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LATE PLEISTOCENE SHASTA GROUND SLOTH (XENARTHRA) DUNG, DIET, AND ENVIRONMENT FROM THE SIERRA VIEJA, PRESIDIO COUNTY, TEXAS

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Abstract.–We present new information about the Late Pleistocene Shasta ground sloth (*Nothrotheriops shastensis*). Spirit Eye Cave in the Sierra Vieja along the Rio Grande provides the newest evidence that the Shasta ground sloth inhabited further south in the mountains of the southwestern Trans-Pecos, Texas, than has been previously documented. The cave is one of only twelve known *Nothrotheriops* dung localities. During excavation of the cave, packrat middens and sloth dung were discovered. Two areas within the cave provide radiocarbon dated ground sloth dung and packrat midden macrobotanical remains which permit the reconstruction of the sloth diet and local biotic habitat at 30,800 and 12,900 calibrated YBP. The local community at 30,800 calibrated years ago was a pinyon-juniper woodland with yucca, sandpaper bush, globemallow, cactus, and barberry in the understory based on the packrat midden from the cave. The dung contents indicate that the diet of the sloth included C_3 and C_4 grasses along with *Agave*. Data for the local vegetation community and sloth diet from 12,900 years ago indicate that during this late glacial time, the region was still a pinyon-juniper woodland but also contained *Celtis*, *Quercus*, and *Larrea*, among other taxa.

Keywords: *Nothrotheriops shastensis, Quaternary, megafauna, phytolith*

The North American ground sloth *Nothrotheriops* (Nothrotheriidae; Xenarthra) is represented by two nominal species and was the smallest of the ground sloths from mainland North America (Hoffstetter 1954). The Texas ground sloth, *Nothrotheriops texanus* (Hay 1916) was restricted to the Irvingtonian Land Mammal Age (LMA), dating first at ~1.7 Ma through the early and middle Pleistocene, was the more widely distributed species, and weighed an estimated 323 kg (Akersten &

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McDonald 1991; McDonald 2005). The larger, more recent Shasta ground sloth, *N. shastensis* (Sinclair 1905) was present during the Late Pleistocene Rancholabrean LMA less than 150,000 YBP and weighed an estimated 463 kg (McDonald 2005). The latter species was restricted primarily to the more arid environments of southwestern North America from the northeastern edge of the Chihuahuan Desert, extending south into central Mexico (McDonald & Jefferson 2008) and Belize (De Iuliis et al. 2015). These authors and McDonald (in press) review the known localities containing *Nothrotheriops* skeletons and cave localities containing sloth dung. Based on the review-work of McDonald & Jefferson (2008), Hunt & Lucas (2018) re-assessed the known locations of *Nothrotheriops* dung. *Nothrotheriops shastensis* skeletal remains and dung are known from southern NM, northwestern TX (from multiple locations), and elsewhere in the Southwest; however, the taxon is not known to occur farther south along the mountainous region flanking the Rio Grande of Trans-Pecos TX or adjacent areas in Chihuahua, Mexico (Harris 1985; McDonald & Jefferson 2008; McDonald & Morgan 2011).

Here we present information about a new cave locality with *Nothrotheriops shastensis* dung and packrat midden macrobotanical fossils from the Chihuahuan Desert in Presidio County, TX (Fig. 1). The Chihuahuan Desert in the arid Southwest is a significant location for Late Pleistocene faunistic, floristic, and climatic studies due to its present moisture-deficient climate pattern. Change in the position of the polar jet streams have been shown to have important effects on the distribution of rainfall in this desert with today over 70% of its precipitation arriving in the summer (Van Devender 1990). Limestone is the predominant rock type in the mountains of Trans-Pecos TX, and because of this, dry caves, rockshelters, and crevices are plentiful and occur throughout this region. Due to these attributes, Late Pleistocene-age packrat middens have been recovered in abundance in many of the desert mountain ranges, allowing an initial reconstruction of past plant communities and late glacial climate regime to be made (Van Devender 1990).

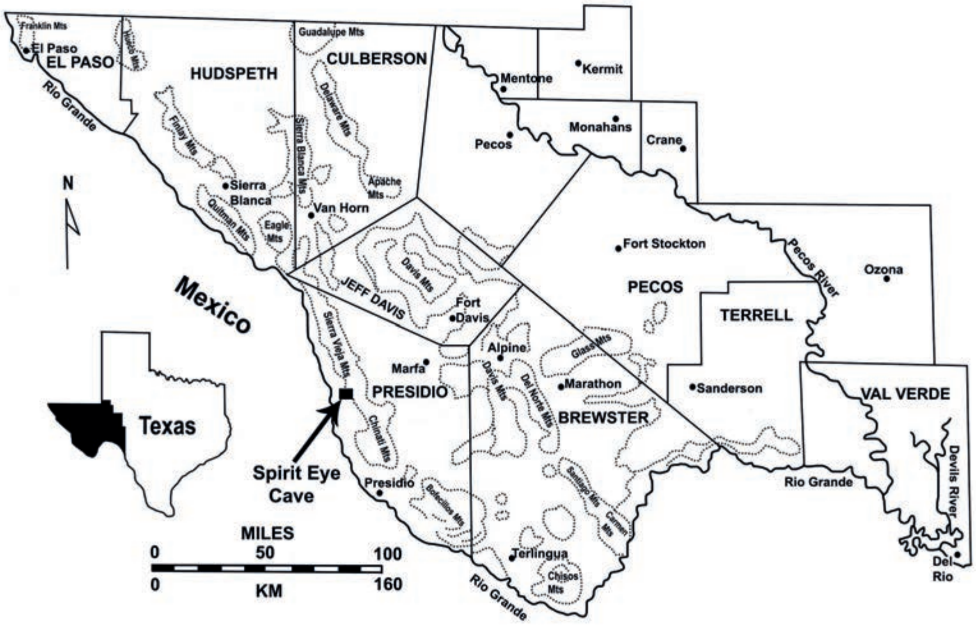

Figure 1. Map of Trans-Pecos TX showing the location of Spirit Eye Cave in relation to local mountain ranges.

The new ground sloth locality is Spirit Eye Cave, an archaeological site (locality number 41PS25) located at 1,433 m elevation along the limestone cliff region of the Sierra Vieja just north of Pinto Canyon and the Chinati Mountains (Fig. 1). The Sierra Vieja is a low-elevation mountain range separating the Rio Grande from the larger Davis Mountains to the northeast. The four main vegetation types in the Trans-Pecos are described by Powell & Worthington (2018) with many intergrading phases of the Chihuahuan Desert presented there and in Henrickson & Johnston (1986) (see also Jameson & Flury 1949; York 1949; Harveson 2016; Davis & LaDuc 2018). The Sierra Vieja and Chinati Mountains consist mainly of desert scrub and woodland species, but the mountain tops have montane woodland vegetation communities. North and east of the mountains the vegetation is dominated by a desert grassland (Powell & Worthington 2018).

Plants common in the vicinity of Spirit Eye Cave are predominantly in the Larrea scrub and mixed desert scrub intergrading phases of the

Chihuahuan Desert (Henrickson & Johnston 1986) and include: *Agave* spp. (agave), *Larrea tridentata* (creosote-bush), *Fouquieria splendens* (ocotillo), *Koeberlinia spinosa* (crucifixion-thorn), *Atriplex canescens* (four-wing saltbush), *Celtis pallida* (desert hackberry), *Lycium berlandieri* (wolfberry), *Ephedra* spp. (Mormon tea), *Senegalia* (=*Acacia*) *greggii* (cat-claw), *Prosopis glandulosa* (mesquite), and *Opuntia* spp. (platyopuntia cactus), among others (Van Devender et al. 1978).

The lower and upper entrances to Spirit Eye Cave provide access to the main chamber of the cave (Fig. 2). Today much of the main chamber is buried deep in bat guano with evidence that organic decay is common due to occasional inflowing rainwater. Beyond the entrance chamber are two inclined passageways (Shafts A and B). Although wet in the main chamber towards the lower entrance, areas towards the upper entrance and within the two shafts are dry. It is within these dry areas of the cave that archaeological perishable artifacts were discovered and analyzed (Schroeder 2018). During excavation for the Archaic archaeology by B.A. Schroeder (BAS), packrat middens and sloth dung were discovered. The cave was revisited in September 2019 to document the midden and sloth dung fossils presented here.

