Phytoliths of the Barstow Formation through the Middle Miocene Climatic Optimum: preliminary findings

Katharine M. Loughney [1,2] and Selena Y. Smith [1,]
[1] *Museum of Paleontology, University of Michigan, 1109 Geddes Ave., Ann Arbor, MI 48109*
[2] *Department of Earth & Environmental Sciences, University of Michigan, 1100 North University Ave., Ann Arbor, MI 48109*

Abstract—The Middle Miocene Climatic Optimum (MMCO) was an interval of significant warming between 17.0 – 14.0 Ma, and a record of the interval is preserved in its entirety in the type Barstow Formation (19.3 – 13.3 Ma) of southern California. In order to understand the biotic impacts of the MMCO, it is necessary to understand vegetation; however, macrofloral records from the middle Miocene in this region are rare and do not span the MMCO. Phytoliths (plant silica) can be preserved in continental sediments even when macrofossil or pollen remains are not, and they can be diagnostic of specific plant clades and/or functional groups, some of which are useful environmental indicators. Sixty-eight sediment samples were collected from 12 stratigraphic sections measured within the Barstow Formation in the Mud Hills, Calico Mountains, and Daggett Ridge, and 39 samples were processed for phytoliths. Ten samples yielded phytoliths, although phytoliths were rare in most of these samples. Paleosols from the uppermost part of the Barstow Formation yielded the most abundant and most diverse phytolith assemblages, including grass bilobates and echinate spheres of palms; grass phytoliths were also identified in samples from the Owl Conglomerate and Middle members but were rare. These phytolith data provide evidence that grasses were present throughout deposition of the Barstow Formation, and that they coexisted with palms in mixed-vegetation habitats. While more sampling is needed to fill in stratigraphic gaps in the phytolith record of the Barstow Formation and few phytoliths have so far been recovered from samples, these preliminary data show that phytoliths can be used in the Barstow Formation to better understand Miocene ecosystems and how they may have changed through the MMCO.

Introduction

Global climate over the course of the Cenozoic became generally drier and cooler but was punctuated by several major and short-lived periods of warming (Zachos et al., 2001). One of these warming intervals, the Middle Miocene Climatic Optimum (MMCO), occurred between ~17.0 – 14.0 Ma as recorded from both marine (Foster et al., 2012) and continental records (Retallack, 2007). In North America, few continental units capture this interval. The Barstow Formation of the Mojave Desert, eastern San Bernardino County, California, is one such unit that encompasses the MMCO.

The fluvial and lacustrine sediments of the Barstow Formation were deposited between 19.3 and 13.3 Ma (MacFadden et al., 1990; Woodburne et al., 1990), and the formation potentially records the responses of the local fauna and flora to this warming interval. The mammalian fauna of the Barstow Formation has been well studied, and some studies have focused on interpreting the lacustrine paleoenvironments represented in the Barstow (e.g., Park, 1995; Park and Downing, 2001). The rarity of plant macrofossils has made it difficult to interpret the terrestrial ecosystems in the formation, and the limited Barstow floral record does not currently span the MMCO. Phytoliths (plant silica), however, can be sampled from sediment layers throughout the formation and may provide a record of ecosystem change through this interval that is not dependent on macrofossil preservation. Here, we present preliminary results of an investigation of paleoenvironments and vegetation change in the Barstow Formation through the MMCO.

Background

Multiple lines of evidence have been used to interpret the timing and geography of the spread of grasslands in the Neogene, and fossils from the Barstow Formation will add information to help refine our understanding of when, where, why, and how this major ecosystem change happened. Carbon isotopic data from paleosol carbonates and fossil mammal teeth capture this transition to open grassland habitats and the adaptations of herbivores to a new food source during the Cenozoic (e.g., Koch, 1998). Likewise, plant macrofossils, pollen, and phytoliths constrain the timing of these ecosystem changes and provide direct evidence of the types of plants in these increasingly open, grass-dominated habitats (Strömberg, 2011). Macrofossils, however, are typically rare, and pollen may be allochthonous or not regularly preserved, so reconstructions of grassland expansion are typically regional or local in scale. Phytoliths are amorphous silica bodies that are precipitated in plant tissues; they are autochthonous and are either taxonomically diagnostic for many groups, including grasses and palms, or diagnostic of certain plant functional types, such as woody plants (Piperno, 2006). Phytoliths of certain taxa may also be useful as indicators of past climatic conditions; such indicator taxa have modern relatives that range within well-defined climatic or floral regimes (Chen and Smith, 2013; Strömberg, 2004). Therefore, phytoliths are a potentially useful tool for understanding vegetation change through the MMCO due to their ability to record different types of vegetation and key ecosystem/climatic indicator taxa.

