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DIAGNOSTIC PHYTOLITHS FOR A PONDEROSA PINE-BUNCHGRASS COMMUNITY NEAR FLAGSTAFF, ARIZONA

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ABSTRACT—Phytolith analysis could play an important role in understanding vegetation dynamics in southwestern ponderosa pine (*Pinus ponderosa*) forests, which have been dramatically altered by fire suppression and other factors. My objectives were to develop a phytolith reference collection and classification system for a ponderosa pine-bunchgrass community found near Flagstaff, Arizona. I examined 27 species of grasses found in and around the study area and ponderosa pine for diagnostic phytoliths. Twenty other species common to the area were examined for redundant phytolith forms. Eight phytolith forms were identified, including a diagnostic phytolith for ponderosa pine, the spiny body. The general Poaceae subfamily system validated by numerous researchers is applicable to this community. Examination of phytolith shape frequencies show that for 7 species in the subfamily Pooideae, and 1 species in the Panicoideae, very few (0 to 5%) nondiagnostic phytolith forms were present. Nondiagnostic phytoliths, particularly rondels, were more common (7 to 22%) for the 3 species from the Chloridoideae subfamily. This result is consistent with the observation by other authors that all grasses produce rondel forms and indicates that rondels will be over-represented in phytolith assemblages in comparison to actual vegetation. The ponderosa pine spiny body appears to be a useful diagnostic for this area and vegetation reconstructions using soil phytolith assemblages based on the system developed in this study could be used to understand grass-tree and grass vegetation dynamics.

RESUMEN—Los estudios de fitolitos pueden jugar un papel importante en la comprensión de la dinámica de la vegetación en los bosques de pino ponderosa (*Pinus ponderosa*) del sudoeste de los Estados Unidos, los que han sufrido modificaciones drásticas debido a la eliminación de incendios y a otros factores. Mis objetivos fueron desarrollar una colección de referencia fitolita y un sistema de clasificación para una comunidad de pino ponderosa y zacate cercana a Flagstaff, Arizona. Examiné 27 especies de pastos encontradas en y alrededor del sitio de estudio y en pino ponderosa para fitolitos diagnósticos. Se estudiaron otras 20 especies comunes en el área para ver si presentaban formas de fitolitos redundantes. Se identificaron 8 formas de fitolitos, incluyendo un fitolito diagnóstico de pino ponderosa: el cuerpo espinoso. El sistema general de subfamilias de Poáceas anteriormente presentado por otros investigadores es válido para esta comunidad. Examinación de la frecuencia de formas de fitolitos indicó que para 7 especies de la subfamilia Pooideae y una especie en la subfamilia Panicoideae presentaron muy pocos fitolitos no diagnósticos (0 a 5%). Estos mismos fitolitos, especialmente los circulares (rondels), fueron más comunes (7 a 22%) en las tres especies de la subfamilia Chloridoideae. Este resultado coincide con la observación de otros autores de que todos los pastos producen rondels, e indica que es esperable que las formas circulares estén sobre-representadas en el banco de fitolitos en comparación con la abundancia de los pastos en la comunidad vegetal. El cuerpo espinoso del pino ponderosa parece ser una forma diagnóstica útil para esta zona. El sistema presentado en este trabajo puede usarse para reconstruir la vegetación, y así entender mejor la dinámica vegetal de pasto-arbol y pasto.

The use of diagnostic phytoliths, or phytolith analysis, is playing an increasingly important role in environmental reconstruction and interpretation of plant community dynamics

(Rovner, 1971; Carbone, 1977; Kurmann, 1985; Jiang and Piperno, 1998; Fredlund et al., 1998; Kealhofer and Penny, 1998; McClaran and Umlauf, 2000). Phytoliths are plant silica remains that can be diagnostic at various taxonomic levels and occur throughout the plant kingdom (Piperno, 1988). Upon death and decay of plant material, phytoliths remain in the depositional environment and can be used to examine vegetation history and dynamics. As a method for determining prior reference conditions, phytoliths have several advantages over other types of plant fossils such as pollen. For example, they are persistent in oxidizing environments such as soil (Wilding et al., 1977). Moreover, it is difficult to use pollen analysis to distinguish ecologically diverse groups within the grass family (Ritchie, 1976; Kurmann, 1985).

Prior to Euro-American settlement, frequent (2 to 12 per year), low-intensity, surface fires characterized semi-arid ponderosa pine (*Pinus ponderosa*)-bunchgrass communities typical of the Intermountain West (Cooper, 1960; Dieterich, 1980; Covington and Moore, 1994*a*, 1994*b*; Swetnam and Baisan, 1996; Covington et al., 1997; Fulé et al., 1997). Beginning in the early part of this century, fire suppression, overgrazing, and a warm and wet climatic period led to an irruption of pine regeneration (Cooper, 1960; White, 1985; Savage et al., 1996; Mast et al., 1999). Concurrent changes in understory plant communities are likely; however, quantitative studies regarding prior conditions for understory plant communities in ponderosa pine forests of the Southwest are lacking. Understanding vegetation history is a crucial step in determination of reference conditions, a critical component of ecosystem management and restoration ecology (Kaufmann et al., 1994; Morgan et al., 1994; Christensen et al., 1996).

