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Significance of the Gunflint (Precambrian) Microflora

Photosynthetic oxygen may have had important local effects before becoming a major atmospheric gas.

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The Precambrian, comprising rocks older than about 600 million years and representing by far the greater part of earth history, has so far revealed few structures that are acceptable to the determined skeptic as evidences of life. It is important, therefore, to establish beyond reasonable doubt such records as are firmly demonstrable, both as grounds for considering less convincing but probably valid records and in order to contemplate the bearing of such evidence on questions of larger import. The biota here discussed has been under study for some years by E. S. Barghoorn and the late Stanley Tyler and has been described in detail by them (*1*). For that reason no systematic names are here applied to individual forms, but some of the distinctive fossils and associations are illustrated and possible affinities are briefly considered, primarily as a basis for the reflections that follow.

Like many paleontologists, I personally accept as probably valid records of primordial life, and probably of photosynthetic life at that, many of the stromatolitic structures found in various limestones and dolomites of Precambrian age. But we must admit that such evidence is from gross analogy only and is accepted mainly by those who have some predisposition to accept it. Judgments of this nature would carry more conviction if we could demonstrate at least a few instances of unequivocal biologic remains in the older sediments.

Now, in considering what we may accept as unequivocal Precambrian fossils, the crucial point is not whether materials observed might conceivably be of vital origin, but whether they could have been produced by nonvital processes; and, if not, whether they are surely endemic to authentic Precambrian rocks. Such hard-headed evaluation is necessary, here as in the problem of exobiology, and particularly in the present state of knowledge, if we are to treat these problems scientifically. From this viewpoint, however, some of our most cherished evidence loses force. The mere presence of free carbon in very ancient sediments is not conclusive proof of vital origin, but could have resulted (before life developed) from the degradation of organic molecules of nonvital origin (for example, *1a*). Crystallites, lithophysae, and spherulites in volcanic glasses (*2*), and similar structures in plastics (*3*) and in colloidal materials of sedimentary origin commonly have a degree of organization suggestive of living or fossil organisms. Patterns formed by evasion of gas or water from setting concrete or natural sediments, by impact, and by other physical processes may strikingly resemble structures believed to be or even known to be of vital origin—for example, medusae and the burrows and tracks of soft-bodied organisms.

I have devoted much effort, beginning in 1948, to tracking down structures reported as Precambrian fossils, tracks, or burrows, both in the field and in institutional collections, with mainly negative or equivocal results, especially as regards features attributed to multicellular animals. The most ancient record, so far, of unquestionable early metazoan fossils is that of the Ediacaran fauna of South Australia (*4*), which is reported to occur about 7200 meters stratigraphically above granites dated as 675 to 700 million years old (*5*, pp. 191–92), underlies by but 130 meters or so the lowest definitely Lower Cambrian fossils (*4*), and has elements in common with rocks that elsewhere have been dated as younger than 590 million years (*6*). Taking these facts into consideration, the best that can be said of this occurrence is that it is probably very early Paleozoic or very late Precambrian. No tracks, trails, burrows, feeding or resting marks, or after-death impressions such as are left by soft-bodied metazoans in Cambrian and younger rocks have, to my knowledge, been surely identified in rocks older than 600 million years, either, although delicate contemporaneous physical markings and structures are preserved in various Precambrian sediments that were deposited in environments reaching from the intertidal zone to probably bathyal depths. The only structures I know of that might betoken the presence of multicellular animal life in surely Precambrian rocks are ovoid bodies resembling fecal pellets that are locally abundant in rocks up to 2 billion (2×10^9) years old, but even abrasion-shaped quartz fragments may also take such ovoid form. Until such time as more convincing evidence may be found, therefore, I conclude that there are yet no records of unequivocal Metazoa in rocks of undoubted Precambrian age.

That important point could be

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labored with negative evidence, some of which I expect to present in subsequent papers. Leaving out of consideration also, for the time being, various dubious accounts of alleged Precambrian microfossils, I would like here to consider briefly evidence which I accept as constituting a valid record of Precambrian life and the environment in which it lived.

I mentioned that the presence of primitive plant life in the Precambrian has been rather convincingly inferred from various structurally organized calcium carbonate deposits comparable in gross detail to the stromatolitic structures of later geologic time, some of which can be shown to have formed by aggregation about associations of filamentous and colloform algae. In addition a number of Soviet investigators have published accounts of "spore-like" bodies from the upper Precambrian (Riphean) of the Ukraine and elsewhere, as well as accounts of other microfossils even more ancient. Persuasive as some of these and other accounts (*7*) are, however, illustrations and materials available to me do not carry the same degree of conviction as do the remarkable micron-sized microorganisms from cherts of the middle Precambrian Gunflint Iron Formation of Ontario, first recorded in 1954 by Tyler and Barghoorn (*8*), and believed to be about 1.9 billion years old (*9*). Excellent photographs, supplied by Tyler and Barghoorn, of material from the same locality were subsequently published by a newspaper science writer and by Rutten (*10*). A commonly cited but less satisfactory record from approximately equivalent rocks in Minnesota is Gruner's 1924 account (*11*) of much larger (up to 0.1 mm) filiform structures from chert masses at the base of the Pokegama Quartzite and filling cracks in the erosion surface beneath. Some of the structures illustrated by Gruner (for example, his plate 13, figs. A–C) are evidently the tracks of ambient pyrite crystals, as described by Tyler and Barghoorn (*12*). Others, all from the same thin section (Gruner's slide M821), suggest the threads of aquatic fungi (Gruner's plate 11), but none show structural details such as do the Gunflint material; and the threads, if organic, are of larger and different organisms. New material from the same locality has revealed nothing.