MATERIALS & METHODS

A test pit near the end of Shaft B uncovered scattered fragments of sloth dung 15 cm below the surface. Further testing in 2019 did not uncover additional sloth dung or a dung mat in this area; the sample presented here is from the initial excavation by BAS. A small crawlway connects Shafts A and B (Fig. 2). In this elevated bedrock area is located an approximately 1 by 1 m accumulation of a packrat midden (midden name and number = Spirit Eye #1; containing sloth dung) and loose sloth dung bolus fragments (Fig. 2). The sloth dung samples and the packrat midden from Shaft A were sampled and are presented here. All specimens reported here are curated into the collections at The

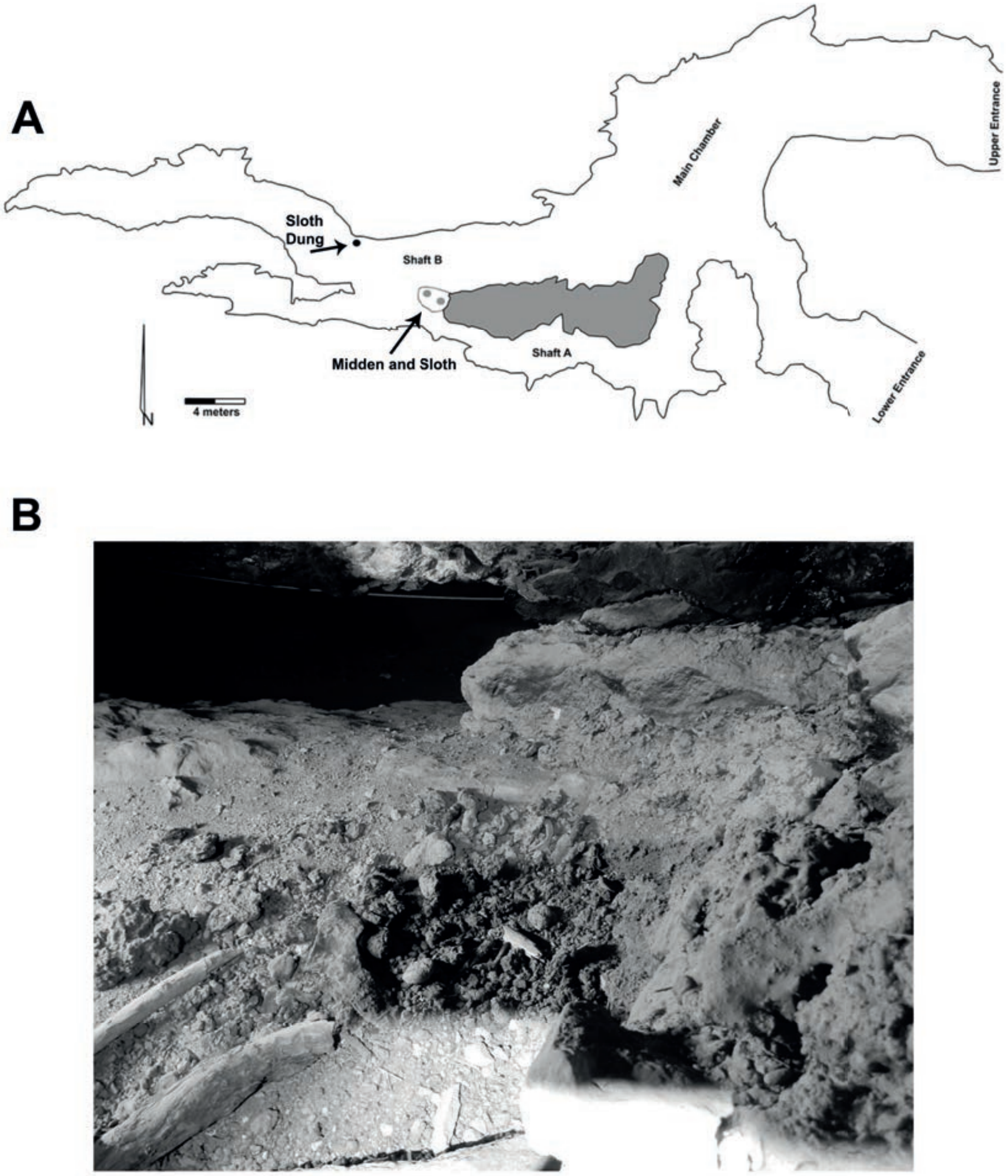

Figure 2. Spirit Eye Cave, Sierra Vieja, Trans-Pecos TX. Map (A) with the location of *Nothrotheriops shastensis* dung remains in Shaft A and B, and (B) close-up of sloth dung and packrat midden in Shaft A.

Mammoth Site, Hot Springs, South Dakota (Mammoth Site Paleontology; MSP).

Identification of the dung (Shaft A and B samples) was determined by direct comparison using a comparative dung collection at The Mammoth Site (Hot Springs, SD) and literature resources. Direct radiocarbon dating of dung and midden contents from Shaft A and B samples were assessed by Beta Analytic Testing Laboratory (Beta; Miami, FL) and DirectAMS Radiocarbon Dating Service (D-AMS; Bothell, WA) labs and presented as calibrated ages (cal YBP) using the IntCal 13 calibration curve. Analysis of the packrat midden follows standard techniques outlined in Betancourt et al. (1990). Angiosperm plant taxonomy follows Powell & Worthington (2018).

Diet of the ground sloth was reconstructed via analysis of the phytolith contents of dung samples from Shaft A (A_p) and Shaft B (B_p). To analyze the silica phytoliths, approximately 0.5 g of dry sloth dung material removed from the center of each sample was placed in a 400 mL beaker and mixed with 20 mL of 37% hydrochloric acid (HCl) to remove carbonates (Table 1). Next, 80 mL of 70% nitric acid (HNO_3) was added to each sample and then heated to 80° C for 2 hr to oxidize the acid soluble organic fraction. Samples were then rinsed five times with reverse osmosis deionized water (RODI). Next, 10 mL of 10% potassium hydroxide (KOH) was mixed into each sample to remove base-soluble organics. After 10 min, the solution color was recorded as a qualitative measure of humic acid (humate) content (Table 1). This step was followed by five rinses with RODI to return the samples to neutral pH. The samples were then transferred to 15 mL centrifuge tubes and dried under vacuum at room temperature. The dried samples were mixed with lithium metatungstate (LMT) set to a density of 2.3 g/mL and centrifuged at 1500 rpm for 10 min. Phytoliths suspended at the surface of the heavy liquid were decanted into new centrifuge tubes and rinsed with RODI. Known quantities of synthetic microspheres were added to each sample in proportion to the volume of each

Table 1. Silica and calcium oxalate (CaOx) phytolith extraction and count summary data. *CaOx extraction samples were split into < 50 µm and > 50 µm particle size fractions after the bleach step to improve visibility for counting.

	#5 Silica	#5 CaOx	#6 Silica	#6 CaOx
Weight started (g)	0.539	0.434	0.451	0.300
10% HCl reaction	Strong	N/A	Strong	N/A
10% KOH step supernatant color	No Rx	N/A	No Rx	N/A
Microspheres added* ($x10^3$)	2	10 (<50 µm)	10	60 (<50 µm)
		60 (>50 µm)		4 (>50 µm)
Microspheres counted*	37	756 (<50 µm)	587	797 (<50 µm)
		200 (>50 µm)		635 (>50 µm)
Phytoliths counted*	660	80 (<50 µm)	479	797 (<50 µm)
		133 (>50 µm)		635 (>50 µm)
Phytolith concentrations (per g)	66,189	17,560	18,093	658,316
Microcharcoal concentrations (per g)	602	N/A	755	N/A

phytolith extract (Table 1). The sample extracts were transferred to 1.5 mL storage vials with 100% ethyl alcohol (EtOH).

To assess the calcium oxalate phytoliths, approximately 0.4 g of dry sloth dung material removed from the center of each sample was placed in a 50 mL centrifuge tube and mixed with 6% sodium hypochlorite (bleach) (Table 1). The samples were periodically agitated with a vortex mixer and allowed to soak in the bleach solution for 48 hr. The samples were rinsed with RODI five times by centrifugation (3000 rpm, 5 min) and decantation of the rinsate. Articulated pieces of lignified plant material were broken into smaller pieces within the centrifuge tube using a metal spatula. The samples were washed though sieves to separate <50 µm and >50 µm size fractions to improve counting visibility. Known quantities of synthetic microspheres were added to each fraction in proportion to the volume of unoxidized residue (Table 1). The residue samples were transferred to 1.5 mL storage vials with EtOH.

A subsample of each phytolith extract was transferred with EtOH to a microscope slide and allowed to dry. The residue was then mixed with and mounted in immersion oil, and coverslips were sealed with fingernail polish. Silica phytolith morphotype names follow the International Code for Phytolith Nomenclature 2.0 (ICPN; Neumann et al. 2019) except where noted in Table 2. Silica phytolith taxonomic interpretations are based on modern reference material and published studies listed in Table 2. Calcium oxalate (CaOx) phytolith morphotypes follow the references listed in Table 3. CaOx phytolith taxonomic interpretations are based on regional plant distributions, modern CaOx reference material, and published studies listed in Table 3.

