis* spp.) and modern (*Oscillatoria* spp.). If the Apex filaments had been discovered in later Precambrian sediments, in which fossil oscillatoriaceans are well known and relatively widespread (23), or if they had been detected in a modern microbial community and morphology were the only criterion by which to infer biological relationships, the majority would be interpreted as oscillatoriacean cyanobacteria. However, because the affinities of these fossils in the Prokaryota cannot be demonstrated unequivocally, I formally describe them as "prokaryotes *Incertae Sedis*"; and because the phylogenetic relations between them and the much (1300 to 2800 million years) younger, predominantly cyanobacterial fossil taxa to which they bear specific resemblance are therefore undetermined, they have not been referred to previously described Proterozoic species (see appendix).

Evolutionary implications. The range of morphologies exhibited by the Apex filaments indicates that if the majority are oscillatoriaceans, this primitive family of

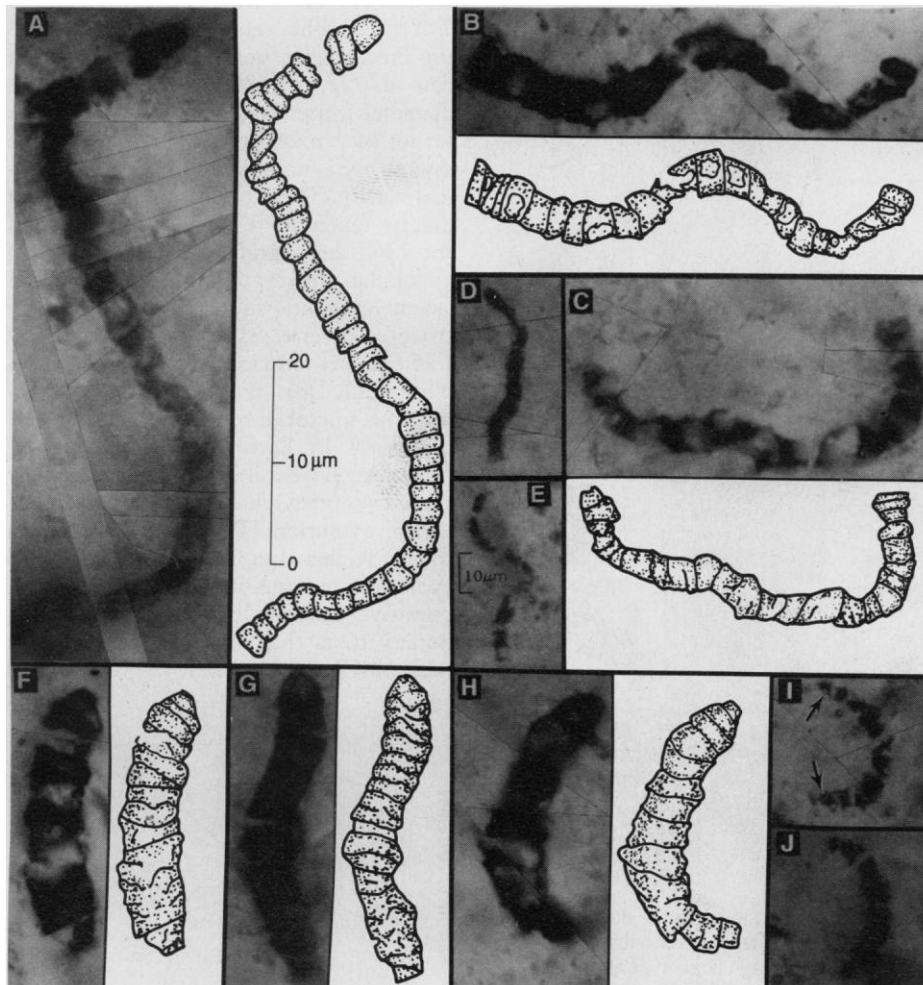


Fig. 4. Carbonaceous microfossils (with interpretive drawings) shown in thin sections of the Early Archean Apex chert of Western Australia. Magnification of (D, E, I, and J) denoted by scale in (E); magnification of all other parts shown by scale in (A). (A, B, C, and D) and (F, G, H, and I) show photomontages of the sinuous three-dimensional microfossils. (A, B, C, D, and E) *Primaevifilum amoenum* Schopf, 1992 (A, holotype) (3). (F, G, H, I, and J) *P. conicoterminatum* Schopf, 1992 (H, holotype) (3); arrows in (I) point to conical terminal cells.