The Barstow Formation is primarily known for its diverse and well-studied mammalian fauna, but few studies have been conducted on Barstow flora. Plant macrofossils are known from only two localities in the Middle Member of the Barstow Formation (Alf, 1970; Reynolds and Schweich, 2013). The Rainbow Loop Flora from the Mud Hills has been dated between 16.3 – 15.8 Ma and preserves impressions and compressions of vegetative and reproductive structures from woody dicots, palms, and juniper, as well as some unidentified remains (Reynolds and Schweich, 2013). Petrified wood from the Solomon Skyline locality below the Dated Tuff marker unit (14.8 Ma, MacFadden et al., 1990) has been identified as belonging to poison oak, juniper, and buckthorn (Alf, 1970). The Barstow Formation has also been sampled for pollen without success (I. Browne, personal commun., October 2014). Indirect evidence for the presence of grasses comes from Feranec and Pagnac (2013), who analyzed the carbon isotopic composition (δ13C) of herbivore teeth and demonstrated that the diets of equids from the Barstow Formation included a small but significant (< 20%) amount of C4 grasses. These isotopic data, then, suggests that grasses were present in Barstow ecosystems, but it has been difficult to reconstruct paleovegetation from fossils that are highly localized in time and space. Phytoliths could help address these issues by providing a microfloral record of the vegetation. Phytoliths are sampled from fine-grained, non-clay-rich sediments and paleosols in which plants are inferred to have lived; although their preservation may be highly variable between or within lithologic units, when present, they nevertheless record a proportion of the paleoflora of a sampled locality.

As part of a broader study of Barstow paleoenvironments, we sampled phytoliths through the formation in order to 1) test whether phytoliths are preserved in Barstow sediments, and 2) examine how paleovegetation as recorded by phytolith assemblages changed through time. Vegetation and landscape reconstructions provide context not only for the habitats of the Barstow fauna but also shed light on floral responses to the changing climate conditions of the MMCO.

Methods

Sixty-eight sediment samples were collected at 20-m intervals through 12 stratigraphic sections measured in the Mud Hills, Calico Mountains, and Daggett Ridge (Fig. 1). These sections include the entire thickness of the Barstow Formation, and all members were sampled. Six samples were collected in the Owl Conglomerate Member, 30 samples were collected in the Middle Member, and 31 were collected in the Upper Member (Table 1). Phytoliths were sampled from sediment ranging in grain size from clay to