Phytolith counting was conducted with a transmitted light microscope equipped with cross-polarizing filters at a magnification of 400x. Silica phytolith counting proceeded until at least 200 Iph (humidity-aridity index) phytoliths (bilobates and saddles) were tallied (Yost et al. 2020). CaOx phytolith counting proceeded until at least 200 were tallied. Silica phytolith percent relative abundance was calculated based on the phytolith sum. Concentrations were calculated from the microsphere counts and normalized to sample weights. Because two different particle size fractions were counted independently for each CaOx sample, CaOx phytolith relative abundance was calculated from the combined morphotype concentration values from each size fraction.

RESULTS

The Shaft B passageway and A-to-B crawlway have extremely low bedrock ceilings and therefore it is unlikely that a sloth visited these areas in the cave. We propose that packrats have transported the dung

Table 2. Silica phytolith morphotypes, taxonomy, sample counts, and index values. *Small caps = ICPN 2.0 morphotype names (Neumann et al. 2019); Sources of other names after the following: [1]Yost et al. (2020), [2]Yost et al. (2018), [3]Collura & Neumann (2017); [4]Yost (2015); [5]This study and Eichhorn et al. (2010); [6]Piperno (2006); [7]Madella et al. (2005).

Silica morphotypes*	Taxonomic interpretations	Sample counts	
		#5	#6
CRENATE (trapeziform sinuate)	Pooideae	2	4
RONDEL (keeled)	Pooideae	1	7
TOTAL C_3 GRASS TYPES		3	11
SADDLE	Chloridoideae	253	165
RONDEL CONICAL (spool/horned)	cf. *Sporobolus*	17	15
BILOBATE: *Aristida* type (long shank)	cf. *Aristida*	11	0
TOTAL XERIC C_4 GRASS TYPES		281	180
CROSS	Panicoideae	8	9
BILOBATE	Panicoideae	54	57
POLYLOBATE	Panicoideae	1	0
RONDEL (panicoid-type)	Panicoideae	6	0
TOTAL MESIC C_4 GRASS TYPES		69	66
Multicellular long cell fragment[1, 2]	Poaceae	9	0
BULLIFORM FLABELLATE	Poaceae	2	11
Substomatal/stomatal complex[1, 2]	Poaceae	0	0
ELONGATE DENDRITIC (dendriform)	Poaceae	0	0
TOTAL INDETERMINATE GRASS TYPES		11	11
ACUTE BULBOSUS (trichome)	Poaceae	53	87
ELONGATE ENTIRE	Poaceae, Cyperaceae	51	76
ELONGATE SINUATE/DENTATE	Poaceae, Cyperaceae	43	18
BLOCKY (Parallelepipedal bulliform)	Poaceae, Cyperaceae	20	22
TOTAL INDETERMINATE GRASS/SEDGE TYPES		167	203
Thin with ridges[1, 2]	Cyperaceae (stem)	18	0

Table 2 Cont.

Silica morphotypes*	Taxonomic interpretations	Sample counts	
		#5	#6
Irregular with tubular projections[1, 2]	Cyperaceae (root)	0	1
Cone cell–verrucate/polyhedral[1, 2]	Cyperaceae (achene)	2	0
TOTAL SEDGE TYPES		21	1
SPHEROID ORNATE (globular granulate)	Trees	0	1
Elongate facetate (Sclereid)[3]	Trees	1	0
Tabular verrucate: *Celtis* sp. drupe[4]	*Celtis* cf. *reticulata*	0	1
TOTAL TREE TYPES		1	2
Prismatic anisopolar[5]	*Commelina* sp.	0	1
Anticlinal sheet[6]	Leaves	1	0
TRACHEARY HELICAL	Leaves / herbaceous stems	8	0
Hair (trichome) base cell[7]	Various plants	99	4
TOTAL VARIOUS PLANTS		108	5
	TOTAL SILICA PHYTOLITHS COUNTED	660	479
	Iph aridity index	80.1	71.4
	C3 grass types (%)	0.8	4.3
	C4 mesic grass types (%)	19.5	25.7
	C4 xeric grass types (%)	79.6	70.0

and plant remains from other areas of the passageways with taller ceilings, main chamber, and areas immediately outside the cave.

Dung identification.–The dung that was recovered along with the skeleton of *Nothrotheriops shastensis* from Aden Crater in southern NM permitted the initial dung morphology-to-species identification (Eames 1930; Lull 1930). Dung of ground sloths is typically composed of linear-connected thick plates that contain a matrix dominated with short-cut twigs in the case of the browser, *Nothrotheriops*, or grass stems with some twigs for the grazer, *Mylodon* from South America (and presumably the North American *Paramylodon*). These are

Table 3. Calcium oxalate (CaOx) phytolith morphotypes, taxonomy, and sample counts. Taxonomic interpretations based on regional plant distributions, modern CaOx reference material, and published studies as indicated. For samples 5 and 6, *a* denotes <50 µm fraction and *b* denotes >50 µm fraction.

CaOx Morphotypes	Morphotype source(s)	Taxonomic interpretations	Sample counts #5*a*	#5*b*	#6*a*	#6*b*
Spheroid	This study	Agavaceae	22	57	50	22
Spheroid cluster	This study	Agavaceae	8	7	9	1
Druse – small	Franceschi & Horner (1980)	Various plants	7	7	50	15
Druse – large	Franceschi & Horner (1980)	Various plants	0	0	5	0
Raphide Type III small	Raman et al. (2014)	Agavaceae	0	0	470	519
Raphide Type III large	Raman et al (2014)	Agavaceae	0	1	5	0
Raphide Type VI small	Raman et al (2014)	Agavaceae	10	10	29	0
Raphide Type VI large	Raman et al (2014)	Agavaceae	0	0	119	39
Prism	Franceschi & Horner (1980)	Various plants	3	1	11	27
Rhomboid twin	Crutcher & Crutcher (2019)	Various plants	2	1	21	2
Domed twin	Crutcher & Crutcher (2019)	*Quercus* sp. leaf	0	0	13	4
MV twin	Crutcher & Crutcher (2019)	*Larrea tridentata* leaf	0	0	1	3
Pinacoidal	Morgan-Edel et al. (2015)	*Larrea tridentata* wood	0	0	1	1
Sand	Franceschi & Horner (1980)	Various plants	28	49	13	0
		TOTAL CaOx PHYTOLITHS COUNTED	80	133	797	653

morphologically distinct from the smaller, disc-shape dung from *Bison* and *Bos* with a dry-diet (or the classical ‘meadow muffin’ of a green grass diet), the large (~25 cm diameter) single-bolus *Mammuthus*, the wedge-shaped masses from *Equus*, or that of the pellet-producing ruminants (Mead et al. 1986; Mead & Swift 2012; Mead et al. in press). The Spirit Eye Cave (MSP 1, 2 14, 17) dung fragments are of the Shasta ground sloth bolus morphology (Fig. 3; Mead & Agenbroad 1989).

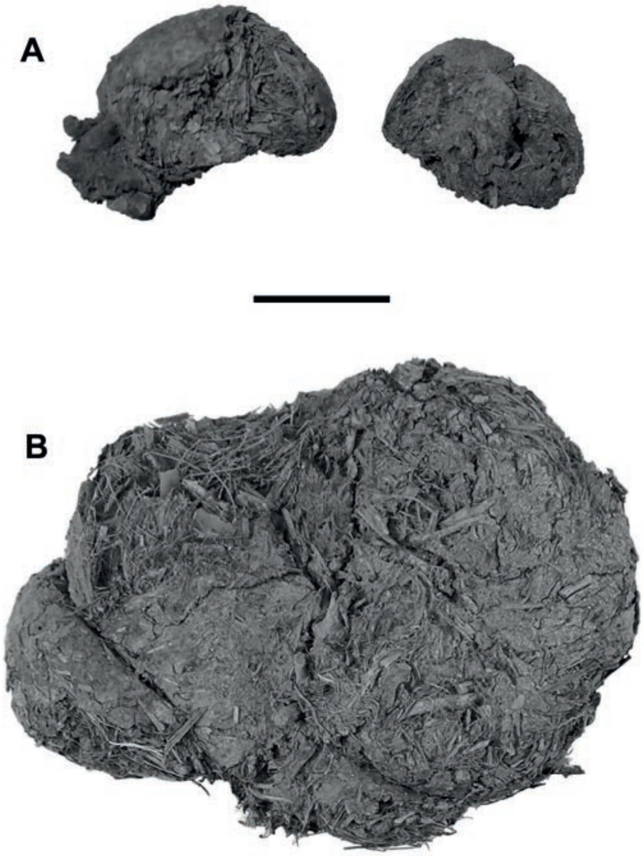

Figure 3. *Nothrotheriops shastensis* dung fragments from (A) Spirit Eye Cave (Shaft A), and as a comparison (B) Upper Sloth Cave (C-08), Guadalupe Mountains National Park. Contents are typically short-cut twigs of browsed plants (see text for details). Scale bar is 2 cm.