filamentous cyanobacteria was already highly diverse at Apex time. Although some cyanobacteria are capable of temporarily carrying out anoxic (bacterial) photosynthesis (24), oxygen-producing photoautotrophy is a universal, presumably early-evolving characteristic of the group. The presence of diverse oscillatoriaceans in the Apex assemblage would thus seem to imply that this relatively advanced level of physiological evolution had been attained at least as early as ~3465 Ma.

Four other lines of evidence seem consistent with the possible Early Archean existence of O₂-producing oscillatoriaceans: (i) Early Archean stromatolites (10) were presumably produced by photoautotroph-dominated microbial communities.

(ii) The reactants required for oxygenic photosynthesis, CO₂ and H₂O, and materials possibly representing products of this process, sedimentary organic matter and oxidized iron minerals, were present in the Early Archean environment (3). (iii) The isotopic compositions of Early Archean organic and carbonate carbon (for example, Fig. 1) are evidently indicative of photosynthetic CO₂-fixation like that occurring at relatively high CO₂ concentrations in extant microbial populations (25). (iv) Calculations based on models of the early global ecosystem, and cerium and europium concentrations in Archean banded ironformations, suggest that O₂-producing photosynthesis and aerobic respiration both date from the Early Archean (26). These

additional lines of evidence, however, are not conclusive; all but the latter, which necessarily incorporates model-dependent uncertainties, would be equally consistent with the presence of solely anoxic bacterial photosynthesizers (3). Moreover, it is conceivable that the external similarity of the Apex microorganisms to younger oxygen-producing oscillatoriaceans masks significant differences of internal biochemical machinery (27); thus, their morphology may provide a weak basis on which to infer paleophysiology. To address this issue, additional data are needed regarding the ecology and community structure of the Apex assemblage and the evolutionary relations that link these prokaryotes to the later, relatively well-documented Precambrian fossil record.

Whether or not O₂-producing photoautotrophs are represented among the Apex fossils, the morphological diversity of the assemblage is striking. In particular, the Apex filaments exhibit a greater range of diameters than those reported from all but 7 of the 70 other septate filament-containing Precambrian units known [Fig. 7 and data in (22, 23, 28)]. Because filament diameter is a principal taxonomic character for such microorganisms (17, 18), the assemblage is notable also for its taxonomic diversity. The Apex assemblage is more diverse taxonomically than 92 percent of the 126 other septate filament-containing or tubular sheath-containing Precambrian assemblages known, and is more than twice as diverse as the average diversity (~5 taxa per formation) of all such assemblages (22, 28). Evidently, cellular filamentous microbes originated and diversified early in Earth's history and have subsequently exhibited an exceedingly slow, hypobryadetic (27) rate of morphological evolution. The Apex microfossils thus provide a glimpse of the diversity and evolutionary status of Early Archean life, a primitive microbial biota having evolutionary roots that must predate, perhaps substantially, ~3465 Ma.