Phytolith analysis could play an important role in understanding vegetation dynamics in these communities; however, examination of local flora is required before phytolith analysis can be reliably applied. Several researchers have investigated diagnostic Poaceae short-cell phytoliths in other grassland ecosystems (Metcalfe, 1960; Twiss et al., 1969; Brown, 1984; Mulholland, 1989; Mulholland and Rapp, 1992; Fredlund and Tieszen, 1994). Early researchers (e.g., Twiss et al., 1969) attempted to place phytolith forms within groups characteristic of the grass subfamilies: Festucoid (Pooideae), Chloridoid (Chloridoideae), and Panicoid (Panicoideae); however, later research indicated that a single plant may produce many types of phytolith forms (multiplicity) and a particular form may be produced by a number of different plant taxa (redundancy—Rovner, 1983). Multiplicity and redundancy complicate the concept of diagnostic phytolith forms. For example, species in the genus *Stipa* of the Pooideae subfamily (C_3) produce lobate forms characteristic of the C_4 species in the Panicoideae subfamily. However, detailed morphological examination and the use of liquid mounts for 3 dimensional phytolith examination has eliminated confusion regarding *Stipa* bilobates (Brown, 1984; Fredlund and Tieszen, 1994).

Phytolith production in gymnosperms often has been described as poor, and as being a less promising area of study for phytolith morphology compared to flowering plants (Piperno, 1988); however, some researchers have isolated diagnostic conifer forms, most notably the bordered pit tracheary elements present in *Pinus* and *Picea*, and asterosclereids produced by *Pseudotsuga menziesii* (Brydon et al., 1963; Klein and Geis, 1978). Bozarth (1993) examined 4 species of conifers and identified several forms which occur only in conifers. These included thin plates with wavy margins common and possibly unique to *Picea glauca*, silicified tracheary elements with bordered pits found in *Pinus banksiana* and *P. glauca*, and the spiny irregular body diagnostic to *P. banksiana*. Norgen (1972:50) observed a possible diagnostic form for ponderosa pine he called the "spiny elliptical blob."

The first objective of this study was to examine local grass species and establish a workable Poaceae short-cell classification system in the context of existing literature. I was also interested in developing a diagnostic phytolith for ponderosa pine. Although this paper focuses on diagnostic phytoliths from the Poaceae and ponderosa pine, 20 other species common to the area were examined for redundant phytolith forms.

METHODS AND MATERIALS—The study area was located within the Fort Valley Experimental Forest, 10 km northwest of Flagstaff, Arizona. This area was chosen because it has never been harvested (hazard

trees have been felled), is currently closed to grazing (area was grazed between 1876 and 1910: Covington et al., 1997), and is proximal to an ongoing ecosystem restoration project (Covington et al., 1997). The area consists of gently rolling topography (0 to 5% slopes) with an average elevation of 2,250 m. Mean annual precipitation is 56.7 cm with approximately half of that falling as snow in the winter, and the other half as monsoonal rains in July through September (Schubert, 1974). Mean annual air temperature is 7.5°C with an average of 94 frost-free growing days. Soils are mapped as a complex of fine, smectitic Typic Argiborolls and Mollic Eutroboralfs that developed on Tertiary basalt flows and cinders (Miller et al., 1995). Present-day plant community structure in the study area is characterized by small patches (0.02 to 0.29 ha) of larger old-growth trees in clumps of 3 or more interspersed with dense stands of younger smaller trees (germination after settlement, ca. 1870), and relict patches (<0.01 ha) of open areas with bunchgrasses and other herbaceous plants (White, 1985; Kerns, 1999).

Grass species were collected from the study area and nearby sites, resulting in a collection of 27 species for diagnostic Poaceae short-cell phytolith investigation (Table 1). Development of this collection was based on personal field experience, consultation with other ecologists and botanists, examination of herbarium notes, and prior botanical studies. Although this species list is not exhaustive for grasses found in ponderosa pine forests of northern Arizona it does include common species from a wide variety of habitats. Several introduced species were also collected. To ensure that the diagnostic phytolith form developed for ponderosa pine was not redundant in other species in the study area, an additional 20 species of trees, shrubs, forbs, and grass floral material were examined (Table 2). A botanist (J. Springer or J. M. Rominger, Northern Arizona University) confirmed all plant identifications.

Plant samples were separated into leaf, needle, or seedhead (if present), soaked and washed with deionized water, and dried at 70°C for 24 h. Samples were then weighed into crucibles and dry oxidized overnight at 400°C. Initially, ash was washed in 1M HCL to remove calcium oxalate (M. Umlauf, Northern Arizona University, pers. comm.). However, samples did not react to this treatment, and no difference between washed and unwashed samples was detected under the microscope. Therefore, this step was dropped. Ash material was then mounted in Canada Balsam. After mounting, slides were placed into a low temperature oven (35 to 40°C) for 48 to 72 h and cooled. Slides were examined at 400× using a Standard 20 Zeiss biological microscope. I examined phytolith forms in a semi-liquid mount that allowed the phytolith to be rotated and viewed in 3 dimensions.

All grasses listed in Table 1 were examined for diagnostic short-cell identification. For many species several plants were available for examination; however, some species were limited to 1 sample (Table 1). Because future application of this system was for examination of soil phytolith assemblages, only Poaceae short-cells were considered, because they are fairly equal in size and silicification and would be equivalently resistant to post-depositional degradation. Phytolith shape frequencies of the leaf epidermis were determined for a subsample of grasses. Species were chosen to represent the most common for the study area and also to span a range of subfamilies and tribes. If more than 1 plant was collected then the sample was randomly chosen. To prepare the slide, ash material was well mixed, and for each sample, the same amount of material was placed on the slide. This amount was determined through trial and error using a small scoop with a mark at the appropriate depth. Slides were then systematically scanned until 100 disarticulated short-cells were counted. If the 100th short-cell was counted in the middle of a field with additional short-cells, the entire field was counted to reduce bias.