Chronology.–Four coprolite samples from the cave deposit establish the chronology of the sloth dung (Fig. 4). Sloth dung from Shaft A is dated directly and indirectly. An isolated dung bolus fragment was AMS dated to 31,254 - 30,879 cal YBP (Beta 518298; 27,040±110 radiocarbon YBP; δ13C - 14.9 o/oo). The urine-cemented packrat midden adjacent to isolated dung boluses contained plant macrofossils and small fragments of sloth dung. One dung fragment removed from the midden was AMS dated to 30,840 - 30,140 cal YBP (D-AMS 036249; 26,158±102 radiocarbon YBP). Two *Juniperus* (juniper) seeds from the same packrat midden that contained the sloth sample were AMS dated to 30,915 - 30,365 cal YBP (D-AMS 036248; 26,320±104 radiocarbon YBP). The ages imply that a packrat collected the sloth dung and the plant remains during the same interval of time (possibly over a few hundred years) approximately 30,800 years ago.

Sloth dung from 15 cm below surface in Shaft B is also radiocarbon dated directly. Two samples of dung date from 12,995 - 12,735 cal. YBP (D-AMS 027565) and 13,045 - 12,787 cal YBP (D-AMS 027566) with an overall approximate age of 12,900 cal YBP. The Shasta ground sloth visited and utilized Spirit Eye Cave at least for short episodes of time approximately 30,800 years ago and about 12,900 years ago. More in-depth dating of additional sloth dung deposits may disclose that sloths utilized the cave for more extensive periods of time.

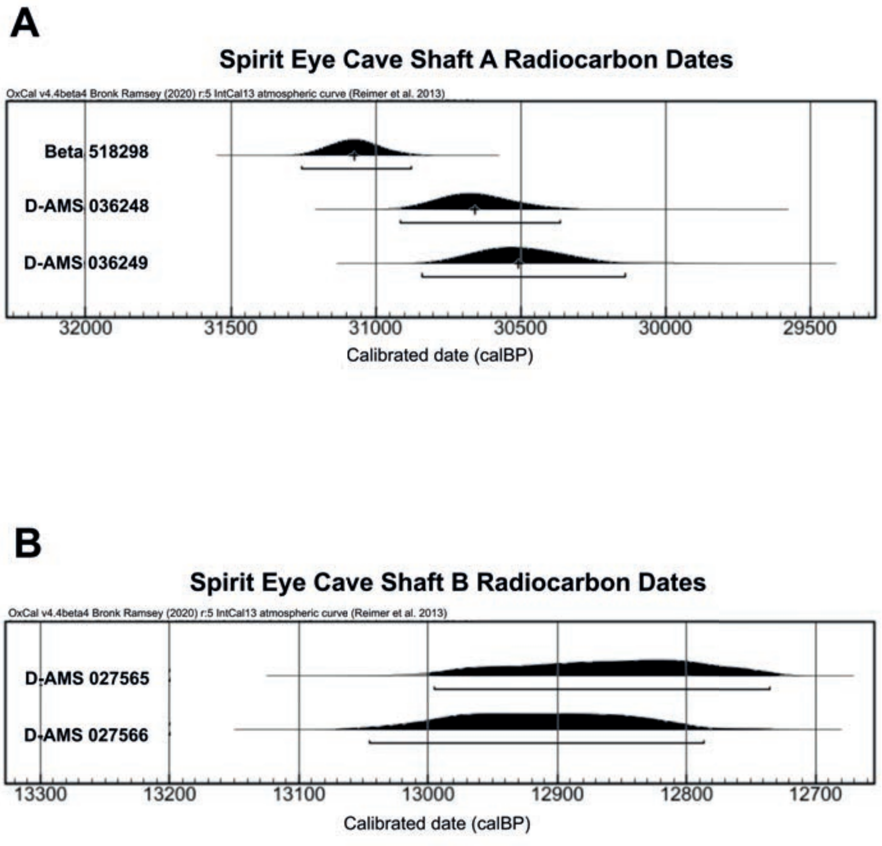

Figure 4. Graph illustrating the calibrated radiocarbon (cal YBP) chronology and overlap of dates for *Nothrotheriops shastensis* dung in (A) Shaft A and (B) Shaft B, Spirit Eye Cave, Sierra Vieja, Trans-Pecos TX.

Diet Reconstruction.–Silica phytoliths were well preserved, and concentrations were 6.6 and 1.8 x 10^5 phytoliths per gram (ppg) for sloth dung samples A_p and B_p, respectively (Table 1). The silica phytolith assemblages from both samples were dominated by morphotypes derived from xeric C_4 Chloridoideae and mesic C_4 Panicoideae grasses (Fig. 5). Phytoliths derived from cool season C_3 Pooideae grasses were rare but present. The Iph aridity index with a value of 80.1 was slightly higher for sample A_p than the 71.4 value for sample B_p (Table 2). The relative abundance of cool season C_3 grass phytoliths was lower in sample A_p (0.8%) than for sample B_p (4.3%). The relative abundance of mesic C_4 grass phytoliths was lower in sample A_p (19.5%) than for sample B_p (25.7%). Silica phytoliths diagnostic of sedges (Fig. 5B:6–7) were slightly higher in sample A_p (3.0%) than in sample B_p (0.2%). Silica phytoliths derived from trees were rare in both samples, but few woody plants in this region produce silica phytoliths. One tree phytolith diagnostic of Celtis drupes, and most likely derived from Celtis reticulata, was observed in sample B_p (Fig. 5B:8). One phytolith diagnostic of seeds from the herbaceous plant Commelina (dayflower) was observed in sample B_p (Fig. 5B:9–10). Silicified hair base cells (Fig. 5B:1) derived from dicotyledonous leaves and stems were relatively abundant in sample A_p (15%) and rare in sample B_p (0.8%).

Calcium oxalate (CaOx) phytoliths were also well preserved. CaOx concentrations were 1.6 and 65.8 x 10^5 ppg for sloth dung samples A_p and B_p, respectively (Table 1). A total of 14 CaOx phytolith morphotypes were recognized (Table 3). The CaOx assemblages were strikingly different (Fig. 6). CaOx concentrations in dung sample A_p were relatively low and dominated by Spheroids (Fig. 6B:6-7) and Sands (Fig. 6B:3) produced by various plants. Some of the spheroids may be fecal spherulites rather than CaOx phytoliths. CaOx concentrations in sample B_p were an order of magnitude higher and overwhelmingly dominated by small raphide type III phytoliths (Fig. 6B:17-18) regionally diagnostic of Agavaceae and produced in high proportions in *Yucca* leaves. Large raphide type VI phytoliths, also regionally diagnostic of Agavaceae and produced in both *Agave* and

