RESEARCH ARTICLE

Life on Land in the Precambrian

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Microfossils have been discovered in cavity-fill and replacement silica that occurs between chert-breccia clasts in 1200-million-year-old paleokarst at the top of the Mescal Limestone, central Arizona, and in ~800-million-year-old paleokarst at the top of the Beck Spring Dolomite, southeastern California. Microbial communities on Precambrian (>550 million years ago) land may have been extensive enough to affect weathering, erosion, sedimentation, and geochemical processes.

During the last three decades, our understanding of the Precambrian biosphere has increased markedly. Studies conducted during the mid- and late 1960s emphasized establishing both the biogenicity and Precambrian age of purported Precambrian microfossils (*1*). Now it is well established that life was present and abundant during the Proterozoic eon (550 to 2500 million years ago) and cyanobacteria-like microorganisms were extant and morphologically diverse more than 3400 million years ago (2). Proterozoic microfossils are now known from more than 400 formations (3). However, nearly all of these occurrences are in marine or probably marine strata, and the rest are in possible lacustrine strata. Unequivocal Precambrian, terrestrial body fossils have been unknown, and the oldest direct evidence for terrestrial life includes trace fossils in Middle Ordovician strata (4) and fossil spores in Middle Ordovician and Lower Silurian strata (5). There are, however, indications that Precambrian alluvial settings may have harbored microbial life. Curled bedding-plane structures in a 1200-million-year-old alluvial sandstone may have formed by a microbially bound sandy layer curling during desiccation (6); stromatolites were reported from a 1000-million-year-old alluvial fan deposit (7); relatively high carbon concentrations were detected in 2700-million-year-old alluvial rocks (8), and in these same rocks the dissolution of gold was considered to be related to decomposition products of organic matter and its precipitation to microbial activity (9). In addition, the chemistry and structure of Precambrian paleosols suggest that terrestrial life was present when the paleosols formed (*10*). Hydrocarbons interpreted as being produced by the breakdown of terrestrial matter were detected in several rocks ranging from ~2500 million to ~600 million years old (*11*), and some extant prokaryotes are so resistant to harsh conditions that it is logical that microbes may have inhabited the Precambrian land surface (*12*). In spite of these indications, the lack of compelling evidence has left standing the view that Precambrian land was devoid of life. Establishing the existence of terrestrial communities during the Proterozoic Eon would have implications with regard to understanding Proterozoic weathering and sedimentation as well as the nature of the Proterozoic biosphere.

Carbon-isotope depletions of up to 10 per mil have been reported for dolostones in ~1200-million-year-old paleokarst at the top of the Mescal Limestone and in ~800-million-year-old paleokarst at the top of the Beck Spring Dolomite (*13, 14*). These paleokarsts represent carbonate rocks that underwent surface and near-surface dissolution and reprecipitation during Proterozoic subaerial weathering (*15*). In recent settings, such depletions normally are attributed to the presence of land plants, which introduce ^{13}C-depleted CO_2 into downward-percolating ground waters. In the absence of land plants there is no mechanism for significant lowering of $^{13}C/^{12}C$ ratios, so carbon in the host rock is recycled into karst-related secondary carbonate phases without significant isotopic change. The low $^{13}C/^{12}C$ ratios in the Proterozoic paleokarsts have been interpreted to indicate that photosynthetic communities were present on land at least 1200 million years ago (*13, 14, 16*). In this article, we document microfossils found within these ^{13}C-depleted paleokarsts. They are interpreted as fossils of Proterozoic terrestrial microorganisms.

Geology and paleontology. A regionally extensive paleokarst is well developed at the top of the Mescal Limestone, Apache Group, central Arizona (Figs. 1 and 2) (*17*). Based upon the age of sills intrusive into the overlying Troy Quartzite and paleomagnetic data, the paleokarst is ~1200 million years old (*18*).