Photographs were made using a LEO 435VP Scanning Electron Microscope at the Northern Arizona University Electron Microscope Facility (Figs. 1–8). The entire reference collection of dry ash, microscope slides, and card catalog, is housed by the Ecological Restoration Institute, School of Forestry, Northern Arizona University.

Phytolith Classification—Eight categories of phytolith forms from leaf and needle material were identified, and these identifications were consistent with existing literature (Metcalfe, 1960; Twiss et al., 1969; Brown, 1984; Mulholland, 1989; Mulholland and Rapp, 1992; Fredlund and Tieszen, 1994). Forms are pictured in Figs. 1–8 and summarized in Table 3 along with their representative taxa. Because numerous researchers have published grass short-cell classification systems, I tried to use previously published nomenclature to avoid further confusion. In the following section I provide more detailed descriptions of the forms and point out usage of terms for comparative purposes. Table 4 shows phytolith shape frequencies for the species subsampled.

Description of Diagnostic Forms—Morphological terminology is standard. The adaxial/abaxial outline is the appearance of the phytolith when looking directly down at the top/bottom. The bottom is defined as the largest, flattest face, or the face not decorated or pointed. The top is opposite to the bottom. Sides are the longest pair of opposite faces, and the ends are the other pair of faces. When I refer to a phytolith shape in cross-section, this is viewing the phytolith on one of its sides. Conversely, the end view is looking down on one of its ends.

1) Rondel. This form is more or less circular to

TABLE 1—Grass species collected and examined for this study. Systematics and common names conform to Allred (1993).

Taxa	Species	Common name
Poaceae		
Pooideae		
Aveneae	*Koeleria macrantha*	prairie Junegrass
Poeae	*Bromus tectorum*[a,b]	cheatgrass
	B. ciliatus	fringed brome
	Festuca arizonica[c]	Arizona fescue
	Poa compressa[a,b]	Canada bluegrass
	P. fendleriana[c]	muttongrass
	P. pratensis[a,b]	Kentucky bluegrass
Triticeae	*Agropyron desertorum*[a,b,d]	crested wheatgrass
	A. smithii[b]	western wheatgrass
	Elymus elymoides[c,e]	bottlebrush squirreltail
	Hordeum jubatum[b,d]	foxtail barley
Stipeae[f]	*Stipa comata*[c]	needle-and-thread
	Piptochaetium pringlei[b,e,g]	Pringle's needlegrass
Arundinoideae		
Aristideae	*Aristida purpurea*[b]	purple three-awn
	Aristida sp.	three-awn
Panicoideae		
Andropogoneae	*Schizachyrium scoparium*[b]	little bluestem
Paniceae	*Panicum bulbosum*	bulb panicum
Chloridoideae		
Cynodonteae (Chlorideae)	*Bouteloua gracilis*	blue grama
Eragrostideae	*Blepharoneuron tricholepis*[c]	pine dropseed
	Lycurus phleoides[b,d]	wolftail
	Muhlenbergia minutissima[c]	least muhly
	M. montana[c]	mountain muhly
	M. rigens	deergrass
	M. virescens[b,g]	screw leaf muhly
	M. wrightii[b]	spike muhly
	Sporobolus cryptandrus[b,d]	sand dropseed
	S. interruptus[b,g]	black dropseed

[a] Introduced (United States Department of Agriculture and Natural Resource Conservation Service, 2000).
[b] Only one plant examined.
[c] Very common perennial species in study area.
[d] Not found in study area.
[e] Synonymous with *Sitanion hystrix, Hesperostipa comata,* and *Stipa pringlei,* respectively.
[f] Some authors (i.e., Watson and Dallwitz, 1992) place the Stipeae within the Arundinoideae.
[g] Species not listed in Allred (1993), name conforms with McDougall and Haskell (1973).

oval in adaxial/abaxial outline and asymmetric in cross-section (Fig. 1). The top can be flat, horned (2 points), decorated (more than 2 points or complex), or crested. The base can be flat, but is more typically slightly to highly indented. Mulholland (1989) also used the term rondel. This form includes the 1a, 1d, 1e categories of Twiss et al. (1969), conical and keel variants of Fredlund and Tieszen (1994), and Brown's (1984) non-sinuous trapezoids. All the C_3 (Pooideae) grasses in this study commonly produce rondels, but *Festuca arizonica, Poa fendleriana,* and *Stipa comata* have high (>90%) percentages of rondels (Table 4).

2) Pyramid. The pyramidal form is roughly square to rectangular in adaxial/abaxial view, edges are smooth and it is trapezoidal in cross-section. This form is not a true pyramid because the top is truncated (Fig. 2). Fredlund and Tieszen (1994) use the

TABLE 2—Other conifer species, understory shrubs, and forbs examined to check for redundant phytolith forms. Except for *Pinus ponderosa,* one plant was examined for each species listed. Nomenclature conforms to McDougall and Haskell (1973) and common names are from the PLANTS National Database (United States Department of Agriculture and Natural Resource Conservation Service, 2000).