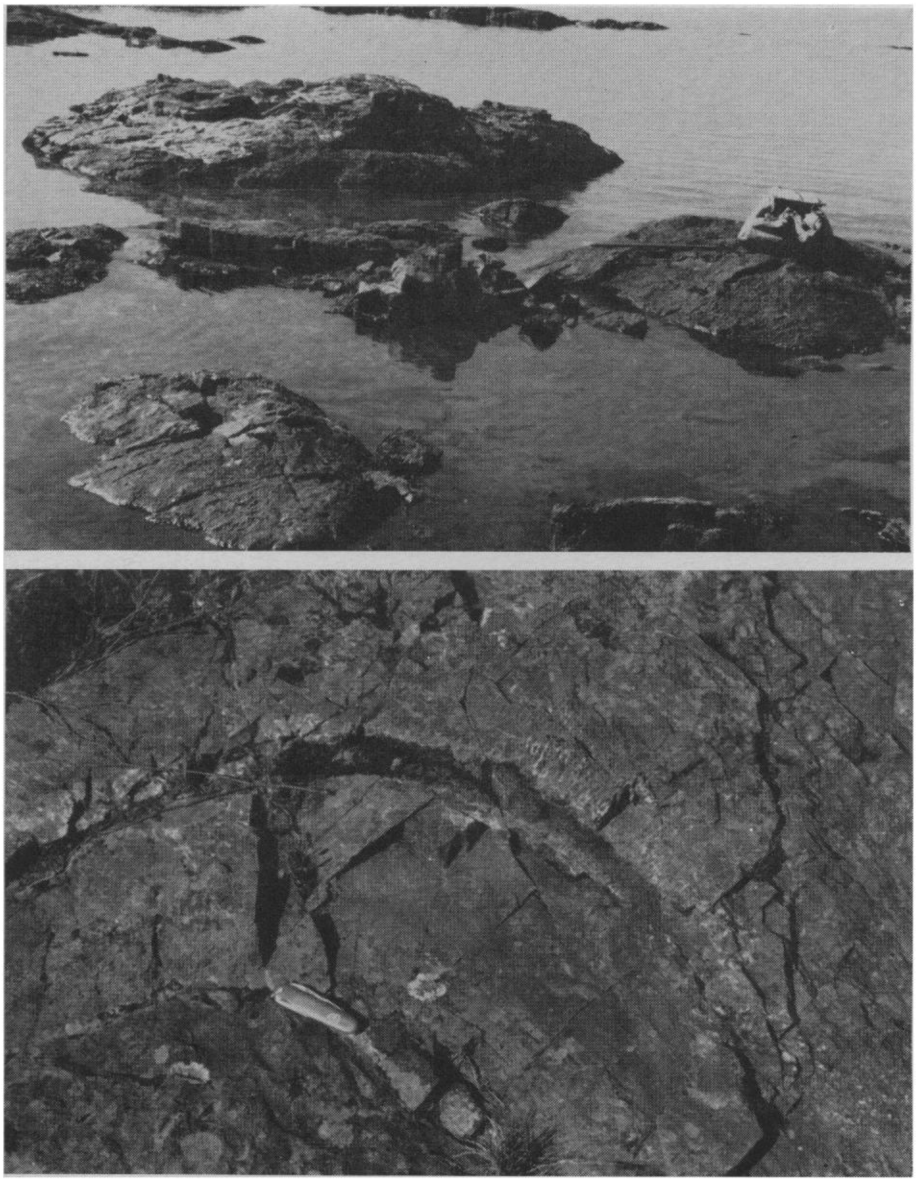

Fig. 1. (Top) Outcrops of Gunflint chert, north shore, Lake Superior. Mounds of chert in Gunflint Formation 4 kilometers west of Schreiber Beach, Ontario, opposite Slate Island. (Bottom) Internal structure of a small chert dome (stromatolite) on back beach, showing radiating "fingers" where the fractured surface intersects the alternating dark partitions of organogenic chert and light interfillings of cherty debris. The core rock below the knife is an individual pillow of Keewatin andesite. The appearance is the same in either vertical or horizontal section. Except as noted, all of the fossils illustrated in Figs. 2–4 come from this or adjacent chert domes which envelop the andesite pillows on the back beach.

Immediate Import of the Gunflint Occurrence

My own studies of cherts from the Gunflint Iron Formation at a locality 4 kilometers west of Schreiber Beach, Ontario, have revealed additional material that preserves such detail and so closely resembles living simple thallophytes as to warrant separate notice, along with considerations of possible biologic affinity. The primary purpose of this article, however, is to confirm and supplement previous work in such a manner as to leave no residual doubt concerning at least this one firm datum in the record of Precambrian life, and to consider its bearing on atmospheric and metazoan evolution. This will then serve as a point of departure for future comment, some of which will, perforce, be negative and other based on much less satisfactory evidence than is here considered.

The importance of the Gunflint fossils is threefold:

1) They are the most ancient recorded structures which closely resemble specific living organisms, namely the group which includes the so-called thread-bacteria and the nostocalean blue-green algae, and which we may

refer to collectively as lower thallophytes.

2) The manner of their preservation, sealed within a primary chert, exemplifies the type of occurrence for which we should search in the continuing quest for the oldest records of life.

3) These organisms tell us something about the environment in which they lived and suggest some thoughts about atmospheric and pre-metazoan history.

The Fossils

Locality, geologic relations, age. All material here described comes from small mounds of stromatolitic chert on the north shore of Lake Superior, opposite a small island locally known as Slate Island or Flint Island, about 4 kilometers west of Schreiber Beach and 6.5 kilometers west-southwest of the town of Schreiber, Ontario. The local geology is described by Harcourt (*13*). Moorhouse and Beales (*14*) mention further occurrences of the stromatolitic chert. And other papers by Moorhouse and by Goodwin (*15*) describe the distribution of the Gunflint in nearby parts of Ontario. A comprehensive description of the regional stratigraphy and lithology of the Gunflint Formation is given by Gill (*16*).

At this locality, which may be called the Schreiber Beach locality, Harcourt describes the fossiliferous chert as lying below a black shale that outcrops on Slate Island, and resting on a basal conglomerate, which, in turn, rests on andesitic Keewatin pillow lavas. At the site from which I collected, the stromatolitic chert, although clearly below the black slate and above the andesite, rests directly on, and partially envelops, the Keewatin pillow lavas, individual stromatolitic mounds growing upward from individual pillows (Fig. 1*B*). According to the regional evidence, however, it would seem that the chert was separated by a stratigraphic break from the pillows on which it grows and is to be referred to the Animikian rather than to the Keewatin. My all too brief personal observations of the outcrop left some doubt about this relation, but such doubt appears to be resolved by a potassium-argon age that corrects to 1.9 ±0.2 billion years on material associated with the chert at the same locality (*9*). This implies an Animikie age for the chert, which may be regarded in round numbers as roughly 2 billion years old.

It should be pointed out that the material dated was fragmental matrix and could be more ancient than the enclosing fossiliferous chert. Isotopic age determinations on presumably equivalent rocks elsewhere, however, indicate an age in excess of 1.7 billion years (*17*), so the 1.9 billion year age given for the Gunflint can be regarded as reasonably secure.