The Beck Spring Dolomite is the middle unit of the Middle and Late Proterozoic Pahrump Group, and it underlies latest Late Proterozoic strata in the basal Wood Canyon Formation (*19*) by at least 2 km (Figs. 3 and 4). An age of ~800 million years for the paleokarst is based on radiometric ages for the underlying basement and for a sill intrusive into the lower Pahrump Group and regional correlation of the Beck Spring and overlying Kingston Peak formations with units dated by radiometric and paleomagnetic methods (*20*). On the basis of sedimentologic studies, the Beck Spring Dolomite has been interpreted as a shallow-water, marine deposit (*21*); and a marine setting is supported by stable isotope studies (*22*).

At both the Mescal and Beck Spring localities, paleokarst intervals contain chert breccia and terra rossa (red soil), which accumulated as insoluble residues during dissolution of the host carbonate by vertically percolating ground water. Secondary silica fills a variety of cavities in the paleokarst, cements breccia clasts together, and replaces much of the breccia matrix formerly composed of very fine-grained carbonate, terra rossa, and hematite. In some cases, the paleokarst surface may have funneled runoff from higher surrounding areas into the subsurface. The collapse breccias could then have acted as sieves for any organic matter that may have been in the sink hole or on the surrounding land mass. Organic matter lodged or living between clasts can be entrapped and preserved in this secondary silica. Inasmuch as the best preserved Precambrian microfossils are in chert, we targeted this secondary silica in our search for terrestrial microfossils.

Silicified collapse breccias and siliceous terra rossa associated with the Mescal pa-

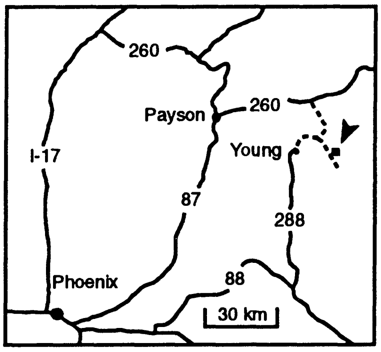

Fig. 1. Locality map for the Mescal terrestrial microfossils.

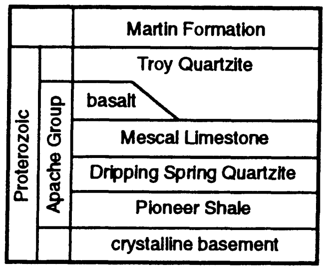

Fig. 2. Generalized stratigraphy for rocks associated with the Mescal Limestone.

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leokarst form a unit up to ∼10 m thick that caps the Mescal Limestone. We found microfossils in cavity-fill fibrous quartz in this siliceous cap, but the best specimens were found in ferruginous chert pebbles in a pebbly sandstone at the base of the overlying Middle Proterozoic Troy Quartzite at Shell Mountain, Sierra Ancha Mountains (*23*). These pebbles were derived from the uppermost, highly siliceous part of the underlying Mescal paleokarst. The microfossils are in a matrix of intergrown blocky quartz crystals ∼100 to 200 μm across. Fine-grained hematite is pervasive throughout the crystals and imparts a bright-red color to the chert except along feather edges of petrographic sections. The microfossils cross grain boundaries without disturbance. Numerous spherulitic arrays of clear fibrous quartz up to 300 μm across are distributed throughout the blocky quartz-hematite matrix. The blocky quartz and fibrous quartz grade into each other; this relation indicates that both silica phases precipitated simultaneously. In thick petrographic sections, microfossils are best seen where the red blocky quartz matrix grades into the clear fibrous quartz.

The most abundant of the well-preserved microfossils are sinuous, unbranched, tubular microstructures defined by a rim of submicrometer-sized hematite particles that surround a hematite-free core that is 0.8 to 1.7 μm wide (Fig. 5, A and B, and Fig. 6). Viewed in thick petrographic sections, some filaments are as much as 150 μm long; this represents a minimum length because many filaments pass out of the petrographic section or become invisible where they descend into highly pigmented parts of the petrographic section. These filaments form intertwining masses that resemble the fabric of a filament mat (Fig. 5A). Associated with these microfossils are wider filaments as well as hollow spheroidal microstructures, which also are defined by fine hematite particles. The microorganisms preserved in these cherts may have actively or passively caused an iron-bearing mineral to precipitate upon their surface, or particles of an iron-bearing mineral or colloidal iron may have adhered to their surface.

