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SILICIFIED MISSISSIPPIAN PALEOSOL MICROSTRUCTURES: EVIDENCE FOR ANCIENT MICROBIAL-SOIL ASSOCIATIONS

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Abstract

Silica-replaced microfeatures in a well-developed, Upper Mississippian paleosol from north-central Arizona, were examined by scanning electron microscopy using back-scattered electron imagery. Preserved microfeatures include hollow and solid tubiform filaments and mycelium-like stringers which radiate from problematic (biogenic?) soil structures. Preservation of these features suggest that microstructures in the soil zone are not uniformly destroyed during post-diagenetic silica replacement and that biological soil symbionts may have occurred as early as the Upper Mississippian (~280 Mya).

Key Words: paleosol, Scanning Electron Microscopy, Upper Mississippian, soil microstructures, Redwall Limestone, secondary silica, microcodium, Arizona.

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Introduction

Recognition of soil microstructures preserved in altered paleosols (ancient soils) may complement data from other sources when trying to distinguish between paleosols and similar clay-rich deposits found in the geologic record. The presence of paleosol microstructures is also important for developing an understanding of the role of soil microorganisms through geologic time. One of the principle drawbacks in the study of paleosols is that ancient soil material is rarely preserved without having been diagenetically altered to some degree. Often the degree of alteration and replacement is considerable making field recognition difficult at best. Because of this, it would be useful to know that certain features which are diagnostic of modern soils are not uniformly destroyed during post-diagenetic replacement events. The results presented herein have significant implications for basic paleoenvironmental and stratigraphic interpretations (i.e., identification and documentation of true paleosols) as well as research into diagenetic effects and processes. Additionally, paleosol horizons previously considered to be (a) of minor paleoecological significance, or (b) unsuitable for detailed analyses (owing to post-diagenetic events), may warrant closer inspections.

We have collected paleosol samples from various localities at the top of the Upper Mississippian (~280 Mya) Redwall Limestone, north-central Arizona, U.S.A. The paleosol samples contained isolated biogenic features and microstructures preserved in silica. The aim of this paper is to describe the features and show that silica-replaced, post-diagenetically altered paleosols still contain preserved features that are recognizable, or interpretable, under microscopic analyses.

Materials and Methods

Scanning electron microscopy (SEM) using back-scattered electron (BSE) imagery was used to investigate soil microstructures preserved in Upper Mississippian (~280 Mya) paleosols. Several profiles in north-central Arizona along Hunter Creek (Fig. 1) were sampled and sectioned. The sections were then polished with progressively finer grit and sputter-coated with 200 angstroms of carbon prior to viewing in a ISI SS40 SEM at 20 kV using a solid state detector surrounding the final lens. BSE imagery was used in order to obtain the z contrast (different average atomic numbers) of the material. BSE imagery permits contacts between the various minerals in fine-grained material to be seen quite clearly.

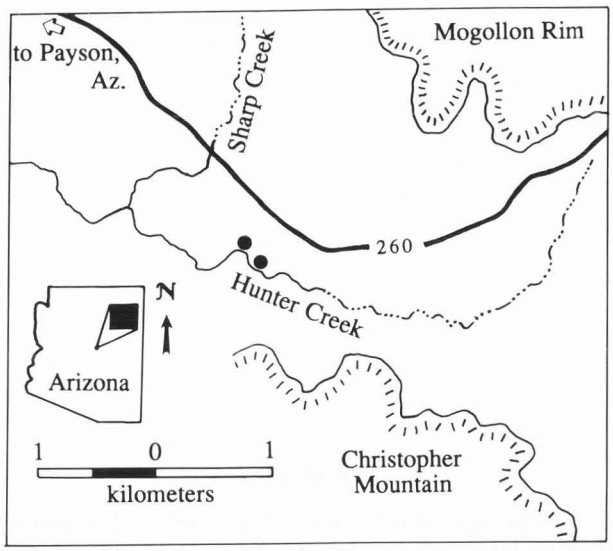

Fig. 1. Index map of main sample sites (solid dots) along Hunter Creek (north-central AZ., (USA).

Paleosol samples containing the greatest concentration of microstructures occur in a silicified zone (Fig. 2) from an exposure south of the Mogollon Rim along Hunter Creek in Arizona (SE 1/4, S33, T11N, R13E, Woods Canyon Quadrangle; Fig. 1). Preserved biogenic structures occur in silicified (a) residual clasts and corroded grains and, (b) rubbly to fine-grained, red-brown, terra rossa soil preserved in fractures and depressions. These depressions may represent former soil carbonate and solution channels in soil.