The matrix. The fossils occur in a matrix of "waffle"-structured chert stromatolites in which thick, anastomosing partitions and fingers of black chert rise in a succession of convex-upward layers between narrower infillings of siliceous oöids and fragmental particles of volcanic materials (Fig. 1, bottom; Fig. 2, *A* and *B*).

The filaments and other fossil struc-

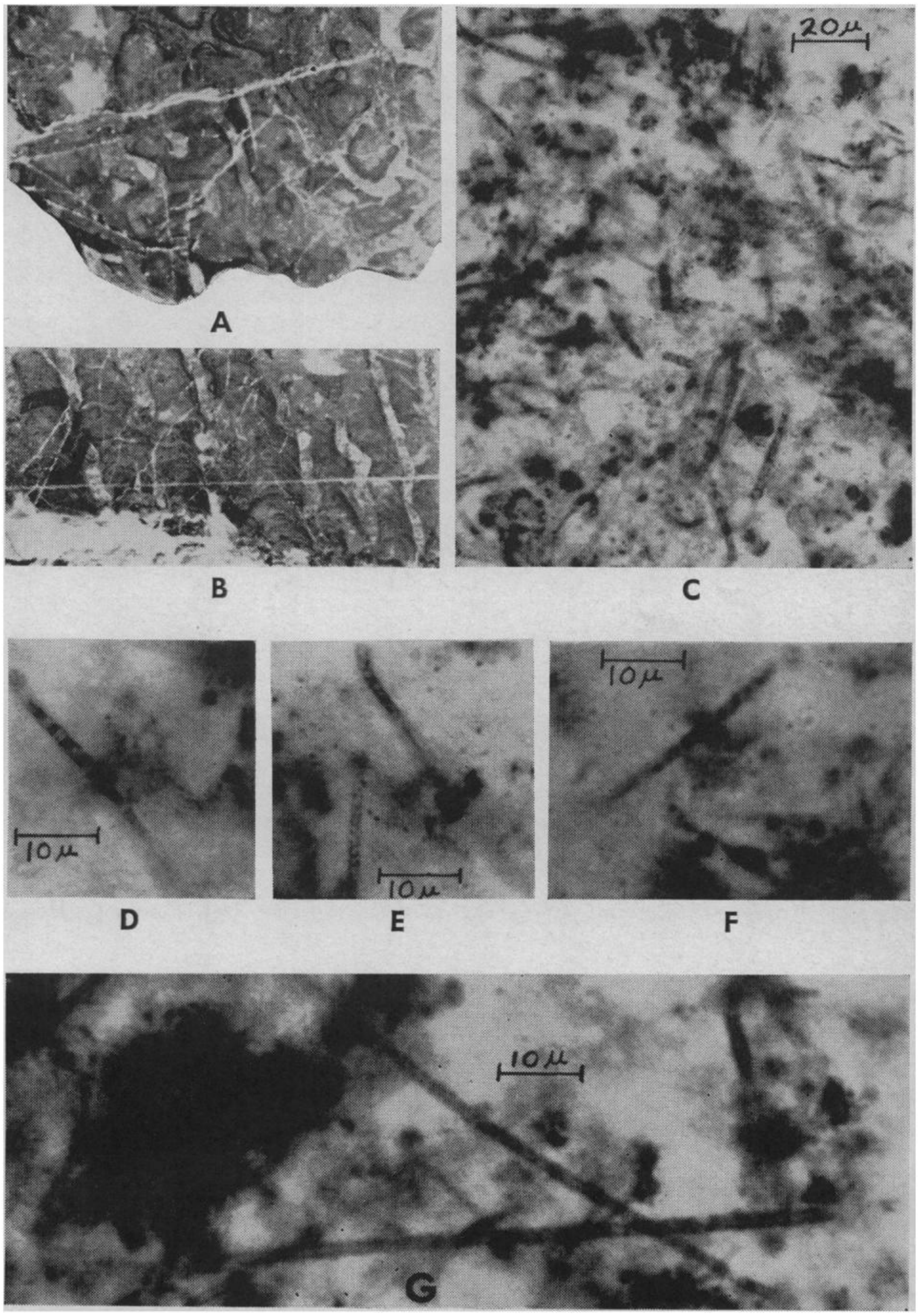

Fig. 2. Structure and microorganisms of Gunflint chert from shore of Lake Superior west of Schreiber Beach, Ontario. (Coordinates given are for the IDKIT stage on the Leitz Ortholux microscope.) (*A* and *B*) Horizontal and vertical sawn faces of structured chert from a small dome similar to that pictured in Fig. 1 (bottom) (slightly reduced from natural size). The black parts contain the microfossils, the light interfillings are of siliceous oöids and detrital material. (*C*) General view of septate threads and spherical structures from thin section C6(3); coordinates, 26.1/125.3. (*D–G*) Thin septate threads of category 1 of text, aff. *Sphaerotilus* and *Oscillatoria*. (*D, E,* and *F*) From thin section C6(4); coordinates of *D* and *F*, 32.9/119.1; coordinates of *E*, 33.0/119.1. (*G*) From slide C6(1); coordinates, 49.6/122.2.

tures appear to be confined to the stromatolitic partitions and fingers, although the nuclei of some of the oöids resemble the same chert without recognizable fossil content. It appears, from the exquisite preservation of the many micron-diameter threads and other minute structures, that the silica was deposited at the time of their growth or very shortly after—probably as a tough gelatinous mass that enveloped the organisms layer upon convex layer and was strong enough to stand with some relief above the oölitic and detritus-containing channels between. Euhedral rhombs of the carbonate mineral ankerite are locally enclosed in the chert matrix. Microstructures can at places be traced across the boundaries between rhomb and chert, indicating that the carbonate crystallized within the matrix while the latter was still in a gelatinous state. If either silica or carbonate at such places were replacement products, we could hardly expect preservation of the fidelity observed. The pattern of dispersal of the cellular threads, which "float" as in a viscous fluid (Fig. 2*C*), also indicates that the threads were suspended and sealed within a matrix of gelatinous silica at a very early stage. These relations show that the rock was not originally precipitated as a carbonate rock and later silicified, as has been claimed by some (for example, *18*). The occasional larger pockets of ankerite and dolomite observed were evidently in part penecontemporaneous with the inferred silica gel, and perhaps in part also the result of later replacement of part of the chert with carbonate minerals.