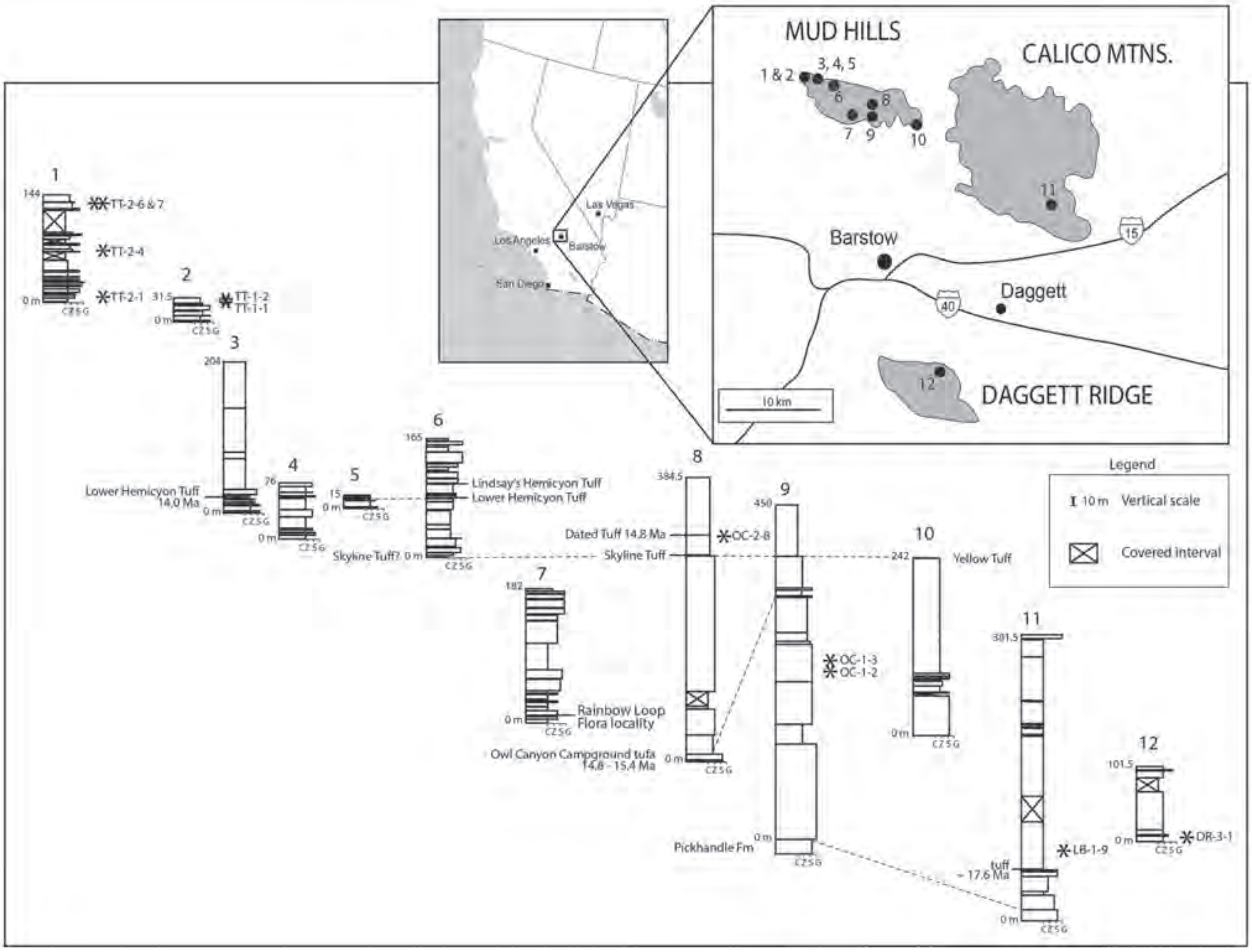

Figure 1. Locations of measured sections from which phytoliths were sampled in the Mud Hills, Calico Mountains, and Daggett Ridge. 1, 2, Truck Top Wash; 3, 4, 5, Falkenbach Wash; 6, Hell Gate Basin; 7, Cal-Uranium Prospect Canyon; 8, 9, Owl Canyon; 10, Copper City Rd; 11, Little Borate; 12, Daggett Ridge. Stratigraphic positions of phytolith-bearing samples are indicated with asterisks. Ages of tuffs are from MacFadden et al. (1990) and Miller et al. (2013), and age of tufa is from Cole et al. (2005).

fine sand. In general, A and B horizons of paleosols should have the highest chance of preserving phytoliths and were typically targeted for sampling. Paleosols in the Barstow Formation are restricted to the uppermost ~100 m of the Upper Member, exposed in Truck Top Wash (Fig. 1), and six samples were collected in weakly to moderately developed paleosols at this location. Given the overall dearth of paleosols in the rest of the formation, sampling efforts were not restricted to any particular lithology, and rather, we sampled a variety of lithologies in each member. We sampled siltstones, claystones, fine sandstones, marls, and ashes to test how phytolith preservation might differ with sediment type in the Barstow Formation.