Background

The Redwall Formation (in the study area; Fig. 1) contains a full spectrum of preserved paleokarst features developed under a regionally extensive, pre-Pennsylvanian exposure surface (McKee and Gutschick, 1969; Sando, 1988). The Redwall Formation is unconformably overlain by a marine carbonate (Pennsylvanian Naco Group). During subaerial exposure of the Redwall Formation an aerially extensive, red residual paleosol and rubble breccia developed at the top of the formation (Kenny, 1989). The color red is attributed to the presence of ferric oxide as hematite. Carbonate was leached from the profile and portions of the paleosol have been diagenetically altered including having been replaced by silica. The paleosol often lacks distinct laminar horizons and is therefore best described as a terra rossa rather than a ferruginized laterite (cf., Weider and Yaalon, 1972). The paleosol is similar in lithology, age and origin to a regionally extensive paleosol that occurs north and northeast of the study area (Power, 1969).

Modern soil studies have documented both a relatively high density of microbial soil populations (Curl and Truelove, 1986) and their critical role in soil development (Starks et al., 1981). Soil microorganisms are an important component in modern soils and yet relatively little is known about paleosol microorganism associations. Only recently has evidence for ancient microbial soil populations been reported (Wright, 1986; Kahle, 1977). The geological range of ancient soil microbial populations is only poorly understood at present, but at least one study suggests that morphologically conservative fungi may extend to the Lower Paleozoic (~400+ Mya; Sherwood-Pike and Gray, 1985).

Modern soils contain three major groups of microflora: the bacteria, fungi, and algae (Alexander, 1977). Microfloral density per gram of fertile soil, as estimated by Nicholas (1965), indicate the following numbers: bacteria 10^6 - 10^9, fungi 10^4 -10^5, and algae 10^1 - 10^3. Given both the relative abundance of modern soil microflora and optimum environmental conditions (i.e., a Ca-rich soil environment), it is likely that at least some partial preservation through calcification will occur. Calcification leading to microfloral preservation (in the Basidiomycetes) has been recently documented in modern soils by Callot et al., (1985a). Calcified microstructures in well-preserved paleosols have also been documented which are consistent with modern microbial-soil microstructures (Wright, 1986; Klappa, 1979).

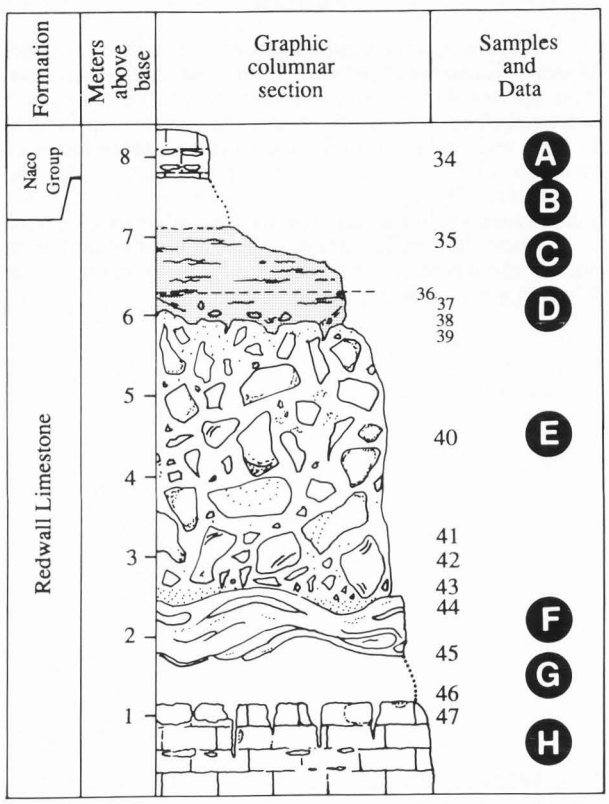

Fig. 2. Diagrammatic columnar section of red residual rubble and paleosol (Hunter Creek, Arizona). Description of lettered items: (A) nodular, mottled carbonate; (B) rubble-covered disconformity; (C) kaolinitic residuum; terra rossa paleosol; noncalcareous reddish-brown to brick red (2.5 YR or redder) with clay skins on peds and micro-slickensides (in thin section); all horizons are discontinuous; composition is not uniform; (D) soil clasts, fractures and channels; zone of silicification below dashed line; (E) cave collapse, rubble material; indurated, disoriented, weathered and corroded cherts (some color banded) in a red kaolin matrix; (F) fine-grained, fluvial flow-like structures of basal cave fill / cave deposits; (G) rubble-covered section; (H) grikes (solutionally opened or enlarged joints) as evidence for percolation of acid waters.