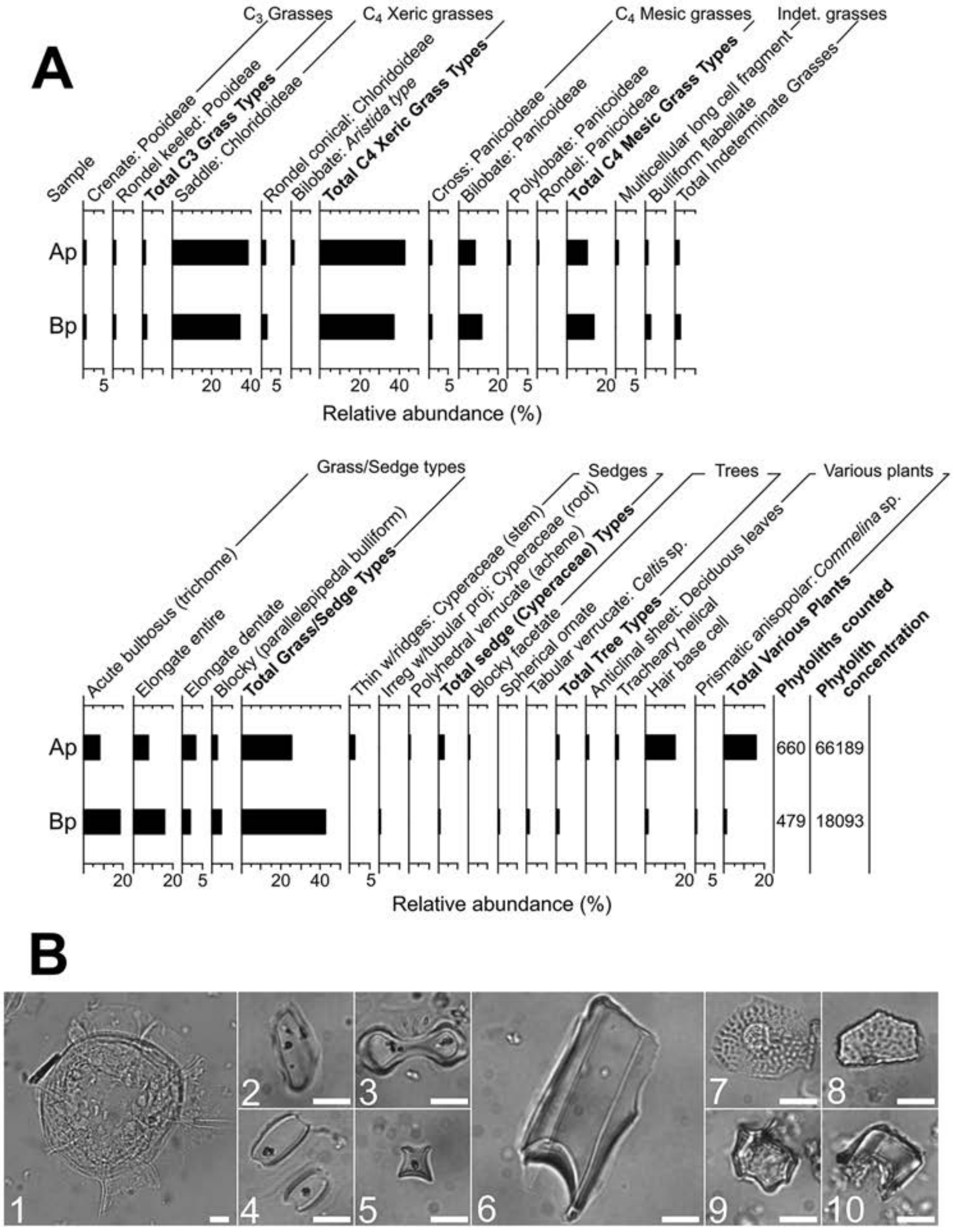

Figure 5. Silica phytolith abundance in *Nothrotheriops shastensis* dung. 1) Silica phytolith relative abundance; B) Micrographs of selected phytoliths recovered from Shasta ground sloth dung samples. Scale bar = 10 µm. A) Silicified hair base cell from a dicotyledonous plant. 2) Crenate phytolith from a C_3 pooideae grass. 3) bilobate phytolith from a C_4 panicoideae grass. 4) saddle phytoliths from a C_4 chloridoideae grass. 5) 'rondel conical' (horned) phytolith from a C_4 chloridoideae grass. 6) 'thin with ridges' phytolith derive from sedge (Cyperaceae) stems. 7) verrucate/polyhedral cone cell from a sedge (Cyperaceae) achene. 8) 'tabular verrucate' phytolith derived from a *Celtis* sp. drupe (fruit). 9) 'prismatic anisopolar' phytolith in outer periclinal surface (OPS) view derived from *Commelina* sp. seeds. 10) Same as I but inside view showing much of the granular pole as broken/dissolved.

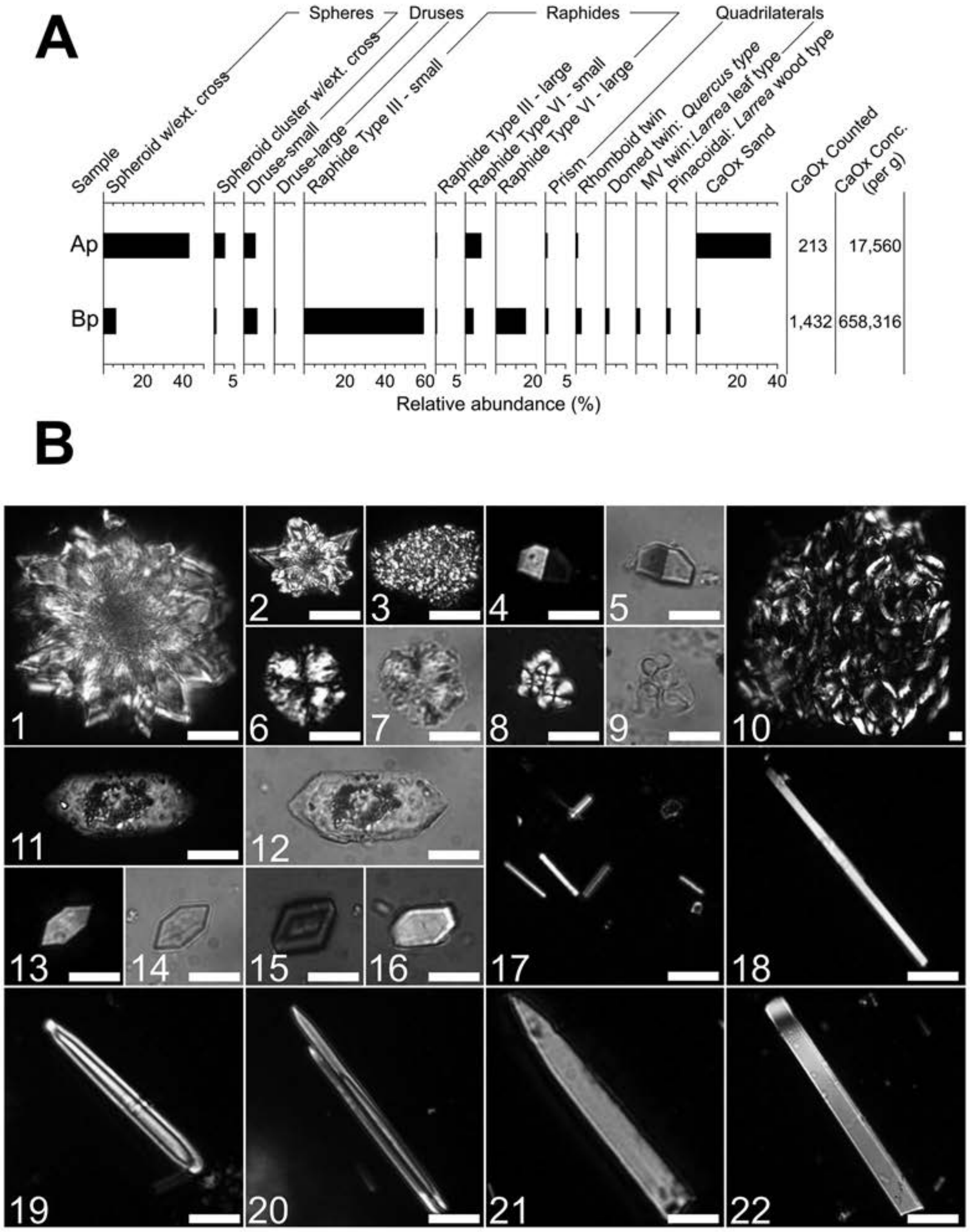

Figure 6. Calcium oxalate (CaOx) phytolith abundance in *Nothrotheriops shastensis* dung. A) Calcium oxalate (CaOx) phytolith relative abundance; B) Cross-polarized light micrographs of selected calcium oxalate (CaOx) phytolith morphotypes and a possible starch granule cluster recovered from Shasta ground sloth dung samples. Scale bar = 10 µm. 1) druse–large. 2) druse–small. 3) sand. 4–5) domed twin. 6–7) spheroid. 8–9) spheroid cluster. 10) possible starch granule cluster. 11–12) pinacoid. 13–14) prism. 12–16) prism/rhombic twin. 17) raphide type III–small. 18–19) raphide type III–large. 20) raphide type III–large cluster. 21) raphide type VI–large in bevel/point view. 22) raphide type VI–large in rectangle view.

*Yucc*a leaves, had the second highest relative abundance in dung sample B_p. Prism (Fig. 6B:13-14) and rhombohedral (Fig. 6B:15-16) phytoliths were present at low levels in both samples. These morphotypes are produced by a wide variety of plants, including species of *Juniperus* and *Atriplex* (saltbush). Druses were observed (Fig. 6B:1-2) but are of low taxonomic value because they are produced by a wide variety of plants, including *Atriplex*. Present only in dung sample B_p were domed twin phytoliths (Fig. 6B:4-5) typical and possibly regionally diagnostic of *Quercus* (oak) leaves, one MV twin phytolith typical and possibly regionally diagnostic of *Larrea tridentata* (creosote bush) leaves, and one pinacoidal phytolith (Fig. 6B:11-12) typical and possibly regionally diagnostic of woody tissue from *Larrea tridentata*.

In the silica phytolith extracts just a few siliceous algae valves (diatoms) and numerous microcharcoal fragments were observed. One *Aulacoseira* sp. valve was observed in sample A_p, and two *Epithemia* sp. values were observed in sample B_p. Microcharcoal concentrations were 602 and 755 fragments per g for samples A_p and B_p, respectively.