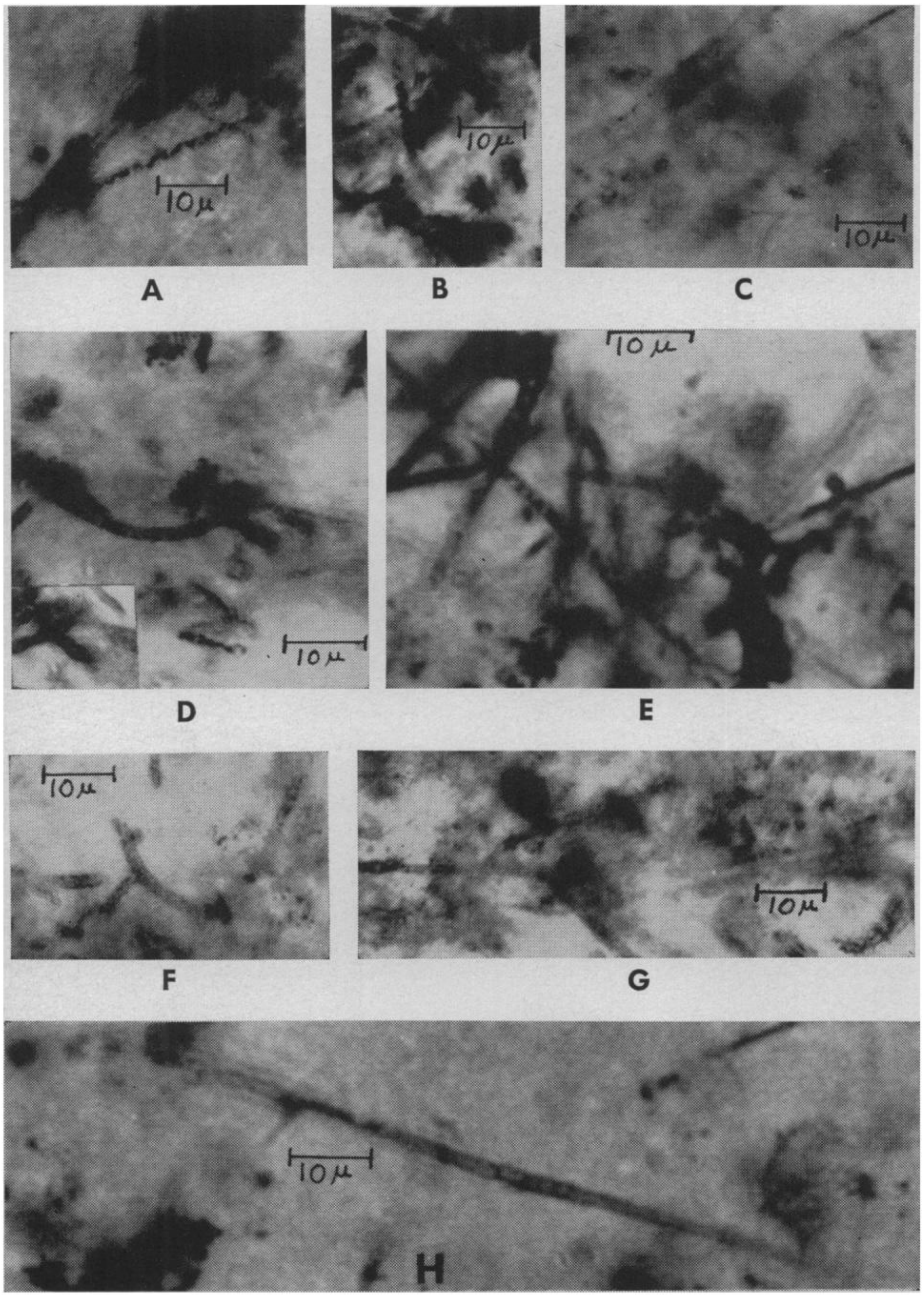

Fig. 3. Microorganisms in Gunflint chert from shore of Lake Superior west of Schreiber Beach, Ontario. (Coordinates given are for the IDKIT stage on the Leitz Ortholux microscope.) (*A* and *B*) Spiral threads of category 2 of text, cf(?) degraded filaments of *Sphaerotilus* and *Oscillatoria*, cf(?) *Gallionella*. Both specimens on thin section C6(4). Coordinates: *A*, 35.0/119.2; *B*, 34.6/118.7. (*C*) *Oscillatoria*-like structure (category 3 of text) dimly shown at upper left above small sphere in center. Thin section C6(2); coordinates 41.5/123.5 (*D–F, H*). Thin septate threads of category 1 of text, cf *Sphaerotilus* and *Oscillatoria*. (*D*) Photomicrograph showing loop. Inset at left (at lower focus) shows structure of loop and septate nature of looped thread. Thin section C6(4); coordinates, 33.0/118.7. (*E*) A group of septate threads. Thread at right seems to have a lump of some sort attached to it, possibly a reproductive structure. Thin section C6(1); coordinates, 55.7/123.7. (*F*) False branching(?). Thin section C6(4); coordinates, 34.7/119.2. (*H*) Thin section C6(1); coordinates, 46.6/122.5. (*G*) Organism of uncertain characteristics showing what may be reproductive structure attached by short necks to threads which either are part of a meshwork or overlap. This might be an aquatic fungus, but more probably is related to category 1. Thin section C6(4); coordinates, 41.0/116.8.

Preservation. Most of the material comprising microstructures observed is a brown to black kerogen-like substance, observable best in very thin thin-section, but capable of being isolated by dissolution in hydrofluoric acid using standard palynological techniques. It gives no diffraction pattern under the electron beam.

Morphology. Microstructures observed are of eight main categories:

1) Thin septate threads mainly 1.5 to 2 μ in diameter, rarely as thin as 1 μ, lengths exceeding 100 μ (Fig. 2, *C–G*; Fig. 3, *D–F, G?, H*). Straight or curved, single or intertwined in masses of threads, rarely looped (Fig. 3*D*). May show false branching (Fig. 3*F*?). Individual cylindrical "cells" 1 to 2.5 μ long, 1 to 2 μ wide, elongate to equidimensional. These threads resemble filamentous bacteria such as the iron-precipitating *Sphaerotilus* [*Leptothrix*] as well as the nostocalean blue-green algae.