Modern Soil Microstructures

Modern soil microstructures attributed to biogenic processes include needle fibres, *Microcodium* (see Klappa, 1978), soil filaments in the soil and around root sections (see Wullstein and Pratt, 1981), and grain coatings (see Wright, 1986; Wright et al., 1988).

Needle fibres are a morphologically rare form of low-magnesian calcite, 1-4 μm wide and up to 100 μm long. Needle fibres have been reported as either bundles or as randomly disposed fibres in Quaternary (Ca-rich) soils (James, 1972; Ward, 1975; Harrison, 1977; Calvet and Julia, 1983; Philips and Self, 1987; Philips et al., 1987). Although the origin of needle fibres is uncertain, the association with soil microorganisms is noteable and a biological origin has been stressed by several workers (Chafetz et al., 1985; Callot et al., 1985b). However, James (1972) explained the occurrence of needle-like fibres to result from inorganic processes. Detailed studies by Wright (1984 and references therein) have shown that needle fibres are intimately associated with soil microorganisms and that growth of the acicular needles may in fact require the "support" of a filamentous organism. If we accept the above reasoning, then it follows that needle fibres in paleosols most likely result from indirect, biogenic precipitation of carbonate by microorganisms, possibly on plant rootlets, in the rhizosphere.

Microcodium is a problematic soil microstructure associated with caliche and paleokarst cavities which has an elongate or spherical, petal-like morphology ranging in size up to about 2 mm in length (Esteban and Klappa, 1983). *Microcodium* is presently interpreted to represent a symbiotic association between fungi and cortical cells of roots (Klappa, 1978). The exact microbiological affinity of *Microcodium* however, is still an open question. Isotopic analyses of organic carbon from *Microcodium* are depleted in ^{13}C, relative to host carbonate, suggesting a biological origin for the *Microcodium* carbon (Bodergat, 1974). Samples containing *Microcodium* have been reported from Recent to Upper Jurassic. A single specimen from Paleozoic (or possibly younger) shales of Missouri has also been reported (Wood and Basson, 1972).

Biogenic soil filaments occur as calcified hollow tubes, borings, or epilithic forms which may be straight, curved, or branched. Soil filaments from Quaternary soils have been reported with diameters that range from 0.5 to 20 μm (James, 1972; Ward, 1975). Klappa (1979) reported hollow and solid tubules from Mediterranean Pleistocene to Recent calcretes; these were interpreted as soil fungi, algae, actinomycetes, and root hairs. Knox (1977) reported filaments from South African caliche; these were interpreted as calcified fungal, algal or bacterial remains. James (1972) reported tubular features from Holocene caliche horizons in the Barbados, interpreted as having algal affinities. Calcified, filamentous soil microstructures have been suggested by various authors to result from microbial-soil interaction and association.

Redwall (Mississippian) Paleosol Microfeatures

As shown in Figure 3, elongate to cylindrical structures with radiating, petal-like features occur in soil clasts and within terra rossa soil joint networks. The exact microbiological affinities of these structures are unknown and may not be determinable because of diagenesis and silica replacement. However, the specimens superficially resemble some form of *Microcodium* based on a morphologic comparsion to Recent and Pleistocene examples, although some morphological differences between the modern and ancient specimens are noteworthy. In cross-section, the ancient specimens resemble columns of *Microcodium* but lack the prominent tubular or elongate structure often associated with modern specimens (Esteban written commun., 1990, 1991). It is possible therefore, that the structures may represent lithified and preserved plant debris (discussed later).

The "microcodium-like", problematic soil structure specimens from the Redwall paleosol occur as single or twin aggregates or as slightly elongate structures with prisms or palisades that radiate from central nuclei. Apparent dimensions range from 100-600 μm in diameter. The nuclei range in diameter from 25 to 150 μm and most have anastomosing fibres or "fine threads" which radiate outward from the core. These internal microfibres range in length up to 200 μm and have occasional "Y" branching patterns. Each specimen is concentrically bound by an aureole of multigeneration fibres (Fig. 4). Microtubules and microborings perforate both the problematic soil structure and enveloping microfibre arrays. These hyphae-like microtubules and microborings support a biological origin. *In situ* growth is indicated by structure truncations within the host paleosol.