The morphology and dimensions of the filaments are consistent with bacterial (including cyanobacterial) affinities. Inasmuch as the best preserved microfossils occur in pebbles derived from the upper, highly siliceous part of the paleokarst, the preserved microorganisms probably lived close to or on the land surface. The manner in which the growing quartz crystals engulfed the microfossils without disrupting them suggests that the silica replaced a mat directly, although the primary precipitate may have been an opaline gel, which subsequently crystallized to quartz.

We found microfossils in paleokarst at the top of the Beck Spring Dolomite at three localities in the Kingston Range, southeastern California. They occur in chert breccias formed by dissolutional collapse and are associated with $\delta^{13}C$ up to 10 per mil less than those in the underlying unkarsted dolostones (*14*). Isotopic data for the secondary silica indicate precipitation in meteoric waters (*15*), supporting the field and petrographic data indicating that the Beck Spring Dolomite was subjected to local karsting during the time of deposition of the lower Kingston Peak Formation (*14*). Microfossils first were found in silica filling voids near the top of the Beck Spring Dolomite in a Proterozoic slide block in the overlying Kingston Peak Formation (*14*); however, they are poorly preserved. Unequivocal, well-preserved microfossils later were found in secondary silica at the other localities. At one locality (*24*), the microfossils are in secondary silica that replaced much of the matrix of a dissolutional-collapse breccia. This matrix originally was composed of fine-grained carbonate and terra rossa. The microfossils are gently curved to highly sinuous chains of 1- to 8-μm crystals of pyrite or hematite pseudomorphs after pyrite (Fig. 5, C to H). Some filaments consist of a single row of relatively uniform-sized crystals, which may be contiguous or separated and evenly spaced. Other filaments are less regular, and there is a greater variation of crystal size within a filament or several crystals are at the same position along the length of the filament. The filaments are commonly isolated or associated with a few other filaments. They do not occur as filament mats. At the other locality (*25*) the most prominent fossils are unbranched, tubular filaments 9 to 19 μm in diameter. They are in silica-filled voids in a dissolution-collapse breccia. The morphology and dimensions of these microfossils are consistent with bacterial (including cyanobacterial) affinities.

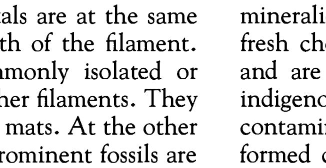
Are they fossils of Proterozoic terrestrial life? Four criteria must be satisfied in order to establish that purported Proterozoic terrestrial fossils actually are fossils of Proterozoic terrestrial organisms. It must be established (i) that the purported fossils are biogenic; (ii) that the fossils are of Proterozoic age; (iii) that the strata containing the microfossils were subaerially exposed during Proterozoic time; and (iv) that the fossils represent preserved terrestrial organisms.

The biologic origin of the Mescal paleokarst filaments is established by their morphology and size. The most convincingly biogenic structures (namely, the 0.8- to 1.7-μm-wide filaments) are curved, unbranched, tubular filaments that maintain a constant diameter along their length. Particularly indicative of their biogenicity are their tubular nature (*26*) and narrow size range (Fig. 6).

The filaments from the Beck Spring paleokarst are similar to chains of pyrite (or hematite pseudomorphic after pyrite) that have been established as biogenic in underlying marine chert in the Beck Spring Dolomite as well as in other Precambrian chert (*27*). Their sinuosity, length, and variability in crystal size along a filament are similar to bona fide Precambrian microfossils composed of pyrite crystals and hematite pseudomorphs after pyrite.