Packrat Midden Contents.–The macrobotanical contents of the packrat midden were not as diverse as seems to be typical for middens in the Trans-Pecos region (Van Devender 1990). The most abundant plant remains were *Juniperus* sp. twigs and seeds (Fig. 7C; MSP 5). These remains did not allow for species identification and the tree does not occur locally today. The seeds are not as large as those that occur on *J. flaccida* (weeping juniper) or *J. deppeana* (alligator juniper), and the twigs do not have the flattened form as found on *J. scopulorum* (Rocky Mountain juniper). A few leaf fragments of *Berberis* (*Mahonia*) cf. *haematocarpa* (red berberis; Fig. 7B; MSP 8) were recovered that have more than three spikes on the leaves (a character of *B. trifoliolata* (algerita) which is a local shrub in the region today). A single fragment of a yucca leaf with minute denticles on the leaf edges is identified as *Yucca* cf. *rostrata* (Spanish bayonet; Fig. 7A; MSP11) which is also not in the immediate region today. We do not know what characters on the leaf permit the identification of *Y. rostrata* from *Y. thompsoniana*. Spines and seeds of a cactus have characteristics that allow an identification as *Opuntia* sp. (MSP 6). Carpels were common and indicate a species of *Sphaeralcea* sp. (globemallow; Fig. 7F; MSP 10). A single highly-denticulate leaf of *Mortonia scabrella* (sandpaper bush; Fig. 7E; MSP 9) was recovered, a shrub that is also found in the region today.

Pine needles were recovered that all indicate a two-needle variety (Fig. 7D; MSP 7). Three species of pinyon live today in the Trans-Pecos. The 2-needle *Pinus edulis* (Colorado pinyon) lives today mainly at the higher elevations such as in the Guadalupe Mountains north of and not nearby Spirit Eye Cave. *Pinus remota* (papershell pinyon) and *P. cembroides* (Mexican pinyon) live in central and southern areas of the Trans-Pecos (Harveson 2016). *Pinus remota* grows today in the upper Sierra Vieja and Chinati Mountains (Keller 2019) but not at the lower elevation of the cave locality. Both of these latter-two species can have 2- and 3-needle varieties (Van Devender 1986b; Wells 1986). Here we used the defining characters of Betancourt et al. (2001) to differentiate *P. edulis* from *P. remota*. *Pinus remota* needles and those from the packrat midden in Spirit Eye Cave have small stomata (compared to those of *P. edulis*), are of a uniform oval configuration, and are sunken in narrow troughs. Thus the fossil pinyon at Spirit Eye Cave area was *P. remota*.

DISCUSSION

Of the four taxa of ground sloths in mainland North America during the Rancholabrean LMA (*Eremotherium*, *Megalonyx*, *Nothrotheriops*, *Paramylodon*; Delsuc et al. 2019), the Shasta ground sloth was the smallest (McDonald 2005). The mylodonts (including the North American *Paramylodon*; with an estimated weight of ~1,393 kg) and the giant *Eremotherium* (estimated weight of ~ 3,962 kg) are both considered grazers (Moore 1978; Naples 1989; McDonald 1996, 2005) in contrast to the feeding strategy of *Megalonyx* (estimated weight ~1,090 kg) and *Nothrotheriops* (463 kg) as both browsers. McDonald (1996) examined the distribution of both *Megalonyx* and *Nothrotheriops* and determined that when one was common at a fossil

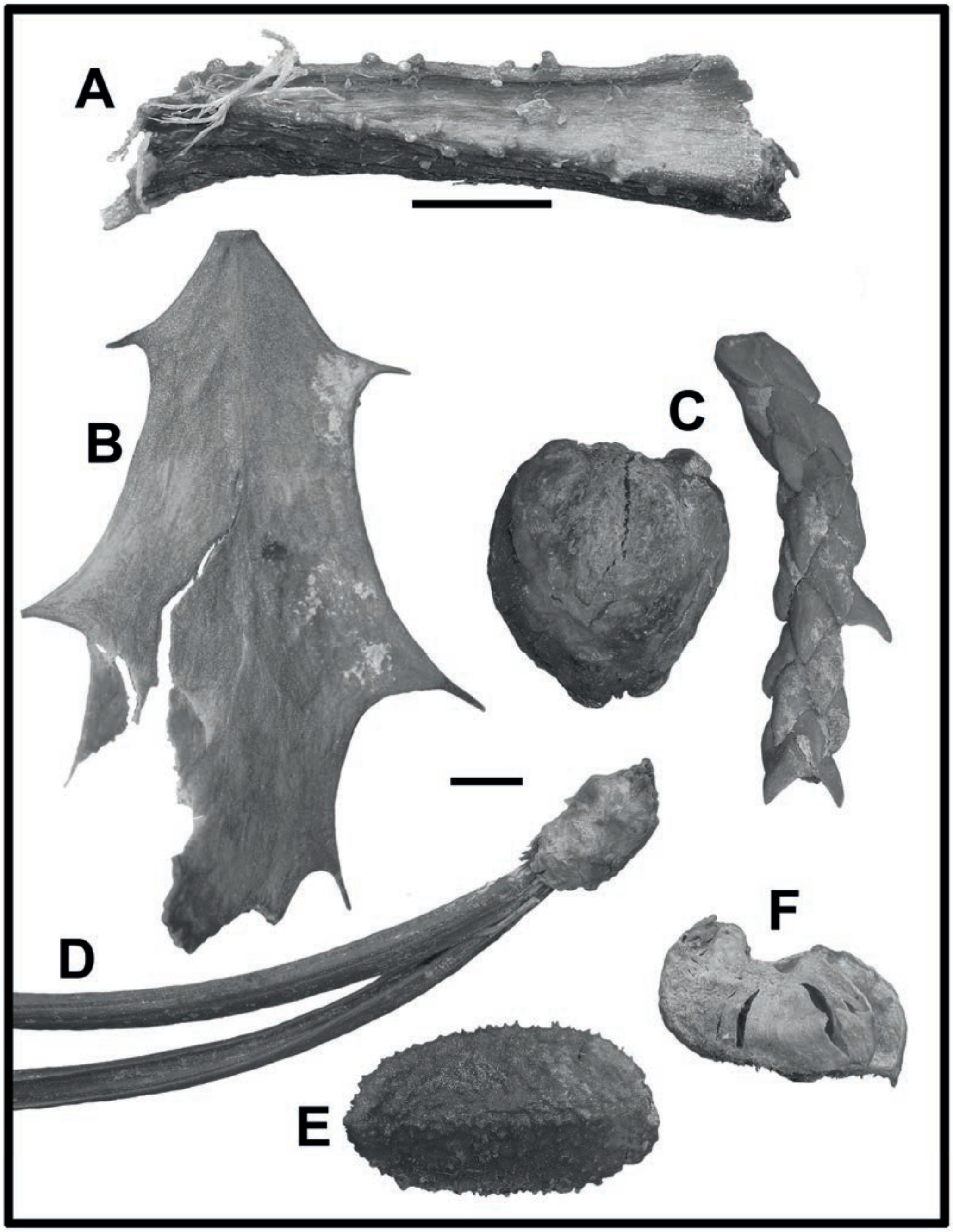

Figure 7. Macrobotanical fossils from the packrat midden in Spirit Eye Cve, ~30,900 cal YBP: (A) *Yucca* cf. *rostrata*; (B) *Berberis* (*Mahonia*) cf. *haematocarpa* (red berberis); (C) *Juniperus* sp. (juniper); (D) *Pinus remota*; (E) *Mortonia scabrella*; (F) *Sphaeralcea* sp. Scale bar is 1 mm.

locality, the other was rare or not present likely due to their differences in their habitat preferences and types of plants they consumed.

In their review of the Late Pleistocene distribution of *Nothrotheriops*, McDonald & Jefferson (2008) provided a detailed list of each locality in Mexico and the USA. Shasta ground sloths are recorded from northern CA through southern NV, AZ, UT, NM, western TX, south into Mexico and Central America at Belize (McDonald 2003; McDonald & Jefferson 2008; De Iuliis et al. 2015). With respect to the Spirit Eye Cave record reported here, *N. shastensis* is known no closer than about 320 km to other sloth dung cave localities such as Dust Cave, Upper and Lower Sloth Caves, and Williams Cave (McDonald & Jefferson 2008; McDonald in press; Fig. 8) and the nearby, non-dung localities such as Carlsbad Cavern and Lechuguilla Cave, all in the Guadalupe Mountains of TX/NM (Hill & Gillette 1987; McDonald & Morgan 2011). These dry caves containing accumulations of sloth dung, along with a few other dry caves in AZ, elsewhere in NM, NV, and UT (Fig. 8) provide unique deposits for a detailed description and reconstruction of the diet for the Shasta ground sloth (McDonald in press).