As shown in Figure 3, numerous subparallel arrays of slightly altered needle-like fibres occur as envelopes around the soil structures. These needle fibres often coalesce and form "bridges" between two or more structures. Individual needles range from 10-60 μm long and occur as bundles and randomly disposed features.

Esteban (1974) introduced the term alveolar (root moldic porosity of Harrison, 1977) to describe cylindrical to irregular pores in soil caliches. Alveolar structure is a petrographic fabric composed of semicircular or irregularly-shaped oval pores or "moulds" that are not recognizable as former biotic grains. The structure has been widely used by geologists (e.g., Esteban, 1974) to describe a network of soil-rootlet channelways. However, the term alveolar has also been used by soil micromorphologists to describe the release of gases during wetting and drying episodes in soils. In the latter case, alveolar structures are not associated with soil septae. Wright (1986) has suggested that the term alveolar be modified to "alveolar-septal structure" when arcuate septal structures are present. This term has been adopted throughout the paper. Figure 5 illustrates features interpreted as preserved alveolar-septal structures. These structures occur in localized areas in both terra rossa residuum and laminar crusts within the Redwall paleosol.

As shown in Figure 6, preserved tubiform structures occur in microfibre aureoles. The structures range from 6 to 10 μm in diameter. The filaments appear to have the same composition as the matrix material and occur as individual laminar crusts and along the periphery of the soil structures; hence, the filaments and borings do not appear to be a later contaminant. Solid rod filaments occur as gently to moderately curved "elongate" features with diameters that range from 5 to 15 μm (Fig. 7).

Considerations

Silicification

During chemical weathering silicate materials (e.g., chert and clays) breakdown releasing silica. Release and accumulation of silica is associated with (a) hydrothermal

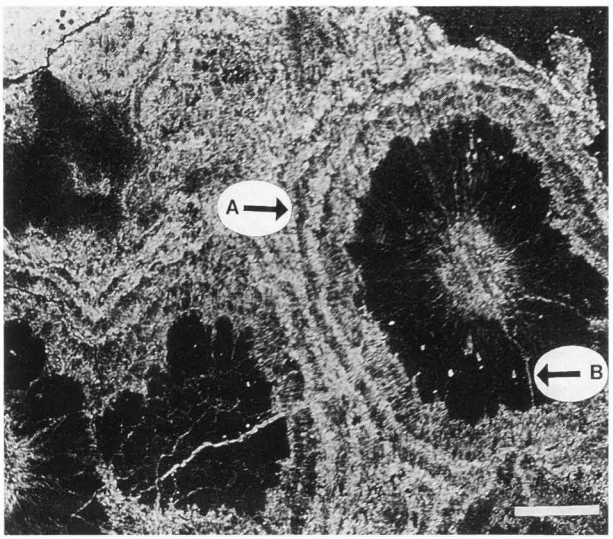

Fig. 3. SEM micrograph using BSE imagery of problematic "microcodium-like" soil structure in post-Mississippian paleosol. Structures are elongate to cylindrical with radiating, petal-like features and occur in the zone of silicification (see Fig. 2; area D). The following citeria suggest a biological origin. (1) Subparallel arrays of needle fibres that form concentric aureoles around the structure (arrow A). (2) Anastomosing filaments or "threads" that radiate from a central core (arrow B). (3) Hollow, tubiform microfilaments that occur in both core and needle fibre sites (see Fig. 4). Several of the soil structures from the paleosol are also cross-cut by late generation silica features. These fracture fills however, are readily distinguished from internal (biogenic) silica replacement features. Structure has been preserved by silica and iron oxide. Apparent dimensions range from 100-600 μm in diameter. Scale bar in lower right represents 100 μm.