Family	Species	Common name
Asteraceae	*Antennaria parvifolia*	small-leaf pussytoes
	Bahia dissecta	ragleaf bahia
	Cirsium wheeleri	Wheeler's thistle
	Hieracium fendleri	yellow hawkweed
	Senecio multilobatus[a]	lobeleaf groundsel
	Solidago sparsiflora[a]	threenerve goldenrod
	Townsendia sp.	Townsend daisey
	Viguiera multiflora[a]	showy goldeneye
Cupressaceae	*Juniperus monosperma*	oneseed juniper
Cyperaceae	*Carex occidentalis*	western sedge
Fagaceae	*Quercus gambelii*	Gambel oak
Pinaceae	*Abies lasiocarpa*[b,c]	corkbark fir
	Pinus edulis[c]	twoneedle pinyon
	P. ponderosa	ponderosa pine
	Pseudotsuga menziesii[c]	Douglas-fir
Rhamnaceae	*Ceanothus fendleri*	Fendler's ceanothus
Rosaceae	*Potentilla subviscosa*	Navajo cinquefoil
Salicaceae	*Populus tremuloides*	quaking aspen
Salicaceae	*Salix scouleriana*[c]	Scouler's willow
Saxifragaceae	*Ribes* sp.[c]	currant

[a] new name *Packera multilobata, Solidago velutina,* and *Heliomeris multiflora* var. *multiflora,* respectively (United States Department of Agriculture and Natural Resource Conservation Service, 2000).

[b] *Abies lasiocarpa* var. *arizonica* (United States Department of Agriculture and Natural Resource Conservation Service, 2000).

[c] Not found in the study area.

pyramid name for this form; it is equivalent to the rectangles of Mulholland (1989), 1b and 1g types of Twiss et al. (1969), and Brown's (1984) non-sinuous trapezoids. The pyramid was a moderately uncommon form for grass taxa examined for this study, but is produced by nearly all Pooideae grasses in small quantities and at a greater frequency by *Elymus elymoides* and *Festuca arizonica* (Table 4).

3) Stipeae Pyramid. The Stipeae pyramid has a bilobate adaxial/abaxial outline and has often been confused with bilobate forms commonly produced by the Panicoideae (Mulholland, 1989; Fredlund and Tieszen, 1994). The more recent practice of 3 dimensional viewing makes distinguishing between Panicoid bilobates and Stipeae pyramids less problematic because the cross-section of the Stipeae pyr-

TABLE 3—Diagnostic phytolith forms, their dominant locally representative subfamilies and genera, and photosynthetic pathway. Genera are listed from most common to least common for that phytolith form.

Phytolith form	Subfamily or tribe	Representative genera	Photosynthetic pathway
Rondel	Pooideae	*Festuca, Poa,* all Pooideae	C_3
Pyramid	Pooideae	All	C_3
Stipeae pyramid	Stipeae tribe	*Piptochaetium, Stipa*	C_3
Crenate	Pooideae	*Bromus, Koeleria, Elymus, Piptochaetium*	C_3
Panicoid lobate	Panicoideae	*Schizachyrium, Panicum*	C_4
Simple bilobate	varies	*Aristida,* all Chlorideae, Stipeae Tribe	C_4/C_3
Saddle	Chlorideae	All	C_4
Spiny body	Pinaceae	*Pinus ponderosa*	C_3

TABLE 4—Phytolith shape frequencies from leaf epidermis material for selected species. Data based on a 100-short cell count from 1 plant for each species.

Species	Rondel	Pyramid	Stipeae pyramid	Crenate	Panicoid lobate	Simple bilobate	Saddle	% Nondiagnostic forms
Pooideae								
Koeleria macrantha	37	5	—	53	—	—	5	5
Bromus ciliatus	7	—	—	93	—	—	—	0
Festuca arizonica	94	6	—	—	—	—	—	0
Poa fendleriana	96	3	—	1	—	—	—	0
Elymus elymoides	71	3	—	27	—	—	—	0
Stipa comata	99	—	1	—	—	—	—	0
Piptochaetium pringlei	14	2	53	31	—	—	—	0
Panicoideae								
Panicum bulbosum	2	—	—	1	85	12	—	3
Chloridoideae								
Bouteloua gracilis	11	—	—	—	—	2	87	11
Blepharoneuron tricholepis	7	—	—	—	—	5	88	7
Muhlenbergia montana	21	—	—	—	1	4	74	22

amid is trapezoidal, with the top being smaller than the base, resembling a pyramid with a bilobate base (Fig. 3). Panicoid bilobates are very flat in cross-section and symmetric. Although several researchers have observed morphological differences between the Stipeae-type bilobates and true bilobates (Twiss et al., 1969; Brown, 1984; Mulholland, 1989), Fredlund and Tieszen (1994) used the term *Stipa*-type, which distinguished this form from other bilobates. I used the tribe designation because the Stipeae pyramid was commonly produced in *Piptochaetium pringlei*, which is in the Stipeae tribe (Table 1). I added the pyramid modifier to reflect the actual 3 dimensional shape of the phytolith, and because it is consistent with Pooideae/C_3 subfamily diagnostic shapes. However, within the flora examined in this