A Proterozoic age for the microfossils in the Mescal and Beck Spring paleokarsts is established by several considerations. The Mescal Limestone underlies the Troy Quartzite, which is intruded by 1100-million-year-old sills. The Beck Spring Dolomite underlies uppermost Upper Proterozoic strata by at least 2 km. In both units the microfossils are encapsulated by the mineralic matrix of the chert, are found in fresh chert away from weathered surfaces, and are not in fractures. Thus, they are indigenous to the rock and are not modern contaminants. These cherts could not have formed during the current exposure event because at both localities similar chert has not been found in outcrops of other stratigraphic intervals. In addition, there is an absence of pollen, spores, or fragments of higher plants that would be expected if this silica was precipitated near an exposure surface during the Cenozoic.

A Middle Proterozoic age for the Mescal fossils is established by their occurrence in ferruginous chert pebbles at the base of the overlying Middle Proterozoic Troy Quartzite. These pebbles are lithologically similar



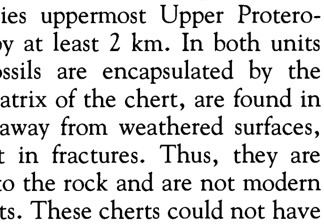


Fig. 3 (**left**). Locality map for the Beck Spring terrestrial microfossils. **Fig. 4** (**right**). Generalized stratigraphy for rocks associated with the Beck Spring Dolomite.

to and obviously were derived from cherts that capped the Mescal paleokarst. Because these pebbles are well rounded and include ventifacts having well-developed facets, it follows that they were fully lithified and abraded at the time they were incorporated into the basal Troy Quartzite. Blocky quartz in one of the pebbles contains well-preserved, tubular, filamentous microfossils. Because this blocky quartz is abraded at the periphery of the pebble, and because the abrasion occurred before, or at the time of, deposition of the basal Troy Quartzite, the filaments are clearly of Middle Proterozoic age. Also, the chert containing these microfossils is dense and the microfossils could not have been introduced into pores during Cenozoic exposure. A Proterozoic age for the Beck Spring paleokarst fossils is further supported by the observation that the filaments show no evidence of compaction; they were silicified before significant burial of the paleokarst and before they could be disrupted by aggrading neomorphism of any precursor carbonate.

Both the Mescal Limestone and Beck Spring Dolomite were subaerially exposed during the Proterozoic. The paleokarst at the top of the Mescal Limestone is extensive (*17*). At Shell Mountain, the chert and terra rossa collapse breccias are more than 10 m thick. At both Beck Spring localities, paleokarst features include chert and terra rossa breccias, collapsed and dissolutionally condensed dolomite beds, and sediment-filled fissures and cavities. One locality (*25*) is overlain by a unit containing a breccia consisting of blocks of Beck Spring Dolomite. These disrupted strata are best interpreted as overlying strata that sagged or collapsed into a karst pit, or as parts of a karst pit wall that slid into the pit. However, exposures are incomplete and the brecciated dolomite could be part of a landslide deposited on a locally karsted Beck Spring surface. It is unclear whether the paleokarst formed before the Kingston Peak began to be deposited or whether early Kingston Peak deposition was interrupted by erosional events that locally stripped