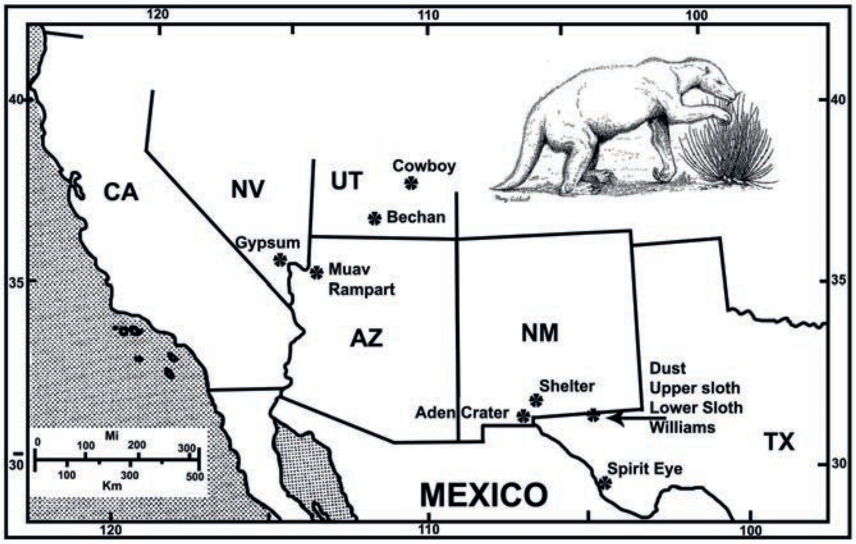

Figure 8. Map of the greater Southwest locating 12 cave sites that contain *Nothrotheriops shastensis* dung. Note that Spirit Eye Cave is the southeastern-most location. Dry cave deposits in Chihuahua, Mexico should also contain sloth dung. Adapted from Thompson et al. (1980).

Diet.–Mammalian herbivores can be grouped into those with either foregut or hindgut digestive strategies. Sloths (all xenarthrans) along with ruminants, camels, etc. lack a caecum, therefore, have an enlarged foregut to provide the main site of microbial activity for digestion (McDonald 2005). Ho (1967) determined that a browsing ground sloth (i.e., *Nothrotheriops*) had a low basal metabolism and therefore a lower core body temperature that may have permitted the sloth to consume nutritionally poor plants (McDonald 2003, 2005).

The reconstruction of an herbivore diet based on analysis of the dung can be assessed multiple ways with varying results: through the use of cuticle (microhistology), phytoliths (the analysis used here), pollen and spores (palynomorphs), and aDNA (ancient DNA for both the coprolite producer and dietary contents). The recovery of pollen and spores from dung has been used extensively for reconstructing the diet (Martin et al. 1961). Palynomorphs provide mixed data sets regarding diet and habitat. The pollen in the dung may not represent the actual plants consumed, but rather the local pollen rain from a variety of plant communities, and it can provide data about season of ingestion (King 1977; Wood & Wilmshurst 2013; Tripathi et al. 2019). Anemophilous pollen from dung does not provide an accurate reconstruction of the local environment as compared to zoophilous pollen. Possibly the most detailed reconstruction of a diet comes from the analysis of the phytoliths, pollen, and cuticular remains (which make up the bulk of a dung bolus). The analysis of cuticles, pollen, and, more recently, aDNA (difficult to preserve well enough for analysis) from the same dung bolus often provides different data sets, yet can be informative about diet and local plant communities (King 1977; Thompson et al. 1980; Poinar et al. 1998; Ghosh et al. 2008; Wood et al. 2013).

Regarding *Nothrotheriops* diet and its habitat, cuticles, pollen, and phytoliths have been utilized for reconstructions. In select scenarios, analysis of the dung contents and packrat middens from the same locality and radiocarbon age do provide a more in-depth reconstruction (Van Devender et al. 1977, 1979; Spaulding & Martin 1979; Thompson et al. 1980; Mead & Spaulding 1995). The diet of *Nothrotheriops* is probably the best known of the four sloths in the North American Late

Pleistocene because of dry-preserved dung remains (McDonald in press).

Silica and CaOx phytolith analysis of the Shasta ground sloth dung samples A_p (~30,800 cal YBP) and B_p (~12,900 cal YBP.) yielded information on both the diets of these individuals and local vegetation habitats. Both individuals consumed a mix of graminoids consisting of mostly xeric and mesic C_4 grasses, some cool season C_3 grasses, and some sedges. However, graminoid silica phytolith concentrations were approximately six times higher in sloth dung A_p. In contrast, *Yucca* (Agavaceae) appears to have been a major component of sloth dung B_p and may not have been present at all in sloth dung A_p. The paucity of raphide type III phytoliths and presence of raphide type VI phytoliths suggests that a small amount of *Agave* (Agavaceae) may have been present in dung sample A_p. Overall, Agavaceae CaOx phytolith concentrations were two orders of magnitude higher in dung sample B_p, and these were likely derived from *Yucca*. Silicified hair base cells from an indeterminant dicotyledonous plant were relatively common in dung sample A_p but were extremely rare in dung sample B_p. A large cluster of what appears to be starch granules with an eccentric hilum were observed in dung sample B_p (Fig 6J) and may be derived from starchy root material. It is thought that some Pleistocene ground sloths may have dug for edible roots and tubers (Bargo et al. 2006). We are unaware of previous reconstructions of Shasta ground sloths having consumed woody root vegetation.

In this region, woody plants are low silica phytolith producers, so silica phytolith assemblages here can significantly underrepresent the abundance of woody taxa. Only a few silica phytoliths diagnostic of woody plants were observed in either dung sample. In contrast, woody tissues and leaves of trees and shrubs are prolific producers of CaOx phytoliths. However, few CaOx phytoliths typical of woody plants were recovered from either dung sample, suggesting that woody plant cover was relatively low during the time periods represented by these two samples or that woody vegetation was not consumed that often and was not in the dung we sampled. Dung sample B_p had the strongest evidence for woody plant consumption, with phytoliths from *Celtis*, *Quercus*, and *Larrea* recovered.

The plants consumed by Shasta ground sloths and recovered from dung B_p suggest that vegetation composition was significantly different at ~30,800 cal YBP than at ~12,900 cal YBP. Dung sample B_p was overwhelmingly dominated by succulents such as *Yucca* and contained much lower concentrations of graminoids (grasses and sedges) whereas dung sample A_p comprised mostly graminoids and dicotyledonous plants. Interestingly, the ratio of xeric (Chloridoideae) to mesic (Panicoideae) C_4 grasses expressed as the Iph humidity-aridity index did not vary greatly between the samples (Table 2). Dung sample B_p with more succulents, had slightly fewer xeric C_4 Chloridoideae grasses (lower aridity index) than dung sample A_p. However, since short-grass Chloridoideae taxa with their lower C:N values are generally more palatable and nutritious than tall-grass Panicoideae taxa (Mattson 1980; Quigley & Anderson 2014), the ratio of these grasses (i.e., the Iph index) likely reflects a dietary signal more than a climatic signal in herbivore dung samples. A stalagmite $\delta^{18}O$ record from Fort Stanton, NM indicates wetter conditions during the winter in the region at ~30,000 cal YBP (30,800 B_p) than at ~13,000 cal YBP (12,900 A_p) (Asmerom et al. 2010), which is consistent with the more mesic plant phytolith assemblage observed in dung sample A_p.

Previous studies indicate that Shasta ground sloths inhabited a wide variety of vegetation communities (McDonald in press), but that their diet typically comprised of arid adapted shrubs such as *Ephedra* , *Yucca*, *Agave*, grasses, *Sphaeralcea*, *Xanthocephalum* (snakeweed), and *Atriplex* (Thompson et al. 1980). While *Sphaeralcea* specifically is not detectible using phytolith analysis (Pearce 2017; Pearce & Ball 2019), *Ephedra* and *Atriplex* produce CaOx phytoliths and *Xanthocephalum* at the family level (Asteraceae) produce silica phytoliths. No CaOx phytoliths consistent with those produced by *Ephedra* nor silica phytoliths diagnostic of Asteraceae were observed in these samples. Druse and Rhomboid phytoliths similar to those produced by *Atriplex* were observed but are identical to those produced by a wide variety of other plants, thus the presence of *Atriplex* in these samples is equivocal. Although cuticle, macrofloral, and phytolith analysis undertaken together would provide the most comprehensive floral analysis of these dung remains, the results of our silica and CaOx phytolith analysis are broadly consistent with the findings of other studies and demonstrate the utility of this approach.