2) Probable degradational remnants of structures of category 1, appearing as dark spiral threads less than 1 μ in diameter, which may be either single corkscrew-like filaments (Fig. 3*A*) or possibly interwoven pairs (Fig. 3*B*). Maximum length observed, 35 μ. Despite their probably degradational na-

ture, these objects are here recorded because of their gross morphological resemblance to spiral threads such as are secreted by the living iron bacterium *Gallionella* (*19*).

3) Larger septate threads up to 5 or 6 μ in diameter, having individual cells shorter than they are wide (Fig. 3*C*). These threads resemble living nostocalean blue-green algae of the genus *Oscillatoria*.

4) Nonseptate or obscurely septate threads similar to structures of categories 1 and 3 and probably degradation products of such structures. Indeed many such threads are indistinctly outlined (Fig. 4*J*) by minute subspherical and rod-shaped bodies that suggest individual bacteria. W. H. Bradley, who has recently been studying the preservation of modern algal filaments, has kindly examined some of these fossils and made the suggestion (*20*) that they may in fact be the bacterially sheathed ghosts of degraded threads.

5) Radiate structures 10 to 30 μ in diameter to outer tips, the individual radial processes suggesting the stubs of septate threads 1 to 2 μ in diameter (Fig. 4, *A* and *B*). These may be independent structures such as the microcolonial manganese- and iron-oxidizing bacterium *Metallogenium* recently described from certain Karelian lakes by Perfil'yev and Gabe (*21*), or they may be the centers of microcolonies from which the threads of category 1 have broken off and moved away during growth or after maturing (*22*).

6) Patterned globular bodies 5 to 15 μ in diameter (Fig. 4, *D–H, J*), of a spherical to slightly flattened spheroidal shape. Different ones appear to consist of an outer layer of cells surrounding a central cavity (Fig. 4, *H, J* center, and *E*?), to be perforated by many small pores (Fig. 4, *D* and *G*), and to be flattened on one end, with possibly a terminal pore (Fig. 4*J*?) or neck (Fig. 3*G*?). These globular bodies may be some kind of fruiting structure, perhaps related to category 1, or they might be independent structures such as the living colonial and planktonic myxophycean alga *Coelosphaerium*.

7) Smooth spheres 1 to 1.5 μ in diameter, possibly reproductive cells or individual bacteria.

8) Subspherical and rod-shaped bodies less than 1 μ in diameter or length which occur mainly attached to or enveloping other objects and which may be individual bacteria (Fig. 4, *H* and *J*). Continuing study of the Gunflint material with the electron microscope, however, has not yet led to discovery of any of these forms, and hence does not confirm (or deny) a bacterial nature.

In addition to the above, I have also observed (i) occasional small curving chains of subspherical bodies or "cells" (not illustrated) that suggest chains of