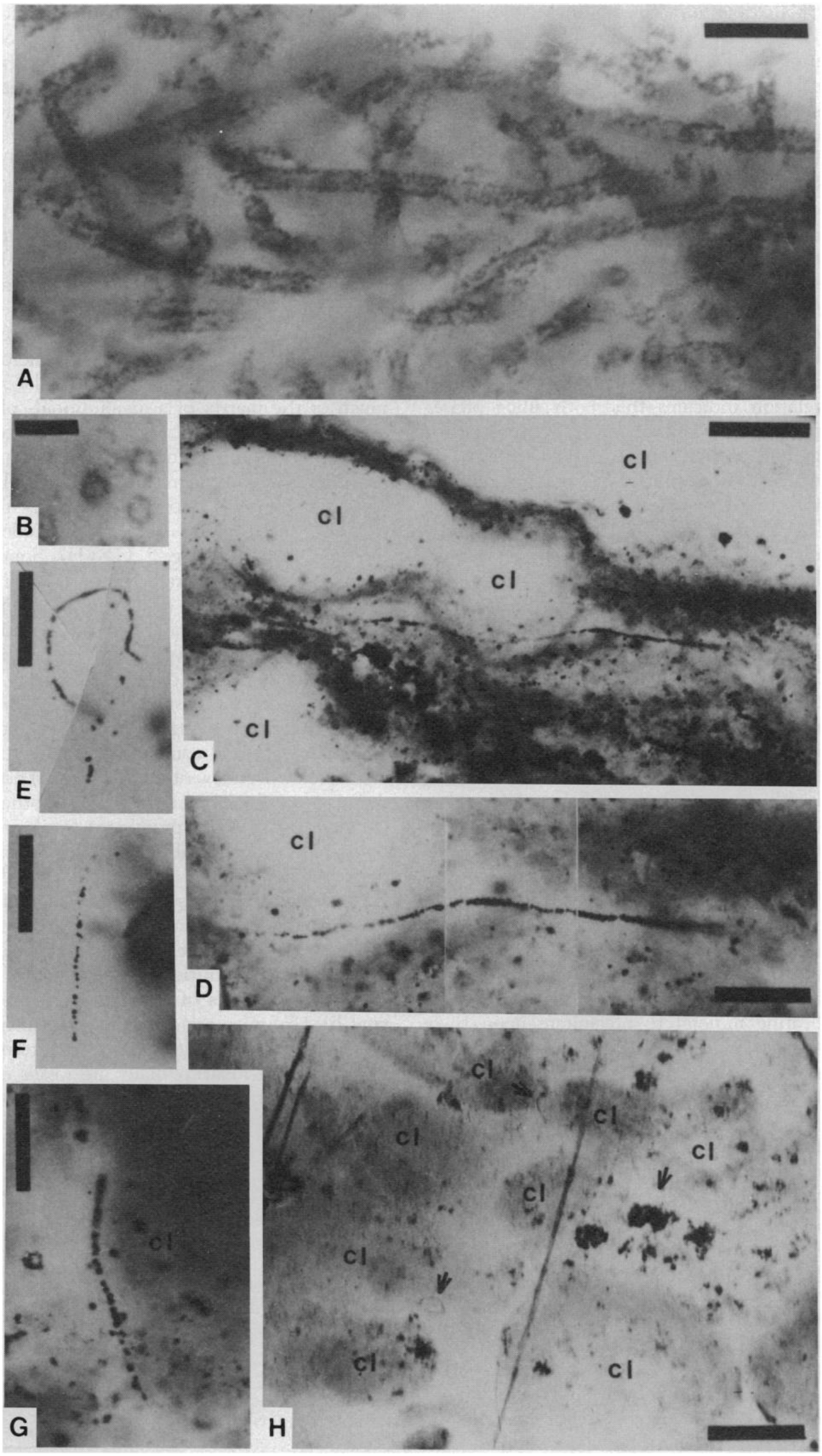


Fig. 5. Transmitted light optical photomicrographs of petrographic sections of chert from paleokarst at the top of the ~1200-million-year-old Mescal Limestone (A and B) and the ~800-million-year-old Beck Spring Dolomite (C through H) showing fossils of Precambrian terrestrial microorganisms (*44*). (**A** and **B**) Filamentous microfossils defined by submicrometer-sized hematite particles. Filament-mat fabric is illustrated in (A) and the circular nature of the relatively clear core of these filaments is illustrated in cross section (B). Bar scale is 10 μm in (A) and 5 μm in (B). (**C** through **H**) Filamentous microfossils defined by a string of 1- to 8-μm pyrite crystals or hematite pseudomorphic after pyrite. Fragments and clasts originating through dissolutional collapse are indicated (cl) in (C), (G), and (H). Microfossils occur between or on the periphery of clasts [the position of three microfossils is indicated in (H) by arrows]. (D) is an enlargement of the microfossil in (C), and (E) and (F) are enlargements of the microfossils shown in the lower left and right center part of (H). Bar scale is 200 μm in (C) and (H), 100 μm in (D), (E), (F), and (G). (D) and (E) are composite photomicrographs taken at different focal levels.

away the basal layers of the Kingston Peak Formation to allow karst formation on the Beck Spring.