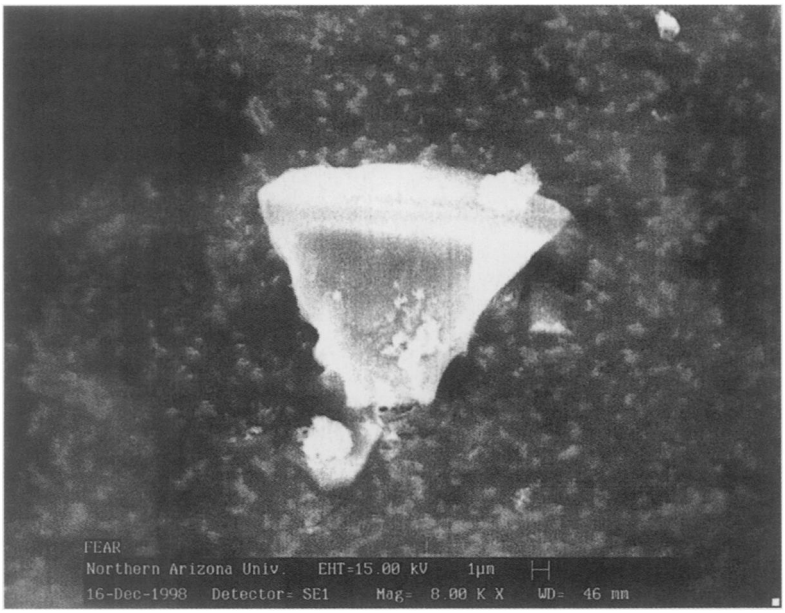

FIG. 1—End view of a rondel from *Festuca arizonica*.

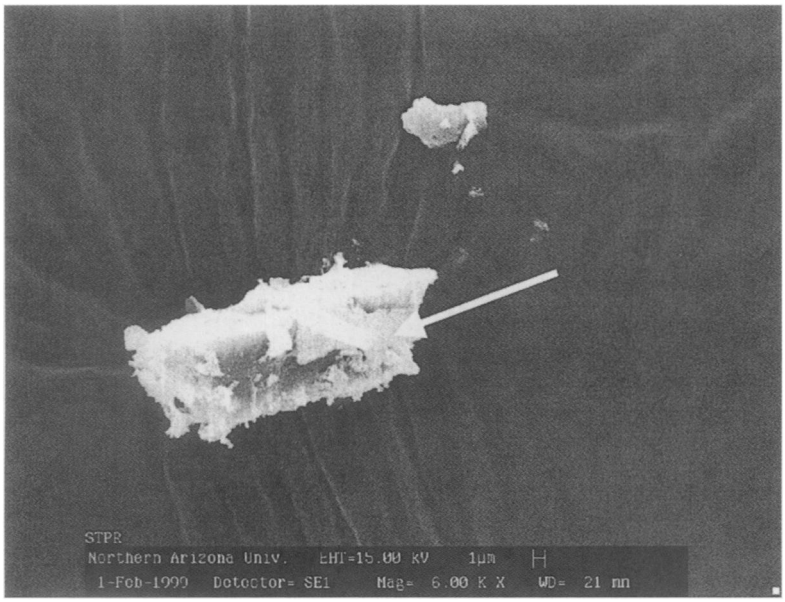

FIG. 2—Cross-sectional view of a pyramid from *Piptochaetium pringlei*.

study, only 2 species from the Stipeae tribe were collected and examined, *S. comata* and *Piptochaetium pringlei* (may also be known as *Stipa pringlei*); thus it remains to be seen if this shape is truly diagnostic for the Stipeae tribe. Both of these species produce the Stipeae pyramid, although it is not commonly produced by *S. comata* (Table 4). These data are supported by Mulholland's (1989) observation that *S. comata* had less than 5% of this form.

4) Crenate. Crenates have sinuous adaxial/abaxial edges and an asymmetric cross-section (Fig. 4). They are frequently longer than wide (although square

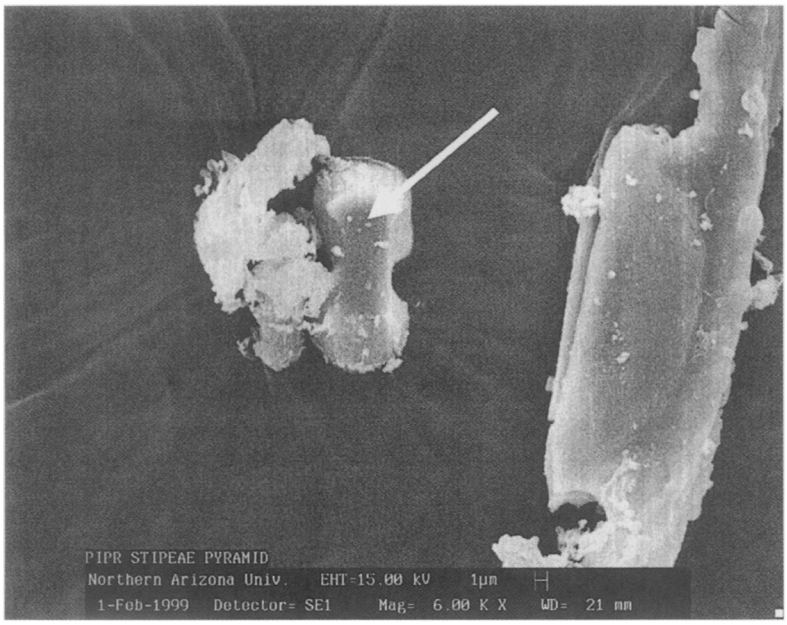

FIG. 3—Looking down on the top of a Stipeae pyramid from *Piptochaetium pringlei*.