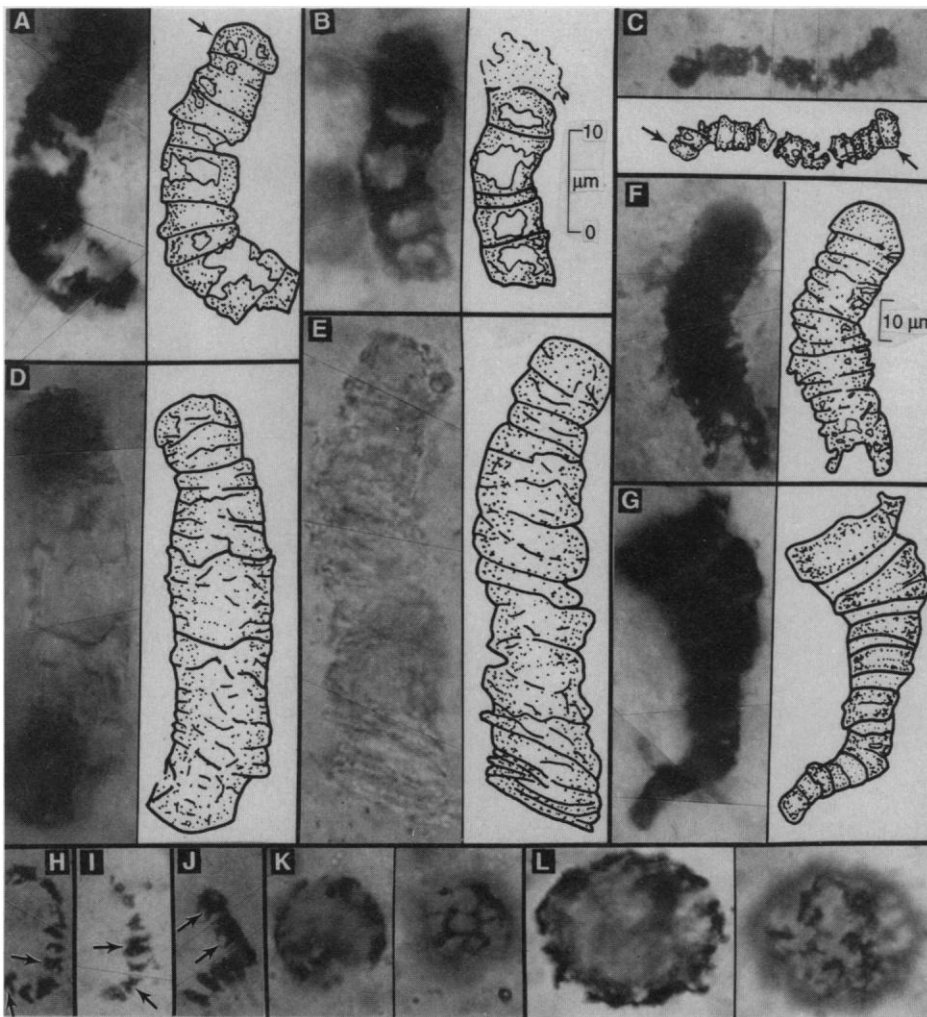


Fig. 5. Carbonaceous and iron-stained (D, E, and F) microfossils (with interpretive drawings) and possible microfossils (K and L) shown in thin sections of the Early Archean Apex chert of Western Australia. Magnification of (C, F, H, I, and J) denoted by scale in (F); magnification of all other parts shown by scale in (B). (A to J) show photomontages of the sinuous three-dimensional microfossils. (A, B, and C) *Primaevifilum laticellulosum*, n. sp. (A, holotype); pillow-shaped terminal cells are indicated by arrows in (A) and (C). (D and E) *Archaeosclerotriopsis grandis*, n. gen., n. sp. (D, holotype). (F) *Archaeosclerotriopsis maxima*, n. gen., n. sp. (holotype). (G) *Primaevifilum attenuatum*, n. sp. (holotype). (H, I, and J) Poorly preserved trichomes showing bifurcated cells and cell pairs (at arrows). (K and L) Solitary unicell-like possible microfossils, in equatorial (left) and polar views (right).