Whole-rock isotopic analyses show that the uppermost surfaces of both carbonate units typically have low $^{18}O/^{16}O$ and $^{13}C/^{12}C$ ratios relative to those of the unkarsted parts (*13, 14*). These low values indicate that meteoric waters were responsible for the dissolution-precipitation events. Secondary carbonate rocks in a paleokarst pit in the Beck Spring Dolomite (*24*) have $\delta^{18}O = +26.9$ and $\delta^{13}C = -4.3$ (*28*), which are indistinguishable from well-documented examples of modern and Cenozoic subaerial alteration (*29, 30*).

A terrestrial origin for the Mescal microfossils is established by their occurrence in secondary, blocky quartz only found on the top of the Mescal paleokarst breccia, by the occurrence of ventifacts in the basal Troy Quartzite, and the fluvial and eolian nature of the lower Troy Quartzite. The Mescal paleokarst lies along an angular unconformity, indicating that karsting was related to tectonic uplift rather than eustatic sea level changes. It is an upland karst rather than a coastal, lowland karst (*31*), which might be an extension of the marine environment. The fossils are not marine fossils reworked from older strata because they occur as mats composed of intertwining, essentially unispecific filaments. These are attributes of a life assemblage.

A terrestrial origin for the Beck Spring paleokarst microfossils is established by several observations. The kilometer-sized slide blocks of Beck Spring Dolomite in the overlying Kingston Peak Formation (*32*) indicate that tectonism followed Beck Spring deposition. The paleokarst most likely developed in response to uplift rather than eustatic sea-level change, so it probably is an upland karst rather than a coastal karst. The microfossils are in secondary silica that replaced a matrix of very fine-grained carbonate and terra rossa in a dissolutional-collapse breccia associated with the paleokarst. This silica differs from the marine, microfossil-bearing chert that occur as clasts in the collapse breccia and as nodules and beds lower in the unit. The secondary silica lacks the silicified arrays of aragonite needles that are relatively common in early diagenetic chert elsewhere in the Beck Spring Dolomite. In some horizons the secondary silica contains many impurities, such as pyrite and hematite, and may appear cloudy in petrographic sections. In other horizons, it is clearer than the marine chert. It is unlikely that the microfossils are marine and were derived from erosion of the Beck Spring Dolomite. Some of the Beck Spring paleokarst fossils consist of crystals that are separated from one another; they could not have been transported in this state. Also, the distinctive elements of the marine Beck Spring fossil assemblage (*33*) are not found in the paleokarst silica. At least some examples should be present if reworking occurred.

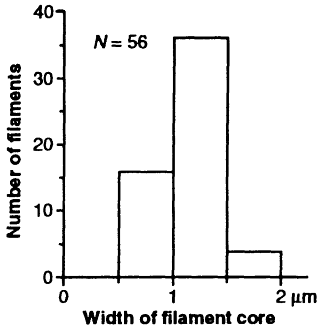


Fig. 6. Size distribution of hematitic filamentous microfossils in a ferruginous chert pebble derived from paleokarst at the top of the Mescal Limestone. Measurements were made on the clear cores of filaments that are oriented nearly perpendicular to the plane of the petrographic section. The measured filaments are in a ~1 mm² area of the section (USNM 448976).

For both the Mescal and the Beck Spring microfossils, it is impossible to discount completely the possibility that the preserved organisms lived in a pond within a karst pit; however, this is considered unlikely because there is no evidence for the existence of ponds in the outcrops examined. Evidence for ponds, such as finely and horizontally laminated fine-grained sediment or stromatolites in growth position, were not observed in the Mescal and Beck Spring paleokarst deposits.