Samples were processed at the Earth System Science Laboratory in the Department of Earth and Environmental Sciences at the University of Michigan, Ann Arbor, following the procedure for extraction and heavy-liquid separation outlined by Strömberg et al. (2007) for 1 g of sediment. Processed samples were mounted on slides using Cargille Meltmount (refraction index 1.534) mounting medium and immersion oil (Cargille Non-Drying Immersion Oil Type A) for rotation to characterize the 3D and surface morphology for initial phytolith identification, and slides were examined on either a Leica DMP-1500 or a Nikon LV-100 transmitted light microscope at 1000x. For this preliminary report, samples were qualitatively, rather than quantitatively, assessed based on initial slides of sample extractions. Phytolith identifications were made using Strömberg (2003) and the modern reference collection compiled by S.Y. Smith at University of Michigan, and following the morphotype terminology of Strömberg (2003) and Piperno (2006).

Table 1. Samples collected for phytolith analysis from the three members of the Barstow Formation in the Mud Hills, Calico Mountains, and Daggett Ridge, San Bernardino County, California (Fig. 1).

Barstow Member	Location	Number of samples collected	Samples yielding phytoliths (total processed)
Owl Conglomerate Member	Owl Canyon	3	2
	Daggett Ridge	3	1
	Subtotal	6	3 (4)
Middle Member	Owl Canyon	10	0
	Cal-Uranium Prospect Canyon	14	0
	Little Borate	6	1
	Copper City Road	1	0
	Subtotal	30	1 (17)
Upper Member	Owl Canyon	1	0
	Hell Gate Basin	6	0
	Falkenbach Wash	15	0
	Truck Top Wash	9	6
	Subtotal	31	6 (18)

Table 2. Lithology of samples, phytolith morphotypes, and morphotype interpretation of samples from the Owl Conglomerate Member (OC), Middle Member (MM), and Upper Member (UM).

Sample number	Location of Section	Lithologic Description	Phytolith type	Interpretation
DR-3-1 (OC)	Daggett Ridge	Brown siltstone, weak paleosol	Globular body	Not previously described
OC-1-2 (OC)	Owl Canyon	Olive siltstone	Druse sphere	Not previously described
OC-1-3 (OC)	Owl Canyon	Brown silty claystone	GSSCs (bilobate, polylobate, short rondel) Elongate Small globular bodies	Grasses Indeterminate Not previously described
LB-1-9 (MM)	Little Borate	Light gray siltstone	Globular bodies	Not previously described
TT-1-1 (UM)	Truck Top Wash	Grayish brown siltstone, moderate paleosol	Echinate spheres GSSCs (bilobates, polylobates, tall rondel) Tracheary elements	Palms Grasses Indeterminate
TT-1-2 (UM)	Truck Top Wash	Graysish brown clayey siltstone, moderate paleosol	Echinate spheres GSSCs (bilobates, polylobates, short rondels) Elongate, tracheary elements.	Palms Grasses Indeterminate
TT 2-1 (UM)	Truck Top Wash	Gray siltstone, weak paleosol	Small globular bodies	Not previously described
TT-2-4 (UM)	Truck Top Wash	Sandy siltstone	Globular body	Not previously described
TT-2-6 (UM)	Truck Top Wash	Brown laminated siltstone, moderate paleosol	GSSCs (bilobate)	Grass
TT-2-7 (UM)	Truck Top Wash	Brown claystone, moderate paleosol	Globular bodies	Not previously described

Results

Of 39 samples that have been processed, 10 contain identifiable phytoliths. In seven of these samples, few phytoliths have been observed in the slides (Table 2), and we do not consider these as robust evidence of phytolith preservation. Of the remaining three samples, two contain phytolith assemblages that are sufficiently well-preserved and abundant to be counted in order to determine the proportion of closed- to open-habitat taxa. The third sample yields very low numbers of not very well preserved phytoliths. The phytoliths in these 10 samples, however, are types that are diagnostic of specific clades or are indicative of climatic conditions, and therefore provide useful paleoenvironmental information (Fig. 2).