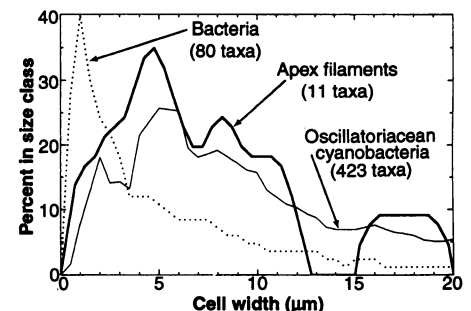
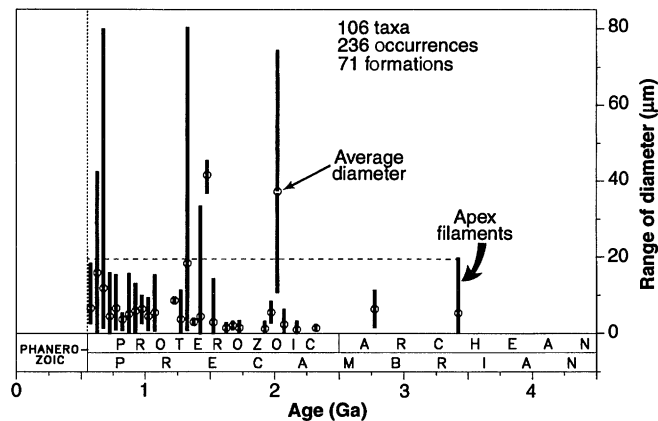


Fig. 6. Cell widths of modern septate filamentous bacteria and oscillatoriacean cyanobacteria <20 μm in diameter (23) compared with those of taxa from the Apex chert (Table 1).

Fig. 7. Range and average diameters of septate prokaryotic filaments reported from Precambrian sediments, grouped in 50-million-year-long intervals based on estimated formation ages (22, 23, 28). The ~3465-million-year-old Apex chert contains broader filaments than those known from 22 of the 28 younger intervals (dashed line); Ga, billion years ago.



Appendix: Systematic Paleontology

Type locality. [Schopf collection 4 of 6/15/82 and Precambrian Paleobiology Research Group collections 1458, 2006, and 2644 (29).] Outcrops of bedded chert from the Apex Basalt (Warraoona Group, Pilbara Supergroup) on a hill immediately south of Chinaman Creek and ~12 km west of Marble Bar, Western Australia (Fig. 2), at grid reference number 799558 on the Marble Bar 1:100,000 Australian National Topographic Map No. 2855, and at 21°11'4" S and 119°42'36" E in Archean map unit "Acj" of the Marble Bar structural belt on the Geological Survey of Western Australia 1:250,000 Marble Bar Geological Map Sheet SF 50-8.