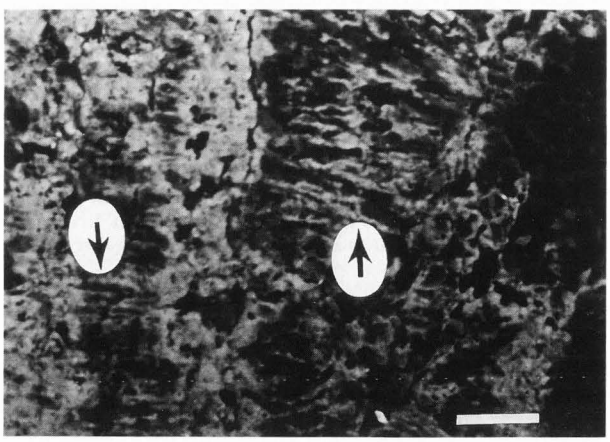

Fig. 4. SEM micrograph using BSE imagery of altered, silica-preserved, multigeneration needle fibre arrays (arrows). Micrograph is an enlargement of the concentric aureole around the problematic "microcodium-like" soil structure in Figure 3. Needle fibres range from 10-60 μm in length. Scale bar in lower right represents 10 μm.

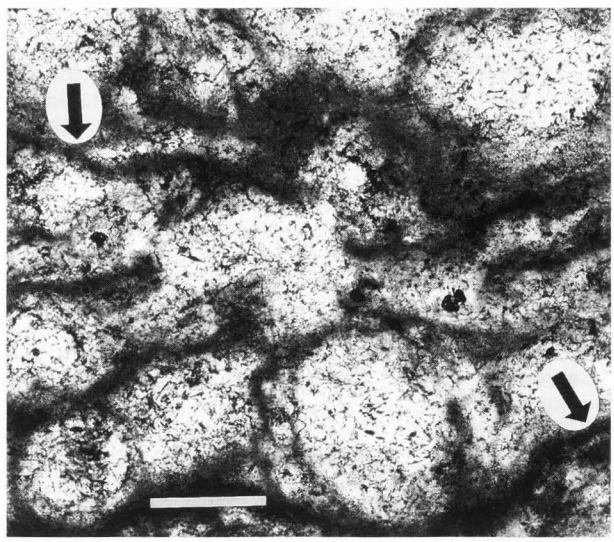

Fig. 5. Photomicrograph showing alveolar-septal structure in upper paleosol (area C on Fig. 2). Arrows point to arcuate septal structures around circular-ovoid pores. Scale bar in lower left represents 0.1 mm.

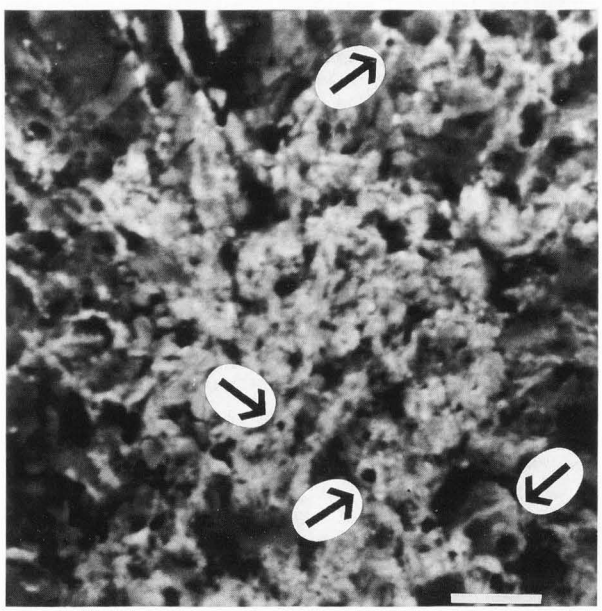

Fig. 6. SEM micrograph using BSE imagery of hollow-center, tubiform filaments (arrows) in problematic "microcodium-like" soil structures from post Mississippian paleosol. Photomicrograph is of tubiform filaments within the concentric aureoles which surround the "microcodium-like" soil structure of Fig. 3). Microfilaments and microborings have apparent dimensions that range from 0.5 to 3 μm. The microfilaments have the same composition as the matrix material suggesting that the features do not represent recent contaminations. Scale bar in the lower right represents 5 μm.

alteration, (b) deep burial, or (c) deep-weathering profiles. In deep-weathering profiles (e.g., terra rossa profiles such as the present study) preciptation of near-surface silica (called secondary silica) occurs at various suitable sites within a profile. The history of silica leaching and precipitation under near-surface processes is extremely complex; we are still far from understanding the kinetics of silica in soil systems or the total role it may play in natural soil profiles (Flach et al., 1969; Mohr et al., 1972; Thomas, 1974). Numerous factors (pH, climatic variations, biogenic activity, soil permeability, etc.) can influence the processes of silicification and desilicification during the development of deep-weathered soils. However, secondary silica precipitated under near-surface conditions must, by definition, be precipitated in the presence of meteoric (fresh) water. Stable isotopic analyses of the D/H and $^{18}O/^{16}O$ ratios of water entrapped within the silica structure at the time of silica crystallization can be used to help constrain the timing of the silicification event and the environment of precipitation. In the present study, it is important to be able to constrain the silicification event to the time of subaerial weathering because silicification events could conceivably occur at any time during the diagenetic history of the sequence.