Owl Conglomerate Member

Two of the processed samples collected in the Owl Conglomerate Member in the Mud Hills have yielded low numbers of phytoliths (Table 2). These samples were collected from thin grayish yellow green (5GY 7/2) siltstone and yellowish gray (5Y 7/2) claystone layers that occur within the thicker sequences of cross-stratified fine- to coarse-grained, pebble-lag-bearing sandstone that characterize the Owl Conglomerate Member (Fig. 1). We observed several morphotypes in these samples, including a bilobate and a polylobate—both grass silica short cells (GSSCs), an elongate, and two as-yet unidentified globular bodies (Fig. 2).

Middle Member

One out of 17 processed samples from the Middle Member has produced phytoliths. This sample was collected at the Little Borate section in the Calico Mountains (Fig. 1) from a ~230-m-thick sequence of thin (0.5 – 2.0 cm), alternating layers of light gray marl, siltstone, and olive claystone. This sequence represents lacustrine sediments that may have experienced increasing evaporative conditions during deposition of the upper part of the section, where gypsum layers occur (Park, 1995). The sample, taken from a layer of siltstone, has produced as-yet unidentified globular bodies and numerous diatoms.

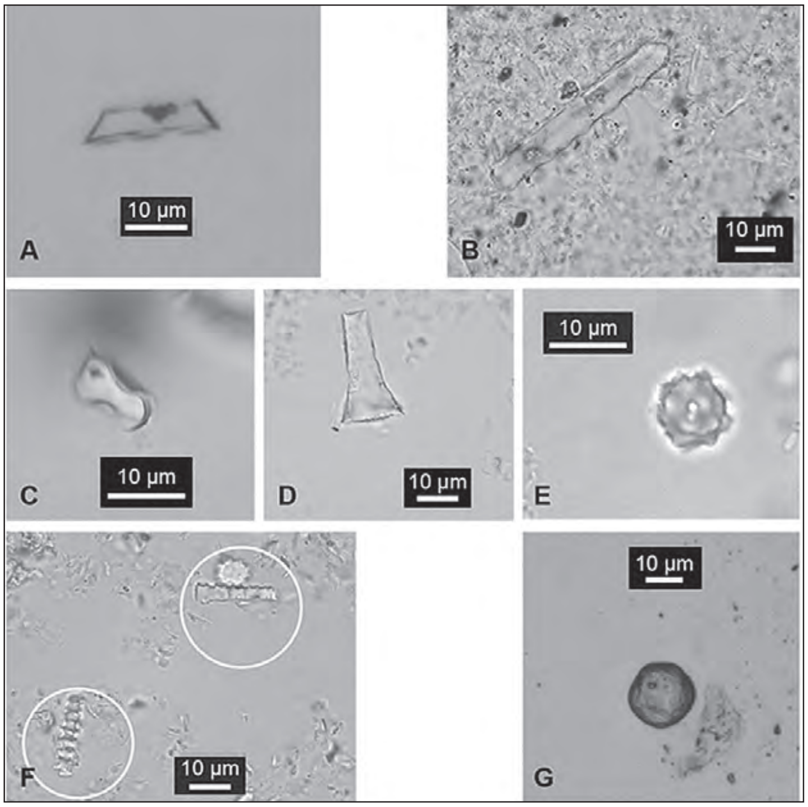

Figure 2. Examples of phytoliths recovered from the Barstow Formation. A, Polylobate; B, Elongate; C, Bilobate; D, Rondel; E, Echinate sphere of a palm; F, Tracheary elements (circled); G, Indeterminate globular body. A, C–D are characteristic GSSC phytoliths of grasses.

Upper Member

The six stratigraphically highest samples collected have the highest numbers of identifiable phytoliths, including the two samples with assemblages suitable for quantitative analysis in the future. These samples were all collected in Truck Top Wash (Fig. 1), where the uppermost part of the Upper Member is exposed. The two assemblages that can be quantitatively characterized in the future come from pale yellowish brown (10YR 6/2) siltstone and clayey siltstone showing moderately developed pedogenic features (slickensides, mottles, redoximorphic depletions, root casts, and filled cracks). In addition, other samples with identifiable phytoliths were collected from light brown (5YR 6/4) siltstone and claystone with moderately developed pedogenic features (slickensides, fine root traces, carbonate nodules, and manganese concentrations), yellowish gray (5Y 7/2) weakly pedogenic siltstone (fine root casts, carbonate nodules), and pale yellowish brown (10YR 6/2) sandy siltstone.