Repository and stage coordinates of figured specimens. (Acquisition numbers for specimens deposited in the permanent collections of The Natural History Museum, Cromwell Road, London SW7 5BD, microscope stage coordinates on Leitz Orthoplan 2 automatic photomicroscope UCLA No. 874-002635 and, in parentheses, England Finder Slide coordinates.) **1982 Collections:** Schopf collection 4 of 6/15/82. Rock specimen 4 of 6/15/82-1; petrographic thin section number 4 of 6/15/82-1B (slide label right) with diamond scribed "X" at front left, stage coordinates 64.4/137.9 (England Finder Slide file 11, row off slide): **Fig. 3K**, Natural History Museum No. V.63164[4], 25.2/118.4 (file 52, row off slide); **Fig. 4B**, V.63164[6], 25.4/120.1 (file 52, row off slide); **Fig. 4C**, V.63164[9], 13.1/105.9 (P64/4); **Fig. 4H**, V.63164[1], 23.9/118.9 (file 53, row off slide); **Fig. 5A**, V.63164[10], 24.0/118.6 (file 53, row off slide); **Fig. 5B**, V.63164[11], 38.8/103.7 (N38/circle); **Fig. 5F**, V.63164[12], 46.1/131.6 (file 30, row off slide). Section -1C (label right) with "X" at front left, 66.6/138.8 (file 9, row off slide): **Fig. 4F**, V.63727[1], 68.0/131.8 (file 9, row off slide); **Fig. 5G**, V.63727[2], 32.0/103.5 (N45/1). Section -1D (label right) with "X" at front left, 64.9/130.0 (file 11, row off slide): **Figs. 3A, B**, V.63165[5], 65.0/97.0 (F11/circle); **Fig. 3H**, V.63165[6], 65.1/97.3 (F11/3); **Fig. 3I**, V.63165[2], 30.2/111.9 (U47/3); **Fig. 3J**, V.63165[7], 65.1/97.9 (G11/1); **Fig. 3N**, V.63165[8], 31.9/112.5 (W45/circle); **Fig. 5K**, V.63165[9], 31.9/112.6 (W45/circle). Section -1E (label right) with "X" at front left, 61.9/139.2 (file 14, row off slide): **Fig. 3L**, V.63728[1], 04.1/108.6 (S74/circle); **Fig. 4C**, V.63728[2], 35.0/123.2 (file 42, row off slide). Section -1F (label left) with "X" at front left, 73.3/137.7 (file 2, row off slide); **Fig. 3D**, V.63166[3], 45.0/97.3 (F32/3); **Fig. 4A**, V.63166[1], 68.3/115.1 (Z8/1). Section -1G (label left) with "X" at front left, 72.1/137.0 (file 4, row off slide): **Fig. 3F**, V.63729[1], 52.3/113.0 (W24/3); **Fig. 3G**, V.63729[2], 53.4/113.9 (X23/3). PPRG collection 1458. Specimen 1458-4; section 1458-4A (label right) with "X" at front left, 70.1/123.8 (file 6, row off slide):

Fig. 3M, V.63730[1], 57.5/112.4 (W19/1). PPRG collection 2644. Specimen 2644-2; section 2644-2B (label right) with "X" at front left, 68.1/123.6 (file 8, row off slide): **Fig. 3C**, V.63731[1], 51.5/102.3 (L25/3); section -2C (label right) with "X" at front left, 69.7/123.6 (file 7, row off slide): **Fig. 3E**, V.63732[1], 50.0/108.3 (S26/2); **Fig. 5L**, V.63732[2], 35.3/116.6 (file 42, row off slide). Specimen 2644-4; section -4C (label left) with "X" at front left, 58.1/112.1 (W18/2): **Fig. 4D**, V.63733[1], 20.3/99.5 (J57/2); **Fig. 5E**, V.63733[2], 19.9/96.2 (E57/2). **1986 Collections:** PPRG collection 2006. Specimen 2006-1; section 2006-1A (label right) with "X" at front left, 71.5/135.4 (file 4, row off slide): **Fig. 4E**, V.63734[1], 58.0/118.3 (file 18, row off slide); **Fig. 4J**, V.63734[2], 53.5/120.4 (file 23, row off slide); **Fig. 5H**, V.63734[3], 47.8/121.4 (file 29, row off slide). Specimen 2006-2; section -2A (label right) with "X" at front left, 69.1/134.9 (file 7, row off slide): **Fig. 3O**, V.63735[1], 40.0/113.4 (X37/1); **Fig. 5I**, V.63735[2], 38.3/110.5 (U38/2); **Fig. 5J**, V.63735[3], 43.0/105.7 (P34/1). Specimen 2006-3; section -3A (label right) with "X" at front left, 71.2/135.9 (file 6, row off slide): **Fig. 4I**, V.63736[1], 40.9/111.8 (V36/3); section -3B (label left) with "X" at front left, 68.3/133.9 (file 8, row off slide): **Fig. 5D**, V.63737[1], 27.4/115.7 (Z50/3); section -3C (label right) with "X" at front left, 67.4/132.4 (file 8, row off slide): **Fig. 5C**, V.63738[1], 28.3/97.1 (F49/circle). Thin sections containing topotypes of Apex taxa have also been deposited in the permanent collections of the Western Australian Museum, Perth, Australia.

Description of new taxa

Kingdom Procaryotae Murray 1968, Incertae Sedis.

Genus Archaeotrichion Schopf, 1968 (30).