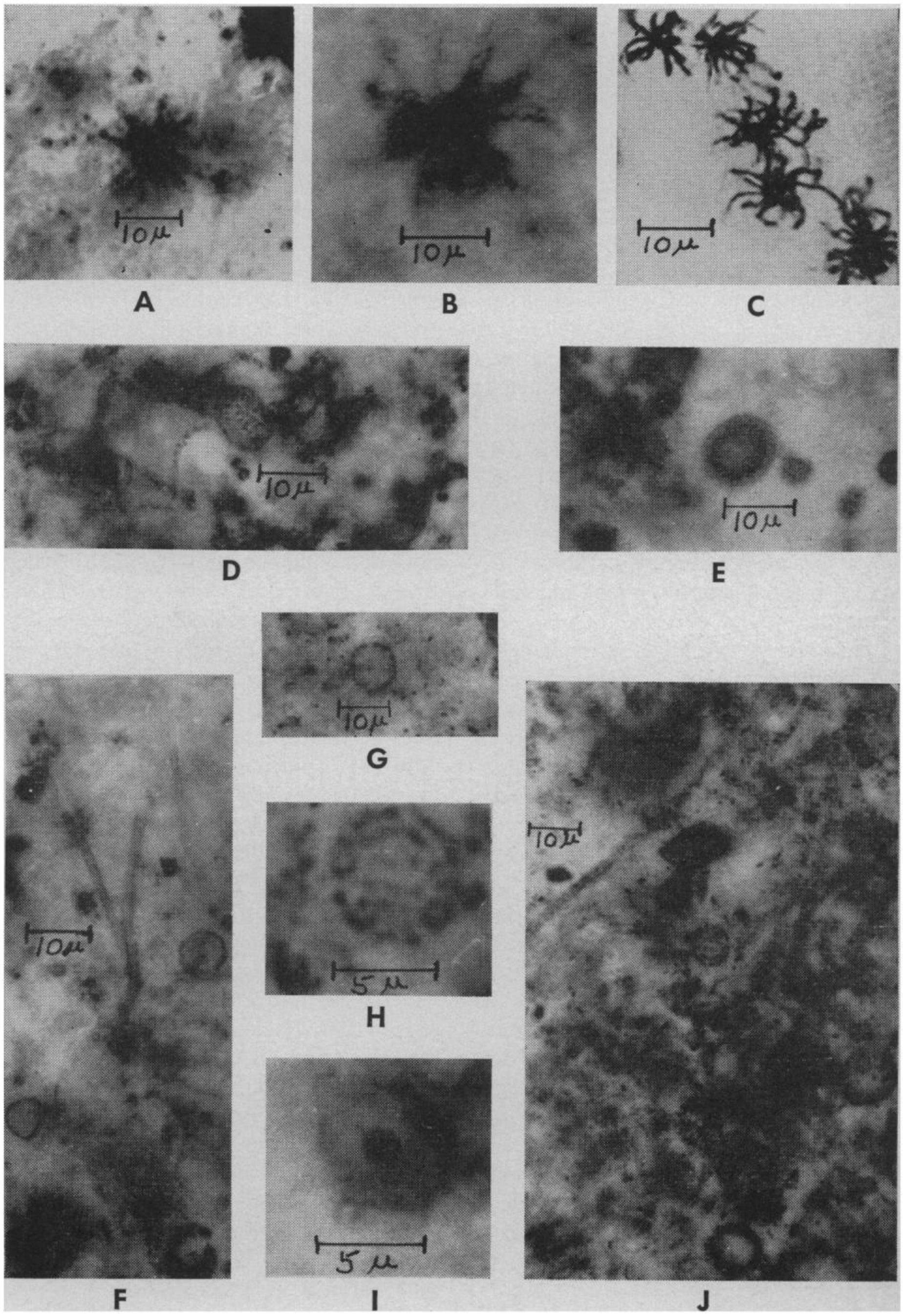

Fig. 4. Globular and radiate microstructures in Gunflint chert (except *C*) from shore of Lake Superior west of Schreiber Beach, Ontario. (Coordinates given are for the IDKIT stage on the Leitz Ortholux microscope.) (*A, B*) Radiate structures of category 5 of text. Note blunt ends and septate structure of radial processes. Compare with *C*, and with microcolony of *Thiothrix* illustrated by Thimann (*22*, p. 713). (*A*) From thin section C6(4); coordinates, 34.9/119.2. (*B*) From thin section C6(1); coordinates, 60.7/126.2. (*C*) *Metallogenium personatum* Perfil'yev 1961, a manganese- and iron-oxidizing colonial bacterium (*21*, plate 7, fig. 3). (*D–H, J*) Globular bodies of category 6 of text showing perforate and apparently cellular walls. Note range in diameter and slight flattening of some specimens. Some may have short stalks (see, for example, Fig. 3*G*) or terminal pores (*G, H*). (*D*) From thin section C6(4); coordinates, 41.1/117.1. (*E*) From thin section C6(2); coordinates, 36.8/127.1. (*F*) From thin section C6(1); coordinates, 55.7/124.0. (*G*) From thin section C15(1); coordinates, 51.8/119.5. (*H, J*) From thin section C15(1); coordinates, 49.0/119.5. (*I*) Sphere, perhaps individual cell, possibly showing cell contents. Thin section C6(1); coordinates, 51.9/124.3.

individual coccoid bacteria, or something like the blue-green alga *Nostoc*, or *Anabaena*; (ii) smooth spheres up to 5 μ in diameter which resemble individual cells, and some of which may show cell contents (Fig. 4*I*); and (iii) a miscellany of possible nannofossils, some of which are probably artifacts of preservation, preparation, or microscopic manipulation.

Affinities. The crucial question—Could the structures here described and illustrated have been produced by nonvital processes?—must be answered in the negative. Not only is the morphological similarity to living microorganisms so strong and so detailed as to make an evolutionary continuity almost certain, but, in addition, the septate thread, the cellular-walled spheroid, and the perforate spheroid have, to my knowledge, never been produced without biologic intervention. What manner of organisms these may be, already suggested in the discussion above, deserves further consideration and summation.

The thin septate threads of category 1, commonest of the microstructures observed, strikingly resemble living thread bacteria (for example, *Sphaerotilus*) and myxophycean algae (for example, *Oscillatoria, Lyngbya*, perhaps *Spirogyra*). They might belong to either of these groups or to an early thallophyte in the common ancestry of both. In the absence of pigmentation or specific biochemical reactions, a choice cannot be made, although it may be noted that the diameters of the threads are smaller than those of most myxophyceans. I have considered but rejected the possibility that these threads are simply chains of Eubacteria.

The larger threads of category 3, however, are big for bacterial threads and most likely represent a nostocalean blue-green alga similar to *Oscillatoria*, or something in the early ancestry of this group.

Categories 2 and 4 probably represent degradational products of the septate threads, but the structures illustrated in Fig. 3*E* (right center) and 3*G* may conceivably represent something different. These structures suggest aquatic fungi, but they are more probably special cases of category 1. The apparently branching structure shown in Fig. 3*G* is probably a simple overlapping of independent threads, but the globular bodies may be attached to the threads by short necks (for example, the upper body in 3*G*?). If so, they may be reproductive structures, possibly similar to structures of category 6. The "false-branching" in Fig. 3*F* may also be a chance juxtaposition.

The possible affinities of other categories are sufficiently considered for present purposes in the preceding section.

Environmental Implications

The preservation of microstructural details which are strikingly like those of living filamentous bacteria and blue-green algae (Myxophyceae) in rocks roughly 2 billion years old substantiates the no longer revolutionary conclusion that an autotrophic mode of existence had evolved by that time. Morphologically similar, and presumably metabolically comparable, living organisms are chemosynthetic or photosynthetic, living normally over a wide range of environmental conditions. The living thread bacterium *Sphaerotilus* [*Leptothrix*] *natans*, which closely resembles the thin septate threads of category 1, tolerates a temperature range of 15° to 40°C, *p*H 5.8 to 8.1, and salinity from that of fresh water to brines (*22*, pp. 710–12). Various related species live in still or running water with or without iron and manganese in solution (*23, 24*), and will tolerate temperatures as low as 5°C (*24*). Although living iron-depositing thread bacteria are not found in the sea (*24*, p. 81; *25*, p. 9), and living blue-green algae are most widely distributed in fresh-water and terrestrial habitats, the latter do, nevertheless, "form an important element in marine vegetation, especially in that of temperate and subtemperate seas" (*26*, p. 862) where they range from the intertidal zone to modest depths in the upper photic zone. Hot-spring myxophyceans will also tolerate temperatures as high as 70°C and perhaps as high as 85°C (*26*, p. 864). With reference to the Gunflint organisms, therefore, we can at this time say only that their presence is consistent with a wide range of environmental capabilities, but that most of their closer modern counterparts prefer a range of temperature and *p*H comparable to averages of the present time.

Turning to other evidence, the presence of presumably primary silica encasing and preserving the observed mass of delicate cellular structures implies either biological precipitation of the silica, or a neutral to acidic *p*H near a source of silica (such as contemporary volcanism or the weathering of older volcanic rocks), or perhaps both. A relatively low *p*H would also be required by the probably high content of dissolved CO_2 in the contemporary hydrosphere; and high atmospheric CO_2 content would be consistent with a relatively warm (nonglacial) climate. The presence of euhedral crystals of ankerite within the chert matrix (and of microstructures that cross from one to the other) implies penecontemporaneity of ankerite and chert, and, in combination with the foregoing, a slightly basic to neutral *p*H. The baffle-structure of the wavy partitions and fingers which make up the siliceous stromatolites and the oölitic nature of much of the material entrapped between these partitions are features of active water movement. This also suggests relatively shallow water, within reach of the action of waves or currents, and presumably within the photic zone, but deep enough to absorb such lethal ultraviolet radiation as was able to penetrate whatever there may then have been in the way of an ozone or atmospheric water-vapor screen above. Relatively shallow depth would also be consistent with the occurrence of conglomerates beneath the stromatolitic zone at some places and clean rock surfaces at others.