Large (~10–15 μm) and small (~ 5–10 μm) echinate spheres are present in two Truck Top Wash samples, and bilobate GSSCs are present in three samples from Truck Top Wash, making them the most common phytolith morphotypes among Truck Top Wash samples. Other GSSCs (polylobates and rondels) as well as less diagnostic morphotypes such as tracheary elements and elongates also occur in these samples but are much less prevalent. Various as-yet unidentified globular bodies and diatoms were also seen in three samples from the Upper Member.

Discussion

Although the results of these phytolith analyses are preliminary, it is possible to identify some components of Barstow Formation vegetation at this stage. The data recovered to date from the analyzed samples do not allow robust estimates of open- vs. closed-habitat taxa, but some morphologies are diagnostic of specific taxa, indicating that the plants from which they derive were present in ecosystems of the Barstow Basin.

At least six observed morphologies can be confidently identified to taxon. Echinate spheres and bilobate GSSCs (Fig. 2) were the most common and most reliably identified morphologies in any of the samples analyzed. Echinate spheres are derived from the leaves and seeds of palms, and bilobates are characteristic of grasses (Piperno, 2006). Polylobates, rondels (Fig. 2), and crenates are also referable to various grass clades; further characterization of the precise morphologies will allow us to identify the clades to which these phytoliths belong. Some globular bodies in these samples superficially resemble druse spheres that are diagnostic of members of the Zingiberales order (gingers and relatives). Phytoliths referable to this clade are found in middle and late Miocene samples from the Great Plains (Strömberg, 2005) and are strong indicators of humid, frost-free conditions (Chen and Smith, 2013). These and other spherical or globular phytolith morphologies in the Barstow samples do not appear to be diagnostic of any particular group and cannot be used to indicate climate. More work is necessary to describe these morphologies and to determine if they can be assigned to a particular taxonomic group or functional type.

Phytoliths through the MMCO

The two stratigraphically lowest samples in this study that bear phytoliths are from the Little Borate and Daggett Ridge sections (Fig. 1). It is difficult to correlate strata between Daggett Ridge and the Calico Mountains, but the estimated ages of these samples place them near and potentially before the onset of the MMCO: the sample from Little Borate came from lacustrine siltstone 28.5 m above a tuff dated at 17.6 Ma (Miller et al., 2013). The age of the Barstow Formation at Daggett Ridge is not well constrained, but the sample was collected below the level of a fossil locality dated biostratigraphically at 16.0 Ma (Reynolds et al., 2010). The phytolith morphologies from Daggett Ridge and Little Borate have not been described and cannot be assigned to a taxon. The rare and indeterminate phytoliths from these sections make it difficult to establish a pre- or early-MMCO flora in the Barstow Formation.

In Owl Canyon, samples from the Owl Conglomerate Member were collected ~60 m below a prominent tufa layer that Cole et al. (2005) dated at 16.14 Ma. Phytolith morphologies from these samples are referable to grasses, in particular the bilobates and polylobates, which may indicate the presence of grasses belonging to the Pooideae or PACCAD (Panicoideae, Centothecoideae, Chloridoideae, Arundinoideae, Danthonioideae, Aristidoideae) clades. Grasses within these clades typically occur in open or dry habitats (Strömberg, 2004). With continued work, we may be able to identify to which of these clades the morphotypes belong and potentially distinguish between grasses using the C_3 or C_4 photosynthetic pathways (see Smiley et al., this volume). Rare druse bodies from these samples are similar to zingiberalean morphotypes, but globular morphotypes are commonly found in numerous plant types and taxa, and cannot be referred to any clade. The diverse identifiable GSSC morphotypes from the sampled layer in the Owl Conglomerate Member may indicate an open ecosystem rather than forest or mixed-forest habitat. The facies from which these samples were collected represent fine-grained interfluve or channel-proximal floodplain environments that may have received too much active deposition and disturbance to allow the establishment of woody forest-dwelling taxa.