Type species: *Archaeotrichion contortum* Schopf, 1968 (30).

***Archaeotrichion septatum*, n. sp.** (Fig. 3, D and E; Table 1)

Diagnosis: Uniseriate unbranched trichomes, possibly enclosed by a thin sheath, having the characteristics specified in Table 1. **Etymology:** With reference to cellularity (for example, Fig. 3D). **Type specimen:** Trichome in Fig. 3D. **Remarks:** The type species (*A. contortum*), first described from the ~850-million-year-old Bitter Springs Formation of central Australia (30), was established to include nonseptate threadlike filaments 0.5 to 0.7 µm in diameter. Although identical in diameter, well-preserved specimens of *A. septatum* are cellular (Fig. 3D).

Genus Eoleptonema Schopf, 1983 (6).

Type species: *Eoleptonema australicum* Schopf, 1983 (6).

***Eoleptonema apex*, n. sp.** (Fig. 3F; Table 1).

Diagnosis: Uniseriate unbranched trichomes, apparently not ensheathed, having the characteristics specified in Table 1. **Etymology:** With reference to occurrence in the Apex chert. **Type specimen:** Trichome in Fig. 3F. **Remarks:** *E. apex* is morphologically comparable to unnamed narrow cellular filaments reported from the ~1425-million-year-old Gaoyuzhuang Formation of China (31) and the ~1050-million-year-old Allamoore Formation of Texas (32), and to the modern bacterium *Beggiatoa minima* [(17), p. 114].

Genus Primaevifilum Schopf, 1983 (6).

Type species: *Primaevifilum septatum* Schopf, 1983 (6).

***Primaevifilum minutum*, n. sp.** (Fig. 3, G and H; Table 1).

Diagnosis: Uniseriate unbranched trichomes, apparently not ensheathed, having the characteristics specified in Table 1. **Etymology:** With reference to small diameter in comparison with other species of *Primaevifilum*. **Type specimen:** Trichome in Fig. 3G. **Remarks:** *P. minutum* is morphologically comparable to unnamed narrow septate filaments reported from the ~2080-million-year-old Gunflint Iron Formation of Canada (33) and the ~1025-million-year-old Valuykhata Formation of Siberia (34).

***Primaevifilum laticellulosum*, n. sp.** (Fig. 5, A to C; Table 1).

Diagnosis: Uniseriate unbranched trichomes, apparently not ensheathed, having the characteristics specified in Table 1. **Etymology:** With reference to large diameter in comparison with other species of *Primaevifilum*. **Type specimen:** Trichome in Fig. 5A. **Remarks:** *P. laticellulosum* is similar in medial cell size and shape to an unnamed oscillatoriacean-type trichome reported from the ~1500-million-year-old Barney Creek Formation of Australia (35) and to the modern cyanobacterium *Oscillatoria tenuis* [(18), p. 223], but differs from these by having pillow-shaped terminal cells (Fig. 5, A to C).

***Primaevifilum attenuatum*, n. sp.** (Fig. 5G; Table 1).

Diagnosis: Uniseriate unbranched trichomes, apparently not ensheathed, having the characteristics specified in Table 1. **Etymology:** With reference to marked attenuation of the trichome. **Type specimen:** Trichome in Fig. 5G. **Remarks:** *P. attenuatum*, croissant-shaped in complete specimens, differs from previously reported filamentous microfossils by the marked attenuation of its trichomes.

Genus Archaeosclatorioopsis, n. gen.

Type species: *Archaeosclatorioopsis disciformis*, n. gen., n. sp.

Diagnosis: Trichomes uniseriate, unbranched, cylindrical or slightly to moderately tapered toward apices, not at all to moderately or markedly constricted at septa, apparently not ensheathed, and commonly slightly to moderately bent or disrupted; medial cells disc-shaped, ranging from 3.0 to 19.5 µm wide and from 0.8 to 6.0 µm long; terminal cells flat-rounded, hemispheroidal, or globose. **Etymology:** With reference to Archean age and morphological similarity to fossil (*Oscillatorioopsis* spp.) and modern (*Oscillatoria* spp.) oscillatoriaceans.