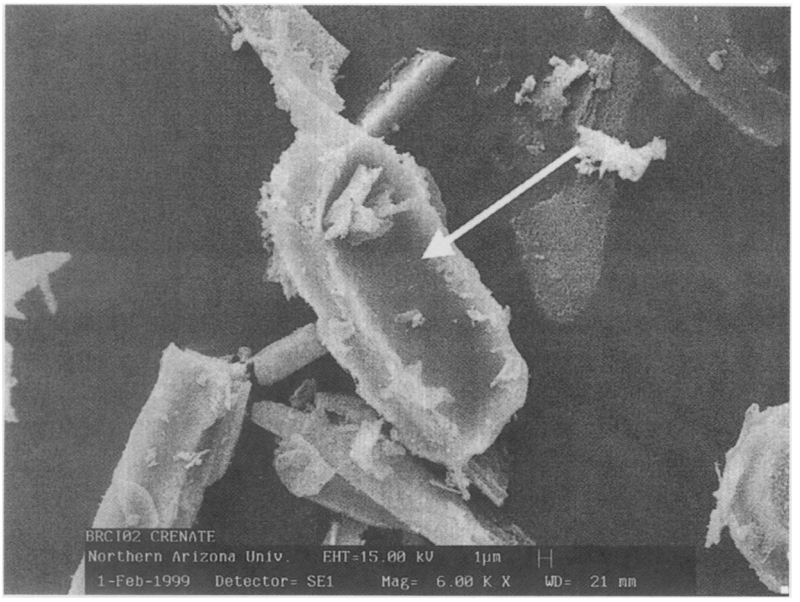

FIG. 4—Crenate in adaxial/abaxial view from *Bromus ciliatus*.

and bullet shapes are common) and range from thin to thick in cross-section. The term crenate was used by Fredlund and Tieszen (1994) and is equivalent to the term sinuate used by Mulholland (1989), sinuous trapezoid by Brown (1984), and the 1h type of Twiss et al. (1969). Many Pooideae grasses produce crenates (Twiss et al., 1969; Mulholland, 1989; Fredlund and Tieszen, 1994). Ninety-three percent of short-cells found in leaf epidermis tissue of *Bromus ciliatus* were of this form (Table 4).

5) Panicoid Lobate. This designation includes several forms diagnostic to the Panicoideae subfamily, including the bilobate, cross, and polylobate. Panicoid bilobates (Fig. 5) exhibit a double lobed adax-

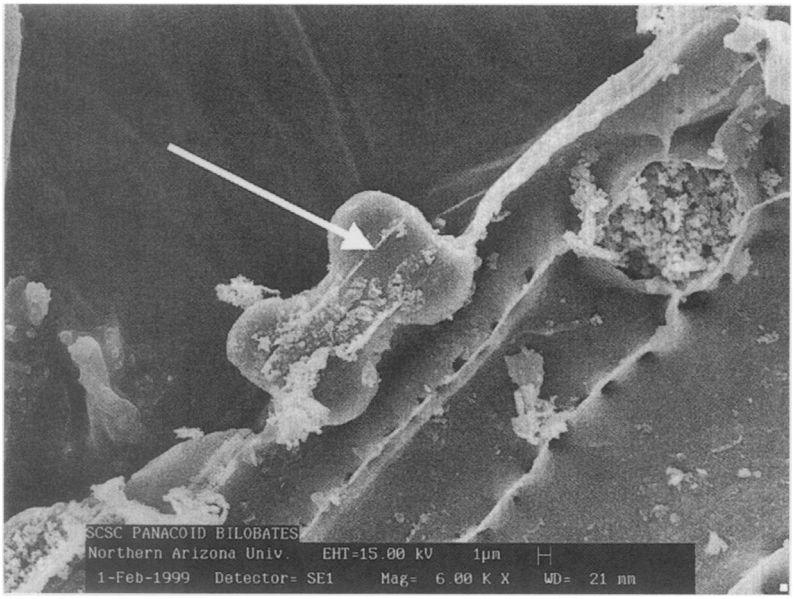

FIG. 5—Adaxial/abaxial views of a panicoid lobate in situ from *Schizachyrium scoparium*.

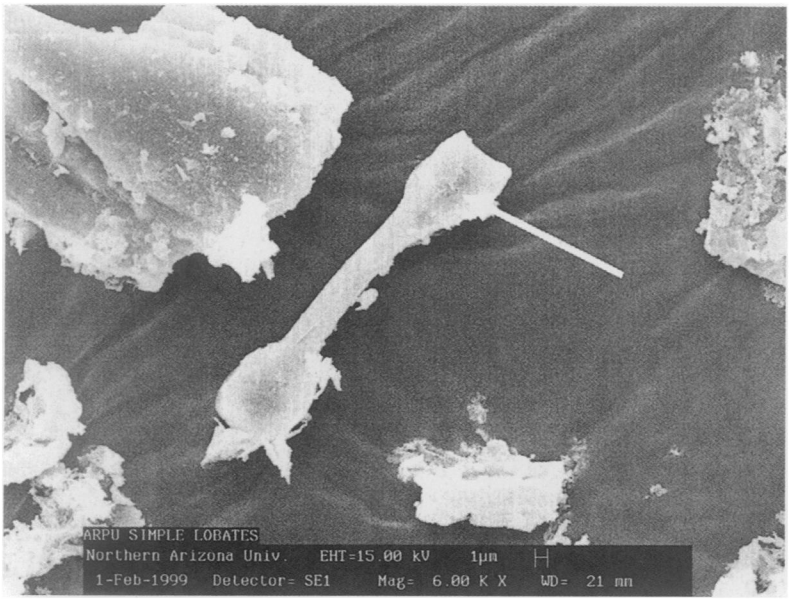

FIG. 6—Adaxial/abaxial view of a simple bilobate from *Aristida* sp.