The stratigraphically highest samples from the Barstow Formation were collected above the Hemicyon Tuff, dated at 14.0 Ma (MacFadden et al., 1990; Woodburne et al., 1990). The paleosols in this part of the Upper Member indicate well-drained floodplain environments that may have experienced seasonal changes in precipitation. The phytolith assemblages from these moderately developed paleosols produce a mixture of palm and grass bodies, and could suggest the presence of a palm savanna-type ecosystem during deposition of the uppermost Barstow Formation.

Barstow environments during the MMCO

Few of the identified phytolith types are referable to taxa used as paleoenvironmental indicators. Palm phytoliths are abundant at the top of the section (Table 2) and are robust indicators of warm, frost-free climates after 14.0 Ma, but their absence in all other samples makes it difficult to compare these conditions to those during the MMCO. It is unclear whether grasses were present on the Barstow landscape by the beginning of the MMCO, but GSSC morphotypes in the Owl Conglomerate and Upper members show that grasses were present before deposition of the 16.14 Ma tufa of Cole et al. (2005). The diversity of GSSC morphotypes is highest at the top of the formation, which was deposited after the end of the MMCO. It is unclear at this stage whether the increase in occurrence of grass phytoliths through the section is related to progressive opening of environments with time or instead a taphonomic artefact.

Palms were reported as present in the Rainbow Loop Flora in the Middle Member of the Barstow Formation (Alf, 1970). Aquatic, riparian, woodland, and upland floral communities are suggested by this assemblage from the middle part of the MMCO (Reynolds and Schweich, 2013). In their analysis of the Rainbow Loop Flora, Reynolds and Schweich (2013) expected the presence of grasses in the woodland community, and this prediction seems more likely in light of the findings of this study. More sampling is needed to demonstrate the presence of grasses at the level of the Rainbow Loop Flora and elsewhere within the Middle Member in order to indicate how grass abundance may have varied through the MMCO.

Conclusions

These initial results provide a glimpse into the changing Barstow ecosystems during the MMCO and add to our understanding of Barstow flora, heretofore known only from the Rainbow Loop Flora and Solomon Skyline localities. These initial results indicate that siltstones and claystones preserve phytoliths more readily than the sandstone, marl, or ash layers sampled, although phytolith preservation is highly variable. Paleosols in the Barstow seem to have the highest potential of preserving phytoliths, although the Upper Member sample from Owl Canyon demonstrates that identifiable phytoliths can be extracted from drab-colored facies. Continued sampling and sample processing will potentially yield more phytoliths and provide additional evidence of vegetation composition in the Barstow Formation and how it may have changed in response to changing Miocene climates.

Acknowledgments

We thank Robert Reynolds for his generous guidance in planning fieldwork and locating sections for stratigraphic measurements. We also thank Catherine Badgley and Tara Smiley for suggestions and comments, as well as Ethan Hyland for reviewing the manuscript. This study was supported by grants from the Evolving Earth Foundation, the University of Michigan Rackham Graduate School, and the University of Michigan Department of Earth and Environmental Sciences Scott Turner Award.

References

Alf, R.M., 1970, A preliminary report on a Miocene flora from the Barstow Formation, Barstow, California: Bulletin, Southern California Academy of Sciences, v. 69, no. 3-4, p. 183-189.

Chen, S.T., and Smith, S.Y., 2013, Phytolith variability in Zingiberales: A tool for the reconstruction of past tropical vegetation: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 370, no. 0, p. 1-12.

Cole, J.M., Rasbury, E.T., Hanson, G.N., Montanez, I.P., and Pedone, V.A., 2005, Using U-Pb ages of Miocene tufa for correlation in a terrestrial succession, Barstow Formation, California: GSA Bulletin, v. 117, no. 3-4, p. 276-287.

Feranec, R.S., and Pagnac, D., 2013, Stable carbon isotope evidence for the abundance of C_4 plants in the middle Miocene of southern California: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 388, p. 42-47.

Foster, G.L., Lear, C.H., and Rae, J.W.B., 2012, The evolution of pCO_2, ice volume and climate during the middle Miocene: Earth and Planetary Science Letters, v. 341-344, p. 243-254.