The evidence here considered does not in itself warrant a clear choice within the wide range of salinities that have been suggested for the waters of that area and time (*27*). Living iron bacteria are unknown from the marine environment (probably because of the near absence of iron in modern sea water), and the marine blue-green algae are mainly near-shore species, yet the wide range of salinities that both will tolerate and the abundance of pyrite (FeS_2) in the Gunflint and equivalent rocks are consistent with a marine habitat for the Gunflint flora. A likely (but not the only possible) source of abundant primary sulfide would be from the bacterial reduction of marine sulfate.

Implications for Early History of Atmosphere and Metazoa

Terrestrial deficiencies of the noble gases, as compared with their cosmic abundances (*28, 29*) tell us that, whatever the composition of the primary atmosphere, it has in large part long since escaped the earth's gravity field. On this and other grounds (*29*) it is now generally agreed that the components of the present atmosphere came ultimately from within the earth, mainly by volcanism. Free oxygen, however, is not directly available from such sources; nor, in the absence of green-plant photosynthesis, is it formed secondarily except in trivial and readily scavenged quantities from photolytic dissociation of CO_2 and H_2O. All who have considered the problem critically, therefore, agree that at an early stage in its history the terrestrial atmosphere was essentially anoxygenic, or reducing (*28–32*). Only at a later date, after the appearance of a photosynthetic source of oxygen, could the atmosphere evolve toward its present oxygenic (and oxidizing) state. And the metazoan level of evolution could arise only after the oxygen content of the atmosphere had reached some relatively high level, so that free oxygen was available in quantity for respiration and for the formation of an ozone layer thick enough to screen out lethal ultraviolet radiation.

The main point of interest here is to evaluate what the paleontological evidence contributes toward identification of the span of time during which a liberally oxygenic atmosphere arose.

The geochemical evidence has recently been exhaustively reviewed by Holland (*31*), who concludes from it that the entry of free oxygen into the atmosphere above certain minimal levels convenient to account for observed geochemical oxidation was more recent than about 2 billion years ago. There is, nevertheless, legitimate disagreement on the interpretation of the geochemical data. Although the presence of supposedly detrital (and easily oxidized) uraninite and pyrite in sediments deposited as recently as 2 billion years ago (*31*, pp. 466–67, citing Ramdohr and Liebenberg) has been taken as the clinching evidence for a reducing atmosphere until that time, there remains some doubt as to whether such uraninite and pyrite are truly detrital, or even contemporaneous with the deposits in which found, as well as their significance if detrital (*33*). Jolliffe (*34*), similarly, has argued, with considerable logic, that a change in the valence states of "weathered" materials at Steeprock Lake, Ontario, indicates the time of change from an essentially anoxygenic to an oxygenic atmosphere to be about 2 billion years ago, but a troublesome possibility lingers that the oxygenic "weathering" observed may be a function of hydrochemical processes much younger than the geologic surface to which it is related. The widespread oxidized iron formations of Precambrian age have been interpreted on the one hand as evidence of a highly oxidative atmosphere (for example *35*, p. 81) and on the other as requiring a reducing atmosphere under which large quantities of iron could be transported to the sites of deposition in the soluble ferrous state (for example, *18, 24*).

The presence of fossil Metazoa in rocks approaching an age of 0.6 billion years (basal Paleozoic, Ediacaran), however, at least establishes an upper limit for the appearance of a relatively oxygenic atmosphere, for metazoan metabolism depends on the continued ample availability of free oxygen (probably at least 1 percent of the present atmospheric level). Fossils here described and referenced demonstrate, in addition, that organisms or predecessors of organisms capable of generating free oxygen through green plant photosynthesis existed roughly 2 billion years ago. They may have existed more than 2.6 billion years ago, if the evidence of the Bulawayan stromatolites of Southern Rhodesia (*36*) is accepted as indicative of green plant photosynthesis this old; but the pegmatitic rocks which have been used to place this minimum age on the Bulawayan occur over 500 kilometers from the stromatolitic structures (*37*) and there is, therefore, at least a little room for reservation about their age, as well as, in the mind of the invaluable persistent skeptic, about their exact nature.

Before about 2 billion years ago, then, the evidence from paleontology and that from geochemistry are not yet in obvious conflict. However, sedimentary (and presumably primary) iron formation younger than 2 billion years is also widely distributed in the Precambrian, raising problems of transport of the source materials if the atmosphere were then oxygenous, and of precipitation if it were reducing.

The presence of structures resembling thread bacteria and of blue-green algae or their probable precursors in the 1.9± billion-year-old Gunflint Formation suggests a working hypothesis that would resolve these apparent contradictions. The early thallophytes, such as are here described, may have been photosynthesizers that either obligatorily or permissively attached any free O_2 that was generated to some convenient oxygen acceptor. Ferrous iron transported to the large water basins or world ocean of the time in reducing surface waters would have been a convenient acceptor for such unwanted or simply available O_2 and possibly an important part of early thallophyte metabolism—the oxidation of soluble ferrous iron is probably the standard source of energy for living iron bacteria, some of which also fix carbon dioxide as the sole source of carbon (*38*). Considerable time might expectably be involved either in the evolution of an organism that could tolerate, let alone use, free metabolic by-product oxygen, or in the oxidation of ferrous iron to the point where free oxygen could begin to evade to and accumulate in the atmosphere in significant quantities. If there were not at that time an interconnected world ocean, but only large separate basins, the time and duration of precipitation of ferric oxide may have varied from basin to basin, until evasion of oxygen to the atmosphere was sufficient to produce an ozone screen and permit the atmospheric transfer of photosynthesizing organisms from one basin to another. This notion of local sources of oxygen antedating its general diffusion was suggested as long ago as 1927 by A. M. Macgregor (*32*).

Although, also, some oxygen (and ozone) would probably always have been available for a little oxidative weathering as a result of photolytic dissociation of atmospheric CO_2 and H_2O, the beginning of buildup of a liberally oxygenic atmosphere should have produced recognizable geochemical and sedimentary effects in the geologic record. Such effects, indeed, should be prominent, owing to the fact that in the early stages of accelerated evasion of oxygen from large water bodies (or an interconnected world ocean) to the atmosphere an ozone layer would presumably have developed at or near the surface of the earth. This should have resulted in a sharp increase in the rate of oxidative weathering, which, in turn, should be recorded by the retention of ferric iron in the weathering profile, the wide appearance of red beds as an important sediment, and great diminution or disappearance of the precipitated siliceous banded-iron-formation so characteristic of Precambrian.