ial/abaxial outline and indented or straight ends and a well developed lateral plane of symmetry (Fredlund and Tieszen, 1994). This form has also been referred to as the dumbbell and is diagnostic for grasses in the Panicoideae subfamily (Twiss et al., 1969; Mulholland 1989). Crosses have a minimum of 3 indentations and are no more than 9.16 microns longer than wide (see Pearsall, 1978; Pearsall, 1986; Piperno, 1988; Mulholland, 1993, for extensive discussions of crosses). Crosses were not common in the Panicoideae grasses examined in this study. Multilobate forms were encountered most often in the grass *Panicum bulbosum,* and can be differentiated from the crenate form. Multilobates are lobed, whereas crenates are sculpted and have more numerous indentations. Crenates are also trapezoidal in cross-section whereas multilobates are flatter and more symmetric.

6) Simple Bilobate. The simple bilobate can be distinguished from the Panicoid bilobate by rounded, rather than indented or straight ends, and asymmetric adaxial/abaxial outline (Fredlund and Tieszen, 1994). The shank on the simple bilobate is generally much longer (Fig. 6). Simple bilobates are typically produced by members of the Chloridoideae subfamily and some Pooideae grasses (Fredlund and Tieszen, 1994). Species in the genus *Aristida* produce many types of simple bilobate forms.

7) Saddle. The saddle has been consistently defined by many researchers (Metcalfe, 1960; Twiss et al., 1969; Brown, 1984; Mulholland, 1989; Fredlund and Tieszen, 1994; Fig. 7). My definition of the saddle is the same as used by Fredlund and Tieszen (1994) and emphasizes 3 planes of symmetry, which are the 2 planes of the adaxial and abaxial surfaces, and cross-sectional symmetry. The adaxial/abaxial outline of a saddle (using light microscopy) has been described as a battle-axe with double edges (Twiss et al., 1969). Grasses in the Chloridoideae subfamily commonly produce saddles (Table 4).

8) Ponderosa pine spiny body type. For the flora examined for this study, the spiny body type is diagnostic for ponderosa pine (Fig. 8), and based on an examination of the literature, a newly identified phytolith form. Characterization and description of this form was based on 5 different samples of needle material from 5 trees spanning various levels of maturity. Nomenclature is based on Bozarth's (1993) description and photograph of spiny irregular bodies from *P. banksiana,* which appear to be very similar to the ponderosa pine spiny body form, and spiny bodies may be diagnostic of the genus *Pinus.* Spiny bodies are irregularly shaped, round to irregularly elliptical (typically shaped like a dolphin) and completely silicified. Spines can be somewhat rounded to sharp, forked or simple, and occur abundantly over the body of the phytolith. This form is similar in size to most short-cells (Fig. 8). A scan (314-cell) of an entire slide of ponderosa pine leaf material from 1 randomly chosen sample indicated that 19% of the silicified material produced was of the spiny body variety, and only 1.9% was the bordered pit tracheary elements diagnostic for many conifers.

Other species, including 5 conifers, were examined and did not produce any form that could be confused with the spiny body diagnostic for ponde-

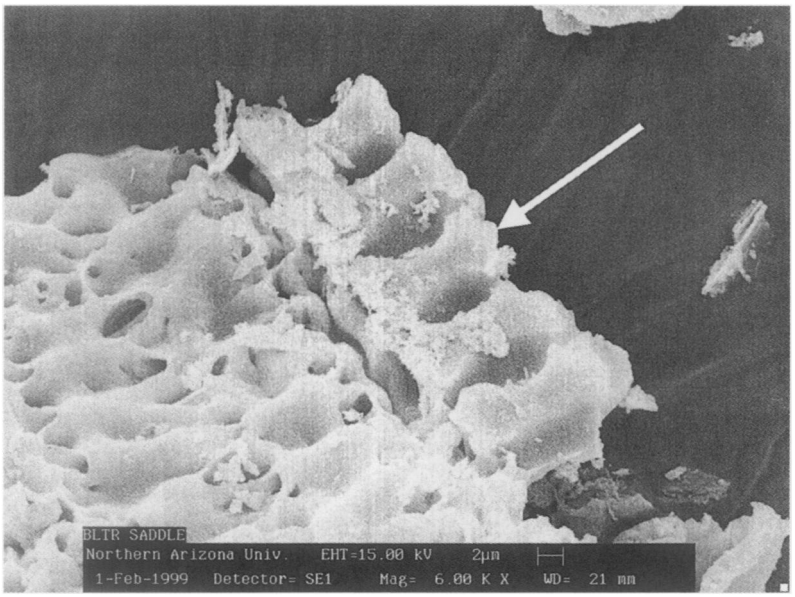

FIG. 7—Cross-sectional view of saddles from *Blepharoneuron tricholepis.*

rosa pine (Table 2). Because some authors have noted that floral bracts of grasses have dendriform and asteriform phytoliths, which may be confused with the spiny body type produced by ponderosa pine (D. Pearsall, University of Missouri, Columbia, pers. comm.; see also Piperno, 1988), material from seed heads was examined for the species where seed heads were present: *Poa fendleriana, Festuca arizonica, Elymus elymoides, Muhlenbergia montana, Blepharoneuron tricholepis, Schizachyrium scoparium,* and *Bouteloua gracilis.* No phytolith forms were noted that could be confused with the spiny body produced by ponderosa pine, which can be distinguished from grass floral silicified material by having an irregular round