As detailed in Knauth and Epstein (1976), D/H and $^{18}O/^{16}O$ ratios of water entrapped within the silica structure can be determined and the results used to see if meteoric waters were involved in the crystallization history of the silica. While it is not the intent of this paper to detail the complexities of this approach (the reader is refered to Knauth and Epstein, 1976; Kenny and Knauth, 1992), we can show that preliminary stable isotopic ratios of the paleosol silica are depleted in ^{18}O and D compared to marine cherts from the Redwall Limestone (Table 1). The depleted isotope values indicate that the paleosol silica precipitated in the presence of lighter meteoric water (relative to heavier marine water values; Table 1).

As mentioned in the Background section, the Redwall paleosol is overlain by a marine carbonate formation (Naco Group). The precipitation of a substantial thickness of marine carbonate in the Naco Group required a major marine transgression. Such a transgression would have completely saturated the permeable paleosol with ocean water and any free silica would have precipitated in the presence of isotopically heavier ocean water (i.e., the D/H and $^{18}O/^{16}O$ ratios of the water in the silica would have a marine isotopic signature). Therefore, the depleted isotopic values obtained for the paleosol silica infer that paleosol silica precipitated (a) in the presence of meteoric waters during the deep-weathering event, and, (b) prior to any large-scale marine transgression and incursion of marine water.

Biogenicity and preservation of soil microstructures

Microcodium-like structures have been recorded from soils as early as the Upper Jurassic (Klappa, 1978). While we maintain a cautious view, the features presented herein may suggest greater antiquity. However, because of the slightly altered nature of the preserved material, it is not possible to determine the actual biological affinity of the soil structures found in the Redwall paleosol. Nevertheless, based on gross morphological features including radial wall prisms, filaments radiating from discrete central nuclei, association with spherical microborings or microfilaments, and needle fibre aureoles, we consider these soil structures to be biogenic and similar to *Microcodium* .

Alternatively the soil microstructures may be interpreted as partly preserved, silicified plant debris because they lack the clearly developed tubular trend often associated with modern *Microcodium*. Plant debris silicification is a permeation or void-filling process (Sigleo, 1978). Silicic acid permeates the cellular structure, replaces the cellular fluids and precipitates between the cell walls thereby preserving, in remarkable detail, the tissue structure of the plant debris (see Hesse, 1989). In the soil structures of the present study, cellular structure of the original tissue is not well-preserved while other unusual and delicate microstructures are preserved (Fig. 5,6 and 7). This suggests that the soil structures should not be strictly interpreted as silicifed plant debris which does occur (well-preserved) elsewhere in the section (also within the zone of silicification).

Initial preservation of biogenic, soil-related microstructures is believed to be achieved via calcification. Callot et al. (1985a) documented calcification in the Basidiomycetes and other workers have recorded direct relationships between mineralization and microbial filaments (Klappa, 1979; Calvet and Julia, 1983; Julia, 1983). The microfeatures preserved in the Redwall paleosol differ from previous investigations because much of the host material has been replaced by silica and iron-rich impurities. The presence of silicified plant debris along with silicified soil-related microfeatures indicates that most biogenic material in the zone of silicification has been replaced by silica. However, direct evidence of precursor calcite replaced by silica cannot be obtained because most of the calcite in the profile has been effectively removed or leached out during the deep-weathering event. Nevertheless, we feel that the association of silicified plant material and silicified