***Archaeosclatorioopsis disciformis*, n. gen., n. sp.** (Fig. 3, L to O; Table 1).

Diagnosis: As for the genus, having the characteristics specified in Table 1. **Etymology:** With reference to disc-shaped medial cells. **Type specimen:** Trichome in Fig. 3M. **Remarks:** *A. disciformis* is morphologically comparable to specimens of *Gunflintia grandis* reported from the ~1950-million-year-old Tyler Formation of Michigan (36) and to the modern cyanobacterium *Oscillatoria grunowiana* [(18), p. 216].

***Archaeosclatorioopsis grandis*, n. gen., n. sp.**

(Fig. 5, D and E; Table 1).

Diagnosis: As for the genus, having the characteristics specified in Table 1. **Etymology:** With reference to large diameter in comparison with most other taxa of *Archaeosclerotriopsis*. **Type specimen:** Trichome in Fig. 5D. **Remarks:** *A. grandis* is morphologically comparable to *Oscillatoriopsis media* described from the ~1250-million-year-old Sukhaya Tunguska Formation of Siberia (37) and reported from the ~900-million-year-old Deoban Limestone of India (38), and to the modern cyanobacterium *Oscillatoria chalybea* [(18), p. 219].

Archaeosclerotriopsis maxima, n. gen., n. sp. (Fig. 5F; Table 1).

Diagnosis: As for the genus, having the characteristics specified in Table 1. **Etymology:** With reference to very large diameter in comparison with all other taxa of *Archaeosclerotriopsis*. **Type specimen:** Trichome in Fig. 5F. **Remarks:** *A. maxima* is morphologically comparable to unnamed broad oscillatoriacean trichomes reported from the ~650-million-year-old Chichkan Formation of Kazakhstan (39) and to the modern cyanobacterium *Oscillatoria antillarum* [(18), p. 242].