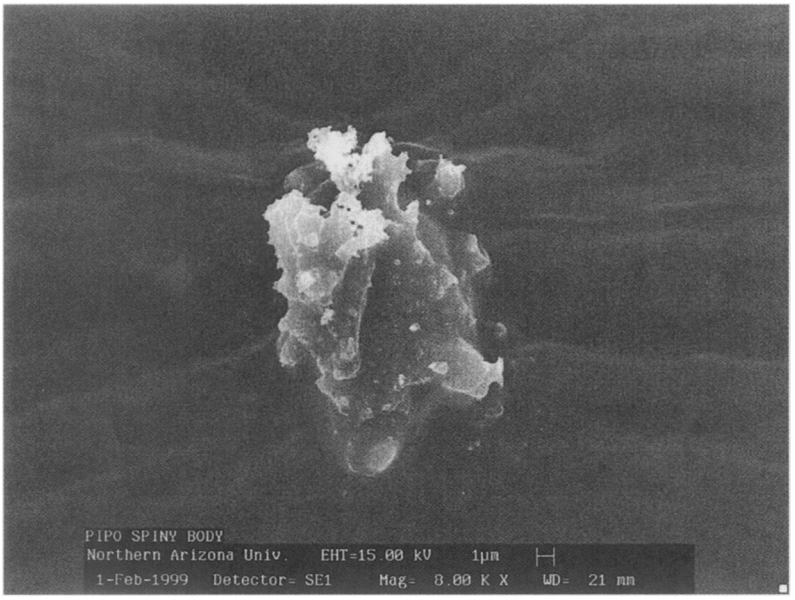

FIG. 8—The spiny body from *Pinus ponderosa.*

to elliptical shape, irregularly and forked spines, having no flat surfaces, and being completely silicified.

RESULTS AND DISCUSSION—Examination of grass flora from this study indicate that the general subfamily system originally defined by Twiss et al. (1969), and validated by other researchers (Brown, 1984; Mulholland, 1989; Piperno, 1988; Fredlund and Tieszen, 1994) can be applied to the ponderosa pine-bunchgrass community examined. Examinations of phytolith shape frequencies indicate that for 7 species in the subfamily Pooideae, and 1 species in the Panicoideae, very few (0 to 5%) nondiagnostic phytolith forms were present. Nondiagnostic phytoliths, particularly rondels, were more common (7 to 22%) for the 3 species examined from the Chloridoideae subfamily. This result is consistent with the observation that all grasses produce rondel forms (Mulholland, 1989; Fredlund and Tieszen, 1994) and indicates that rondels might be over-represented in phytolith assemblages from the study area, and saddles under-represented in comparison to actual vegetation.

The potentially confusing Stipeae pyramid was not common (<1%) for *S. comata* and was much more common in *P. pringlei*. Interestingly, taxonomists consider the Stipeae tribe taxonomically confusing in general (Kellogg and Campbell, 1987; Watson and Dallwitz, 1992). Barker et al. (1995) point out that the Stipeae tribe has been placed both within the Arundinoideae and the Pooideae by various researchers. Using gene sequencing, Barker et al. (1995) reported that the Arundinoideae (including *Stipa, Aristida,* and *Danthonia*) was polyphyletic, meaning that lineages within the subfamily show affinities with all 3 of the other subfamilies. These authors also suggest that placement of the Stipeae tribe in the Pooideae needs further investigation. The Stipeae pyramid phytolith form clearly reflects the polyphyletic nature of species the Stipeae tribe.

With further study of phytolith forms from local grass flora, or application of morphometric techniques, a more specific phytolith Poaceae classification system could be developed. For example, there might be potential to break out the larger and indented rondel form noted for *P. fendleriana* and establish diagnostic crenate forms to separate *Bromus* and *Koeleria macrantha*. Separating these genera and further splitting the species in *Bromus* may be helpful in determining the approximate date of introduction of nonnative aggressive species such as *Bromus tectorum* (cheatgrass). In addition, further examination of grass phytoliths from floral structures may reveal additional diagnostic forms.

The newly identified ponderosa pine spiny body appears to be a useful diagnostic for this area. Although Norgen (1972) noted this form may be diagnostic, no other references to this species were found in the literature. It is possible that this form is common to other species in the genus *Pinus,* although spiny bodies were not observed in *Pinus edulis,* the other pine species examined. Results from this study support other research suggesting that diagnostic phytoliths for conifers can be isolated and conifer species should not be ignored or generally categorized as nondiagnostic (Brydon et al., 1963; Klein and Geis, 1978; Bozarth, 1993).

Examination of soil phytolith assemblages based on the system developed in this study could be used to understand grass-tree and grass vegetation dynamics. Although this study focused on grass and ponderosa pine phytoliths, additional examination of forb and shrub species, including floral parts, may reveal other important diagnostic forms. In addition, examination of multiple individuals of the same species from a variety of soil types, and understanding differences in phytolith form and size due to environmental factors, would strengthen the use of phytolith analysis as a quantitative tool for historical vegetation reconstructions.

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