Koch, P.L., 1998, Isotopic reconstruction of past continental environments: Annual Review of Earth and Planetary Sciences, v. 26, no. 1, p. 573-613.

MacFadden, B.J., Swisher, C.C., III, Opdyke, N.D., and Woodburne, M.O., 1990, Paleomagnetism, geochronology, and possible tectonic rotation of the middle Miocene Barstow Formation, Mojave Desert, southern California: GSA Bulletin, v. 102, no. 4, p. 478-493.

Miller, D.M., Rosario, J.E., Leslie, S.R., and Vazquez, J.A., 2013, Paleogeographic insights based on new U-Pb dates for altered tuffs in the Miocene Barstow Formation, California, *in* Reynolds, R.E., ed., 2013 Desert Symposium: California State University Desert Studies Center, Zzyzx, California, California State University Desert Studies Consortium, p. 31-38.

Park, L.E., 1995, Geochemical and paleoenvironmental analysis of lacustrine arthropod-bearing concretions of the Barstow Formation, southern California: PALAIOS, v. 10, no. 1, p. 44-57.

Park, L.E., and Downing, K.F., 2001, Paleoecology of an exceptionally preserved arthropod fauna from lake deposits of the Miocene Barstow Formation, southern California, USA: PALAIOS, v. 16, no. 2, p. 175-184.

Piperno, D.R., 2006, Phytoliths: A Comprehensive Guide for Archaeologists and Paleoecologists, Lanham, Maryland, AltaMira Press, 238 p.:

Retallack, G.J., 2007, Cenozoic Paleoclimate on Land in North America: The Journal of Geology, v. 115, no. 3, p. 271-294.

Reynolds, R.E., Miller, D.M., Woodburne, M.O., and Albright, L.B., 2010, Extending the boundaries of the Barstow Formation in the central Mojave Desert, *in* Reynolds, R.E., ed., 2010 Desert Symposium: California State University Desert Studies Center, Zzyzx, California, California State University Desert Studies Consortium, p. 148-161.

Reynolds, R.E., and Schweich, T.A., 2013, The Rainbow Loop Flora from the Mud Hills, Mojave Desert, California, *in* Reynolds, R.E., ed., 2013 Desert Symposium: California State University Desert Studies Center, Zzyzx, California, California State University Desert Studies Consortium, p. 39-48.

Smiley, T.M., Hyland, E.G., and Cotton, J.M., 2015, Approaches for reconstructing paleoenvironment in the Crowder and Cajon formations, southern California, *in* Reynolds, R.E., ed., Mojave Miocene: 15 Million Years of History: California State University Desert Studies Center, Zzyzx, Califorina, California State University Desert Studies Consortium.

Strömberg, C.A.E., 2003, The origin and spread of grass-dominated habitats in North America during the Tertiary and how it relates to the evolution of hypsodonty in equids [Ph.D.: University of California, Berkeley.

Strömberg, C.A.E., 2004, Using phytolith assemblages to reconstruct the origin and spread of grass-dominated habitats in the great plains of North America during the late Eocene to early Miocene: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 207, no. 3–4, p. 239-275.

Strömberg, C.A.E., 2005, Decoupled taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America: Proceedings of the National Academy of Sciences of the United States of America, v. 102, no. 34, p. 11980-11984.

Strömberg, C.A.E., 2011, Evolution of grasses and grassland ecosystems: Annual Review of Earth and Planetary Sciences, v. 39, p. 517-544.

Strömberg, C.A.E., Werdelin, L., Friis, E.M., and Saraç, G., 2007, The spread of grass-dominated habitats in Turkey and surrounding areas during the Cenozoic: Phytolith evidence: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 250, no. 1–4, p. 18-49.

Woodburne, M.O., Tedford, R.H., and Swisher, C.C., III, 1990, Lithostratigraphy, biostratigraphy, and geochronology of the Barstow Formation, Mojave Desert, southern California: GSA Bulletin, v. 102, p. 459-477.

Zachos, J.C., Pagani, M., Sloan, L.C., Thomas, E., and Billups, K., 2001, Trends, rhythms, and aberrations in global climate 65 Ma to present: Science, v. 292, p. 686-693.