REFERENCES AND NOTES

1. J. M. Hayes, I. R. Kaplan, K. W. Wedeking, in *Earth's Earliest Biosphere*, J. W. Schopf, Ed. (Princeton Univ. Press, New Jersey, 1983), pp. 93–134.
2. J. W. Schopf and B. M. Packer, *Abstr. 5th Meet. Int. Soc. Study Origin Life*, 163 (1986); *Science* **237**, 70 (1987).
3. J. W. Schopf, in *The Proterozoic Biosphere*, J. W. Schopf and C. Klein, Eds. (Cambridge Univ. Press, New York, 1992), pp. 25–39.
4. _____ and M. R. Walter, in (1), pp. 214–239.
5. J. W. Schopf, in (3), pp. 179–183.
6. S. M. Awramik, J. W. Schopf, M. R. Walter, *Precambrian Res.* **20**, 357 (1983).
7. H. D. Pflug, *Univ. Witwatersrand Econ. Geol. Res. Unit Info. Circ.* **28** (University of the Witwatersrand, Johannesburg, South Africa, 1966), pp. 1–14; _____ and E. Reitz, in *Early Organic Evolution*, M. Schidlowski, S. Golubic, M. M. Kimberly, D. M. McKirdy, P. A. Trudinger, Eds. (Springer-Verlag, Berlin, 1992), pp. 509–518; E. S. Barghoorn and J. W. Schopf, *Science* **152**, 758 (1966); M. D. Muir and P. R. Grant, in *The Early History of the Earth* (Wiley, London, 1976), pp. 595–604; A. H. Knoll and E. S. Barghoorn, *Science* **198**, 396 (1977).
8. M. M. Walsh, *Precambrian Res.* **54**, 271 (1992).
9. _____ and D. R. Lowe, *Nature* **314**, 530 (1985).
10. M. R. Walter, in (1), pp. 187–213; H. J. Hofmann, R. P. Sage, E. N. Berdusco, *Econ. Geol.* **86**, 1023 (1991).
11. G. R. Byerly, D. R. Lowe, M. M. Walsh, *Nature* **319**, 489 (1986); M. R. Walter, R. Buick, J. S. R. Dunlop, *ibid.* **284**, 443 (1980); D. R. Lowe, *ibid.* **284**, 441 (1980).
12. R. Buick, J. S. R. Dunlop, D. I. Groves, *Alcheringa* **5**, 161 (1981); R. Buick, *Palaio* **5**, 441 (1991).
13. A. H. Hickman, *W. Aust. Geol. Surv. Bull.* **127**, 1 (1983); _____ and S. L. Lipple, *Explanatory Notes Marble Bar 1:250,000 Geological Map Series* (Western Australia Geological Survey, Perth, 1978), pp. 1–24.
14. H. Strauss and T. B. Moore, in (3), pp. 709–798.
15. R. I. Thorpe, A. H. Hickman, D. W. Davis, J. K. Mortensen, A. F. Trendall, *Precambrian Res.* **56**, 169 (1992).
16. M. R. Walter, J. P. Grotzinger, J. W. Schopf, in (3), pp. 253–260; J. W. Schopf, in *ibid.*, pp. 1055–1117.
17. R. E. Buchanan and M. E. Gibbons, *Bergey's Manual of Determinative Bacteriology* (Williams & Wilkins, ed. 8, Baltimore, 1974).
18. T. V. Desikachary, *Cyanophyta* (Indian Council Agricultural Research, New Delhi, 1959).
19. A. H. Knoll, S. Rossi, P. K. Strother, *Precambrian Res.* **38**, 257 (1988).
20. H. J. Hofmann, *J. Paleontol.* **50**, 1040 (1976).
21. E. S. Barghoorn and S. A. Tyler, *Science* **147**, 563 (1965).
22. C. V. Mendelson and J. W. Schopf, in (3), pp. 865–951.
23. J. W. Schopf, in *ibid.*, pp. 195–218.
24. D. M. Ward, J. Bauld, R. W. Castenholz, B. K. Pierson, in *ibid.*, pp. 309–324.
25. J. W. Schopf, in *Early Life on Earth*, S. Bengtson, Ed. (Columbia Univ. Press, New York, in press).
26. K. M. Towe, *Nature* **348**, 54 (1990); *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **97**, 113 (1991).
27. J. W. Schopf, in (3), pp. 583–600.
28. _____, in *ibid.*, pp. 1119–1166.
29. T. B. Moore and J. W. Schopf, in *ibid.*, pp. 603–693.
30. J. W. Schopf, *J. Paleontol.* **42**, 651 (1968).
31. _____, W. Q. Zhu, Z. L. Xu, J. Hsu, *Precambrian Res.* **24**, 335 (1984).
32. A. V. Nyberg and J. W. Schopf, *ibid.* **16**, 129 (1981).
33. P. E. Cloud, Jr., *Science* **148**, 27 (1965).
34. J. W. Schopf et al., *Precambrian Res.* **4**, 269 (1977).
35. J. H. Oehler, *Alcheringa* **1**, 315 (1977).
36. P. Cloud and K. Morrison, *Geomicrobiol. J.* **2**, 161 (1980).
37. C. V. Mendelson and J. W. Schopf, *J. Paleontol.* **56**, 42 (1982).
38. M. Shukla, V. C. Tewari, V. K. Yadav, *Palaeobotanist* **35**, 347 (1986).
39. J. W. Schopf and Yu. K. Sovietov, *Science* **193**, 143 (1976).
40. T. S. Blake and N. J. McNaughton, in *Archean and Proterozoic Basins of the Pilbara, Western Australia: Solution and Mineralization Potential*, J. R. Muhling, D. I. Groves, T. S. Blake, Eds. (*Publ. 9*, Univ. W. Aust. Geol. Dept. and Univ. Extension, Perth, 1984), pp. 1–22.
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