Implications for Precambrian geology and paleontology. Dolomite samples along the top of the Beck Spring have $\delta^{13}C$ values as low as -5.4 per mil, implying a depletion of more than 10 per mil relative to the original marine +6 per mil value of the best preserved unkarsted parent rock (*14, 16*). At every locality the depletion in $\delta^{13}C$ values was observed. A depletion of at least 6 per mil was obtained for the Mescal at the Shell Mountain locality (*16*). These depletions are so large that we infer a significant cover of photosynthetic organisms. Carbonate that is dissolved in meteoric waters and then reprecipitated will suffer major changes in $\delta^{18}O$ values because oxygen is a major component of the water molecule, and the carbonate can isotopically equilibrate with this huge reservoir of oxygen. However, carbon recycled into the new precipitates from the host rock reservoir will not undergo any change in isotopic composition; $\delta^{13}C$ values of the secondary carbonate in the paleokarst will be identical to that of the host rock unless carbon with a different isotopic composition is introduced into the system.

The amount of carbon in atmospheric CO_2 dissolved in rainwater is insufficient compared to that derived by dissolution of the carbonate to account for the depletions in ^{13}C in the Mescal and Beck Spring paleokarsts. Carbon dioxide respired into ground waters by land plants and soil bacteria is the conventional explanation for carbon-isotope depletions of this magnitude in Phanerozoic paleokarst. The $\delta^{13}C$ values of respired CO_2 can be lower than -20 per mil, and this carbon makes up a significant component of the dissolved carbon reservoir in ground waters percolating downward through vegetated surfaces. Respired CO_2 is the simplest explanation for the low $\delta^{13}C$ values (*34*).

The morphology of the microfossils that we found is consistent with bacterial (including cyanobacterial) affinities, but it is possible that most of the ^{13}C depletion may actually have been due to organisms that for taphonomic reasons are not preserved in these cherts. It is unlikely that endoliths or highly localized microbial mats restricted to moist, protected areas could supply the pervasive amounts of soil CO_2 implied by the large ^{13}C depletions.

It has been argued that input of respired CO_2 into soils and weathering horizons was absent or greatly reduced relative to modern values before the advent of vascular plants (*35, 36*). However, the rate of weathering of calcium and magnesium silicates is strongly dependent on levels of soil CO_2, and this rate does not appear to have varied significantly over geologic time (*37*). High levels of soil CO_2 were therefore present before the advent of vascular land plants, and this condition has been attributed to higher levels of atmospheric CO_2 (*36, 37*). Little is known about CO_2 levels in soils beneath primitive microbial covers, and the arguments for negligible weathering effects of such covers have recently been challenged (*38*).

The low carbonate $\delta^{13}C$ accompanying the microfossils in our examples suggests that amounts of carbon respired into soil as CO_2 were comparable to those of terrains with vascular land plants (*39*). Our results are at odds with models that assume that the Precambrian land surface either was sterile or that respired CO_2 in soils was insignificant. If the nonkarst terrains were as extensively covered as the karst terrains, then microbial enhancement of silicate weathering in the Proterozoic could have been as great as that encountered on many terranes occupied subsequently by vascular land plants. It may not be necessary to invoke increased levels of atmospheric CO_2 to account for the apparent constancy of weathering before vascular plants evolved.

The presence of Precambrian terrestrial communities has additional significance. For example, microbial communities bind sediment and form protective layers over sediment. As a result, erosion by runoff and wind is inhibited. Microbes are important in the chemical weathering of minerals by directly or indirectly producing acids, bases, or chelating agents (*40*). Microbes also cause minerals to precipitate (*41, 42*). Interestingly, the hematite that defines the Mescal microfossils and occurs in the Mescal terra rossa could have originated by iron-oxidizing bacteria or by bacteria taking up chelated iron compounds (*41*). If land was continuously vegetated between 1200 and 800 million years ago, this would represent a substantial interval during which evolutionary innovations could have occurred on land (*43*).