My scanning of published stratigraphic columns for the Precambrian suggests that there are no important unequivocal red-beds of greater age than the upper Keweenawan and Beltian sediments of North America and their approximate time-equivalents such as the Jotnian of Fennoscandia, with ages of 1.1 to 1.3 billion years (*17*, p. 5; *39*, p. 239). Nor are there yet acceptably dated records of important banded-iron-formation of the Lake Superior type younger than about 1.7 billion years (*18*).

The combined evidence of paleontology and stratigraphy, therefore, indicates that the potentiality for the evolution of oxygen by green plant photosynthesis existed at least 1.7 to 2.1 billion years ago, and that atmospheric oxygen first began to be available in *relatively* large quantities probably about 1.2 billion years ago (a conclusion independently reached on a different line of reasoning by Lepp and Goldich, *18*). From the time of first available photosynthetic O_2 until about 1.2 billion years ago, ferrous iron, carried into the large water bodies or world ocean of the time by reducing surface waters, may have served as a vast oxygen sump, retarding the evasion of free O_2 to the atmosphere.

Once free oxygen began to accumulate on a large scale, there should be accompanying decreases in the partial pressure of CO_2 in both atmosphere and hydrosphere, leading to accelerated precipitation of carbonate sediments. Could this be why limestone and dolomite appear to be so much more abundant and widespread among the younger Precambrian deposits, in contrast to those older than about 1.2 billion years?

Perhaps the existence and facies of Precambrian iron formation itself reflect the onset and nature of early photosynthesis. Typical Precambrian iron formation rocks are known to range in age from about 2.7 or 3 to 1.7 billion years before the present. The oldest stromatolites of possibly algal nature are apparently somewhat older than 2.6, perhaps as much as 3 billion years old. Could it be that the onset of oxygen-generating organisms in the hydrosphere was necessary to trigger the deposition of this type of iron formation, and that it ceased at some point of compensation or evolution between about 1.7 and 1.2 billion years ago? The associated facies of iron formation (*27*) are also consistent with such a concept of biological control. Ferric oxides (hematite) would precipitate near centers of relatively high-level oxygen-generating activity, ferrous-ferric oxides (magnetite) in laterally or temporally adjacent parts or other areas of lesser oxygen availability, ferrocarbonates peripherally or above as a result of increase in available CO_3 consequent to CO_2 assimilation at the photosynthetic centers, and ferrous sulfides in more distant or deeper parts of the sedimentary basins beyond or below a source of oxygen or carbonate ion.

At any time after atmospheric (and hydrospheric) oxygen had risen to sufficiently high levels for respirational, as compared to fermentative, metabolism [the "Pasteur point" = 1 percent of present atmospheric oxygen (*40*, p. 117)], probably somewhere between about 1.2 and 0.6 billion years ago, Metazoa could have arisen. The fact that Metazoa are not unequivocally recorded in the geologic record before about 0.6 billion years ago may mean that there was not sufficient atmospheric oxygen for metazoan metabolism until that time. Or it may mean that the biological event or events which led to the Metazoa did not occur until some time after physical conditions made their ultimate emergence inevitable, or that the evolution of such organisms required a long chain of events that could not begin until the advent of ample free oxygen. One would expect some lag, not only in the build-up of O_2 and the development of an ozone layer thick enough to serve as an ultraviolet screen, but also in the appearance of the Metazoa after these conditions were satisfied. And it is also likely that an event or culmination of events of such potential for the occupancy of then unoccupied ecologic niches as the evolution of multicellular animal life would have been followed by rapid diversification at the new grade of biological organization. This may be exactly what we observe in early Paleozoic time (*40*, *41*).

Summary

Several categories of biological microstructures 1.9± billion years old are here described, illustrated, and referred to a group of early thallophytes that includes the thread bacteria and the blue-green algae. These microstructures were almost surely autotrophic and in the line of evolution toward green-plant photosynthesis, if not themselves oxygen producers. Geochemical evidence has been interpreted by some to imply that the contemporaneous atmosphere was essentially anoxygenic (reducing), and by others to indicate an atmosphere rich in oxygen. These conflicting interpretations may be reconciled by a hypothesis, based on demonstrable fossil organisms, that calls for local centers of biologic oxygen generation.

The ancestors of the first green-plant photosynthesizers were presumably anoxic autotrophs, and the first organisms to produce free oxygen may have found it an objectionable by-product. The abundant ferrous iron in solution in the water bodies of that time would, then, have been a convenient acceptor for oxygen as well as a possibly important metabolic-energy source. Even after free oxygen had become a tolerable part of the environment of such organisms, accumulating dissolved ferrous iron would have had to be precipitated (during time of some duration) before oxygen could have begun to evade to the atmosphere on a relatively large scale.

If the major Precambrian water bodies were not connected into a single world ocean, such events would probably have occurred at different times, and over different spans of time, in different water basins, and such a situation could account for the different ages of Precambrian banded-iron-formation in different parts of the world. Organisms could not have been moved through the atmosphere from one water body to another until after enough oxygen had evaded to the atmosphere to generate an ozone screen thick enough to absorb lethal ultraviolet radiation.

As early as about 1.2 billion years ago there was enough oxygen (and ozone) near the surface of the earth to produce extensive red beds, and CO_2 pressure was concomitantly lowered to the point where extensive precipitation of carbonate sediments ensued. By the beginning of Paleozoic time, about 0.6 billion years ago, enough oxygen had accumulated to permit the evolution and diversification of the Metazoa. It is not to be expected, of course, that metazoans would have evolved until some time after atmospheric (and hydrospheric) conditions were suitable for metazoan metabolism. Evidence currently available indicates that such conditions arose between about 1.2 and 0.6 billion years ago, and that the Metazoa made their debut about 0.6 billion years ago. The beginning of the Paleozoic might, then, be defined operationally as the base of the range-zone of Metazoa (or Eumetazoa if we ex-

clude sponges). But a boundary (or a transition) should be limited from both sides, so I have added to this working definition the further limitation that the top of the Precambrian paleontologically approximates the top of the range-zone of the distinctive conical stromatolite conophyton (*42*). The younger Keweenawan and its correlatives stand as a special division of the Precambrian, during which the atmosphere began to approach its present composition and the stage was set for the appearance and expansive diversification of the Metazoa.

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