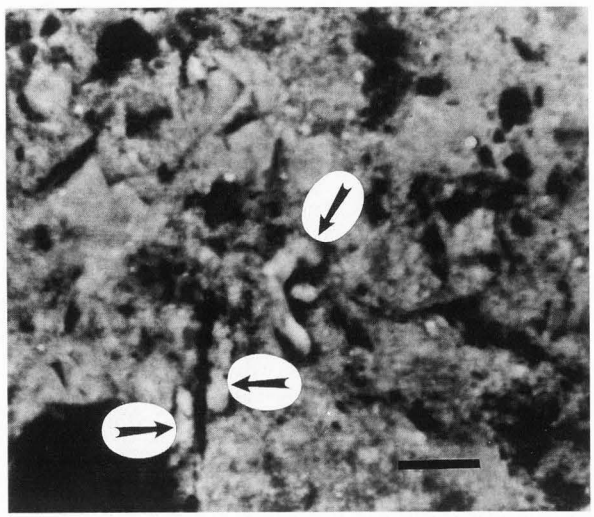

Fig. 7. SEM micrograph using BSE imagery of altered, solid rod filaments from post Mississippian paleosol. Solid filaments occur within the concentric aureoles which surround the "microcodium-like" soil structures and at the edges of the void-filling silica (paleoroot channels?). Solid rod filaments have been replaced by silica and occur as gently to moderately curved, *in-situ* features with diameters that range from 5-15 μm. These solid rod-like forms are locally but irregularly preserved in the paleosol. The rods appear too thick to be flagella. Observed rods resemble microorganisms reported by Wullstein and Pratt (1981) which were associated with rhizosheaths of modern, xeric grasses. Scale bar in lower right represents 5 μm.

microstructures is sufficient to infer that the initial material involved in the delicate preservation of the soil-microstructures (most likely calcite) was replaced by silica.

It is also unlikely that the soil-related microstructures are detrital; the delicate features that are preserved could not have survived any significant mechanical transport. Although the specimens may or may not be directly analogous to modern *Microcodium* samples (owing to the slightly different morphology), we nevertheless interpret the "microcodium-like" specimens to be biogenic.

Another possibility is that the soil structures may represent preserved popcorn-like concretions which form in the shallow vadose zone of certain subaerial exposure surfaces. Morphologically, inorganically-precipitated concretions form as continuous concentric bands and lack fungal microborings as an integral part of the structure. Given that the specimens have preserved, biogenic microtubules and filaments, we believe that it unlikely that these soil structures formed as abiotic, inorganic concretions.

Conclusions

Several biogenic soil features have been identified from the Upper Mississippian Redwall paleosol: (a) hollow tubiform, filamentous microstructures resembling remnants of microbial organisms or microborings; (b) needle fibre textures; (c) problematic "microcodium-like" soil structures in soil clasts bounded by multigenerations of concentric needle fibres; (d) alveolar-septal structures considered diagnostic of paleoroot channelways or networks; and, (e) rod-shaped filaments. We interpret the collective occurrence of these features as evidence of geologically early soil microbial activity.

The findings presented herein (a) suggest that minor post-diagenetic alteration and replacement by silica does not uniformly destroy soil features and microstructures associated with the microbial-root environment; and (b) lend additional support to the studies of Wright (1986) who suggested that microbial-root associations and related biogenic structures may have appeared as early as the mid Mississippian.

Table 1. Stable isotopic data, type and location of silica and chert, Redwall Limestone (Az.). Data are presented in the standard δ notation in ‰ relative to standard mean ocean water (SMOW). Reproducibility of $\delta^{18}O$ is ± 0.2‰ and ± 2‰ for δD.

sample	δD	water content (wt. %)	$\delta^{18}O$ (SMOW)	type
fr-58	-58	0.15	29.5	nd-e-tr+gm-wh+rd
fr-72	-63	0.20	29.8	nd-e-tr+gm-wh+rd
fr-39	-85	0.30	18.9	s-fb+gm-wh+rd
fr-38	-90	0.20	20.2	s-fb+gm-wh+rd
fr-38a	-87	0.18	20.8	s-fb+gm-wh+rd

Notes: All samples are from Hunter Creek, AZ.
wh = white rd = red nd = nodular
tr = translucent e = early diagenetic chert
fb = fibrous s = subaerial silica (in zone of silicification)
gm = granular - microcrystalline quartz