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23. Chert pebbles containing the best-preserved microfossils were collected on a bench ~450 m southeast of the summit of Shell Mountain [*U.S. Geol. Surv., Young, Ariz., 15′ Topographic Quadrangle, Sierra Ancha Mountains, central Arizona* (1961)]. Microfossils in the chert cap occur ~350 m northeast of the summit of Shell Mountain.
24. This locality is near a drainage on a hillside 380 m N17°W of the northeast shaft of the Snow White Mine, [*U.S. Geol. Surv. Blackwater Mine (California) Provisional 7.5′ Topographic Quadrangle Map, Kingston Range, southeastern California* (1985)].
25. This locality is on a saddle 1000 m S33°E of the northeast shaft of the Snow White Mine.
26. Their tubular nature strongly supports biogenicity [see R. Buick, *Palaios* **5**, 441 (1991)].
27. A. V. Gutstadt and J. W. Schopf, *Nature* **233** 165 (1969); J. H. Oehler, *Alcheringa* 1, 315 (1977). The filaments in the secondary silica associated with the Beck Spring paleokarst are sinuous and unbranched, and many are composed of regularly spaced crystals suggesting mineralization within cells or within a sheath. In other Proterozoic chert, similar chains of hematite crystals grade laterally into pyrite crystals, and chains of these crystals pass laterally into chains of crystals that are enclosed by tubular, organic-walled microfossils and finally into tubular organic-wall microfossils lacking these crystals. Similar chains of hematite and pyrite occur in the marine Beck Spring chert lower in the section; however, this is a common mode of preservation for Precambrian microfossils, and it cannot be used to argue that the microfossils associated with the secondary silica in the paleokarst are marine. Views of different focal planes using oil-immersion optics show that these microstructures actually are filaments and not sheets.
28. $\delta^{18}O$ is the per mil difference between $^{18}O/^{16}O$ ratios in a sample and that in standard mean ocean water; $\delta^{13}C$ is the same for $^{13}C/^{12}C$ ratios where the Pee Dee belemnite is the standard. Sample was taken from matrix between paleokarst clasts.
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33. This includes the abundant coccoidal microfossils [G. R. Licarri, *J. Paleontol.* **52**, 767 (1978)] and vase-shaped fossils [R. J. Horodyski, in (*6*), appendix I (microfiche)].
34. Carbonate minerals precipitated from hydrothermal fluids can be depleted in ^{13}C relative to sedimentary carbonates, but these minerals are also greatly depleted in ^{18}O relative to the observed values. The paleokarst carbonate is different in isotopic composition from known hydrothermal carbonate minerals in both areas (*13, 14, 16*). Additionally, there is no field or petrographic evidence that the samples analyzed have been altered hydrothermally.
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39. Keller and Wood (*38*) argued that the amount of respired soil CO_2 attributed to primitive plants may have been lower but that high concentrations can still be achieved because of slow diffusion rates in the soils. Low $\delta^{13}C$ values, however, imply not only high concentrations of soil CO_2 but also an extensive biomass to supply the light carbon.
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43. There even may have been animal protists or metazoans exploiting this source of food, and some of their early evolutionary development could have occurred on land. Although we have not seen features in secondary silica from the Mescal and Beck Spring paleokarsts that would indicate the presence of eukaryotic organisms, this is a topic that should be investigated.
44. Specimens are curated in the Department of Paleobiology, U.S. National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC USNM numbers are provided and the location of each specimen is given in millimeters from the "X" inscribed in a corner of each slide, with the *x*-axis being parallel to the length of the slide and the *y*-axis parallel to the width of the slide. Figure 5, A and B, USNM-448976, 20.9*x*/8.7*y*; Fig. 5, C and D, USNM-448977, 10.0*x*/12.1*y*; Fig. 5E, USNM-448978, 12.9*x*/21.6*y*; Fig. 5F, USNM-448978, 11.8*x*/22.4*y*; Fig. 5G, USNM-448979, 26.3*x*/16.9*y*.
45. We thank C. Dennis Jr., K. A. Freedman, and A. M. Leverentz for assistance. B. Troxel alerted us to a chert concentration at the top of the Beck Spring Dolomite and to additional field localities in southeastern California. Field and laboratory studies were supported by NSF grant EAR-9105534 to L.P.K. and NSF grant EAR-9105159 and a Newcomb Foundation grant to R.J.H. Earlier field studies of R.J.H. in the Beck Spring Dolomite were supported by a grant from the National Geographic Society.

6 July 1993; accepted 22 December 1993