The macrobotanical remains from the packrat midden provide additional direct evidence of the vegetation community outside the cave about 30,800 cal YBP. *Juniperus* was abundant in the cave midden and likely common in the local community, yet today there are no *Juniperus* trees at the cave or in the immediate community. They are also not found today in other low-elevation communities such as the Livingston Hills (just east of the Chinati Mountains). However, junipers do occur north in wet canyons at higher elevations and at the top of the ridge-crest of the Sierra Vieja (Van Devender et al. 1978; Keller 2019). *Juniperus* sp. was recovered in the Shafter #1 packrat midden in the Livingston Hills (radiocarbon dating 15,595±230 YBP; 18,558-19,173 cal YBP).

The 2-needle fascicles of *Pinus emota* were recovered indicating that it too was in the local community outside Spirit Eye Cave. This pinyon does live today in the higher, mountainous elevations in the Trans-Pecos TX, but it is not located near Spirit Eye Cave. It and the higher elevation-tolerant *P. edulis* are recorded in many of the Late Pleistocene caves and packrat middens in the region including the Shafter #1 midden (Van Devender et al. 1978). These authors also discuss the extant and Late Pleistocene record of other related species of pinyons (Van Devender 1986b; Wells 1986; Betancourt et al. 2001).

No *Quercus* was found in the Spirit Eye Cave packrat midden; however, it was apparently growing in the lower Livingston Hills at about 18,000 cal YBP (Van Devender et al. 1978). A seed and a single leaf with minute denticles along the edges were recovered from the sloth cave midden and provisionally identified as *Yucca* cf. *rostrata*. This species today occurs in Chihuahua, Mexico, at lower elevations. It was also recovered in the Shafter #1 midden in the Livingston Hills (Van Devender et al. 1978). Today *Y. torreyi* (Torrey yucca) grows in the local community. Numerous seeds and spines of *Opuntia* sp. were recovered in the packrat midden. *Opuntia imbricata* (cane cholla) and *O. phaeacantha* (variable prickly-pear) were identified in the Late Pleistocene community of the Livingston Hills (Van Devender et al. 1978). Thus, a Late Pleistocene pinyon-juniper woodland mixed with some form of desert scrub was growing outside of Spirit Eye Cave at the time the Shasta ground sloth was present approximately 30,800 cal YBP. The Shafter #1 packrat midden approximates the local pinyon-juniper woodland community during the late glacial for the region and when the Shasta ground sloth also visited Spirit Eye Cave.

Habitat.–McDonald (in press) and Table 4 provide a list of all cave localities in North America containing Shasta ground sloth dung remains including the reconstructed diet and the local biotic community in which the sloth inhabited. The diverse details about the reconstructed diet and habitat can be found in each of the cited references.

CONCLUSIONS

Spirit Eye Cave in the Sierra Vieja Mountains along the Rio Grande of southwestern Trans-Pecos, TX, provides the newest evidence that the Shasta ground sloth inhabited much of the Arid Southwest of North America during the Late Pleistocene. It is one of only twelve *Nothrotheriops* dung localities. Two areas within the cave provide radiocarbon dated dung and packrat midden macrobotanical remains which permit the reconstruction of the ground sloth's diet and the habitat of the region at 30,800 and 12,900 cal YBP. Today the area is a classical Chihuahuan Desert biotic community. The local community immediately outside the cave at 30,800 cal YBP was a pinyon-juniper woodland with desert scrub species such as yucca, sandpaper bush, globemallow, cactus, and barberry in the understory based on the packrat midden from the cave. The dung contents indicate that based on the diet of the sloth, the local community also contained C_3 and C_4 grasses along with *Agave*. Based on this study and that of Van Devender et al. (1978), more data is available for the local vegetation community and sloth diet from 12,900 (sloth dung contents) to approximately 19,000 calibrated years ago (Shafter #1 midden). During this late

Table 4. Updated list of 12 dry shelters in Southwestern North America that contain dung of the Shasta ground sloth, *Nothrotheriops shastensis*. Radiocarbon ages derived from direct analysis, but some ages are associated chronologies (*, see reference). All dates are reported as radiocarbon ages with a few as calibrated (cal YBP) Caves with associated name designations (C-05,08, 09) represent the sloth caves of Guadalupe Mountains National Park. Inferred community inhabited by the sloth from macrobotanical fossils in cave fill and packrat middens; see details in referenced literature.

Locality Name	Radiocarbon Age (YBP)	Inferred Sloth Community	Primary Literature Citations
Aden Crater NM	11,080±200	Woodland: *Juniperus Berberis, Celtis, Rhus, Yucca, Agave*. (Based on Bishop's Cap and Shelter Cave data)	Eames 1930; Simons & Alexander 1964; Long & Martin 1974; Van Devender & Everitt 1977; Thompson et al. 1980
Bechan Cave UT	11,670±300-13,505±580*		Mead et al. 1984; Mead et al. 1986; Mead and Agenbroad 1989; Mead & Agenbroad 1992
Cowboy Cave UT	11,000–13,000*		Hansen 1980; Spaulding & Petersen 1980
Dust Cave (C-09) TX	11,760±610*–13,000±730*	Subalpine forest community: *Picea, Pinus flexilis, Juniperus communis, Quercus, Pseudotsuga, Ostrya knowltoni, Yucca*	Van Devender et al. 1977, 1979; Logan & Black 1979; Spaulding & Martin 1979; Harris & Hearst 2012
Gypsum Cave NV	11,360±260–11,690±250		Laudermilk & Munz 1934; Long & Martin 1974
Lower Sloth Cave (C-05) TX	11,590±230	*Pseudotsuga menziesii, Pinus edulis, P. strobiformis, Juniperus*	Van Devender et al. 1977, 1979; Spaulding & Martin 1979

Table 4 Cont.

Locality Name	Radiocarbon Age (YBP)	Inferred Sloth Community	Primary Literature Citations
Muav Caves AZ	11,140±160 – 11,290±170	Open woodland dominated by *Juniperus, Fraxinus anomola with Atriplex confertifolia, Coleogyne ramosissima, Ribes, Symphoricarpos*	Mead & Agenbroad 1989; Long & Martin 1974; Phillips & Van Devender 1974; Hansen 1978; Van Devender et al. 1987
Rampart Cave AZ	10,035±250– >40,000	Open woodland dominated by *Juniperus, Fraxinus anomola with Atriplex confertifolia, Coleogyne ramosissima, Ribes, Symphoricarpos*	Martin et al. 1961; Long & Martin 1974; Phillips & Van Devender 1974; Hansen 1978; Van Devender et al. 1987
Shelter Cave NM		Woodland: *Juniperus, Opuntia* spp., *Agave, Ephedra, Gutierrezia*	Thompson et al. 1980
Spirit Eye Cave TX	12,858—12,912 cal YBP and 31,254—30,879 cal YBP		This paper; see conclusions
Upper Sloth Cave (C-08) TX	10,750±140– 11,060±180	High-elevation forest: *Picea, Pinus flexilis, Juniperus communis, Quercus, Pseudotsuga, Ostrya knowltoni*	Van Devender et al. 1977, 1979; Logan & Black 1979; Spaulding & Martin 1979
Williams Cave TX	11,930±170– 12,100±210	*Pinus edulis, Quercus, Ostrya knowltoni, Juniperus, Artemisia, Atriplex*	Ayer 1936; Van Devender et al. 1977, 1979; Spaulding & Martin 1979

glacial time, the region was still a pinyon-juniper woodland but also contained *Celtis*, *Quercus*, and *Larrea*, among other taxa. The record of *Larrea* for this area at 12,900 cal YBP is only from the Spirit Eye sloth dung contents (having no record of it in local packrat midden), and thus, is of interest. Although the oldest record of *Larrea* in this region is from packrat middens in the area of Big Bend south of Spirit Eye Cave and dating to approximately 30,600 cal YBP (and believed to be contaminants; Van Devender 1986a), it is thought to have been local in the community by at least approximately 21,000 YBP (Van Devender 1990). *Larrea* is not typically recorded as a component in the diet of the Shasta ground sloth.

The caves and shelters in this region of the Rio Grande and its multitude of flanking mountain ranges clearly contain dry-preserved organic remains (Van Devender 1986a). Although well-known for many decades for their archaeological contents (e.g., Smith 1934), especially along the Pecos River region (Ross 1965; Dibble & Lorrain 1968; Bryant 1974), the more northern expanse to the border with NM and up into the Guadalupe Mountains is less well studied. Paleoecological resources, such as packrat middens, are known from the region (Van Devender 1990) and, with more recent studies, including those presented here, indicate that there is an unrealized and underutilized wealth of additional well-preserved organic remains in terms of dung (Mead et al. in press), especially from dry caves, suitable for Pleistocene-age environmental reconstructions.

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