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Discussion with Reviewers

V.P. Wright: Perhaps the authors can speculate further on the whether they are dealing with Endo / ectomycorrhizae.
Authors: In order to accurately determine whether or not a specimen contains one or the other mycorrhiza the specimen should be either Modern (with the mycorrhizal relationship with the cortical cells of the roots clearly observable) or extremely well-preserved; in this paper we are dealing with neither. One of the main points of our paper is that we no longer have primary calcite preserving these features but instead have some intriguing specimens that are completely replaced by silica. While we would enjoy speculating on this topic and we appreciate the importance of it, we feel that it would be difficult to justify this "speculation" scientifically (in our case). Additionally, such a determination is not the thrust of this paper; the topic has been dealt with in detail by Klappa (1978). The key issue is not whether we are dealing with endo- or ecto- mycorrhiza - rather it is the preservation of these microstructures in a diagenetically altered paleosol (which could open up a whole new area of research). Finally, while we often divide mycorrhizal systems into endotrophic and ectotrophic systems (for convenience), as in all biological systems, there is often no clear-cut distinction between the two. Numerous intermediates occur and have been labelled ectendotrophic in recognition of the difficulty of placing them in either catagory. We feel that our samples do not provide enough unambiguous relationships to allow us to speculate further than we already have. We would also like to note that the term endomycorrhiza has essentially been replaced by the more descriptive term, 'vesicular-arbuscular mycorrhiza' (VAM).

V.P. Wright: Why are the filaments in your specimens so regular?
Authors: Klappa (1978) also noted that in some of the *Microcodium* samples he studied, the filaments formed a very organized pattern; this may be why the radial filaments in our specimens are so regular.

J.A. Raven: What reasons could be suggested for preservation of the problematic soil structures, but not of plant debris?
Authors: This is a very insightful question. In fact, we have some features which have been interpreted as silicified wood pieces and scattered plant debris; we also plan on persuing this topic. We have amended the text so that the reader understands that there is also silicified plant debris. However, we should also point out that the silicified, biogenic microfeatures are only locally preserved and are surrounded by ferric oxides (terra rossa). The accumulation of ferric oxides generally indicates a lack of preserved organic material for one of the following reasons:

(a) permanent or seasonal aridity;
(b) high temperatures coupled with an active microbiota; or
(c) infertility of the soil.

The first two possibilities - in particular the first - seem the most likely because the climate was humid enough to permit exceptionally deep and prolonged weathering. However, the evidence we present suggests that the presence of ferric oxide does not 'automatically' indicate that organic material will not be preserved.

D.C. Bain: What is the evidence for the calcite being ferruginized and replaced by silica?
Authors: This is an excellent question but again gets back to understanding the basic concept of complete silicification

within the part of the profile that we are dealing with (zone of silicification - see Figure 2). As mentioned under the 'consideration' section (new material) we also have a minor amount of wood pieces and scattered plant debris which have also been partly silicified. This indicates to us, albeit indirectly in regards to the present problem, that biogenic material within this zone has been replaced by silica. Direct evidence of calcite being replaced by silica cannot be obtained from material in a profile in which all of the calcite has been effectively removed or leached-out during the episode of prolonged and deep weathering. The replacement therefore, is infered based partly on the consideration given above. Many of the features that we observed in section are morphologically similar to features precipitated as calcite in a modern soil zone. Based on these striking morphologies (preserved in silica along with the ubiquitous ferric oxide - coupled with the documented ability of silica to replace material on a cell-by-cell basis), we infer that these features are silica-replaced. We have made this point - that this is an inference - more clear in the revised text.

D. Jones: What do the authors mean by 'would lack fungal microborings as an integral part of the structure'?
Authors: The question refers to an alternative hypothesis that we thought might be responsible for the observed structures. Specifically, we were refering to features known as 'soil popcorn' which may precipitate in the vadose zone in some areas. In fact, these popcorns are concretions; concretions form through concentric precipitation of inorganic calcite. The key here is that the calcite precipitation is inorganic. Hence, it is unlikely that fungal microborings (endo- or ecto -mycorrhiza) would be a part of an inorganically precipitated microstructure; put another way, it is unlikely that the fungi would be an integral part of the (inorganic) structure. In light of the question, we have changed the text so that it is clear that popcorn-like concretions are inorganic precipitations.

W.J. McHardy: Why did the authors not try secondary electron imaging of the same fields of view?
Authors: As pointed out in the new section dealing with analytical methods, the specimens were all prepared as polished thin sections and not resin-impregnated chips. This preparation was done specifically so that we could locate the various specimens first using a polarizing light microscope and then work with the SEM. Hence,we specifically used BSE imagery on these samples; secondary electron imagery on the polished sections provide little additional evidence. The advantages of the BSE imagery is that we are not just dealing with surface topography (as in the SE mode) but are viewing incident electrons which are back-scattered out of the specimen itself allowing us (among other things) to get the z contrast of the material (since initially we were looking for trace calcite). The fact that these were prepared as polished sections should have been pointed out in the first version of the manuscript and this oversight has been corrected in the analytical methods section.