Hunt et al., eds., 2012, Vertebrate Coprolites. New Mexico Museum of Natural History and Science, Bulletin 57.

LATE PLEISTOCENE (RANCHOLABREAN) DUNG DEPOSITS OF THE COLORADO PLATEAU, WESTERN NORTH AMERICA

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Abstract—Here we review the literature about Late Pleistocene, Rancholabrean-age, dry-preserved dung from cave and rock shelters on the Colorado Plateau of the Intermountain West of North America. The Colorado Plateau covers about 337,000 km2, and most of it has not be adequately prospected for Late Pleistocene-age fossil deposits. Dried dung deposits are restricted to dry caves, rock crevices, and rock shelters. The most intensively-studied and best known Late Pleistocene taxa on the Colorado Plateau are those with added data due to their dung samples being analyzed. These species include the living packrat (*Neotoma*) and the extinct mammoth (*Mammuthus*), Harrington's mountain goat (*Oreamnos harringtoni*), and Shasta ground sloth (*Nothrotheriops shastensis*). Dried dung identified to species provides superb data to analyze detailed aspects of chronology (plus possible time of extinction/extirpation), dietary reconstruction, and molecular phylogeny of extinct species.

INTRODUCTION

Here we review the unique Late Pleistocene (Rancholabrean Land Mammal Age) dung deposits preserved for millennia in the dry cave deposits on the Colorado Plateau (CP) of the Intermountain West of North America.

The Colorado Plateau is a unique physiographic province positioned west and south of the Rocky Mountains, and east and north of the Basin and Range province. Covering an area of approximately 337,000 km2, the CP covers portions of the states of Arizona, Colorado, New Mexico, and Utah (Fig. 1). With an average elevation of 1525 m, the CP ranges from a low of 360 m at the lower reaches of the Colorado River in western-most Grand Canyon to about 3850 m at the crest of the San Francisco Peaks immediately south of the Grand Canyon. The spine of the CP is the Colorado River which rises in the Rocky Mountains and exits the Grand Canyon at the Grand Wash Cliffs on its way south to the Gulf of California. Major tributaries to the Colorado River on the CP include the Little Colorado, San Juan, and Green rivers. These riparian corridors have played an important, yet passive role in floral and faunal movements during the Pleistocene and Holocene, including the present. The CP has an arid climate today. In general, precipitation decreases from high elevations to low elevations; summer precipitation decreases from the southern CP northward (Higgins et al., 1997). Vegetation and animal community distributions act in response to the arid regime. Details about modern climate and vegetation of the CP can be found in Anderson et al. (2000).

Perhaps due to the rugged terrain and the few roads over the CP, surprisingly little is understood about the Late Pleistocene paleoecology. A review of the paleobotanic and paleoclimatic records of the CP can be found in Betancourt (1990), Cole (1990), and Anderson et al. (2000). Late Pleistocene faunal remains are less well known than the paleobotanical. No single publication thoroughly reviews the Late Pleistocene faunal deposits of the CP (see Harris, 1985); although, most of the deposits containing vertebrates are found in the Grand Canyon and are therefore referenced in Mead (2005; amphibians and reptiles) and Mead et al. (2005; mammals and description of localities). Probably the best-understood mammalian taxa on the CP are the rodent (*Neotoma*, woodrat, packrat; see below), mammoth (*Mammuthus*), Harrington's mountain goat (*Oreamnos harringtoni*), and Shasta ground sloth (*Nothrotheriops shastensis*) (Agenbroad and Mead, 1989).

Most of the bedrock exposed at the surface of the CP includes Paleozoic and Mesozoic sedimentary units, many which permit the

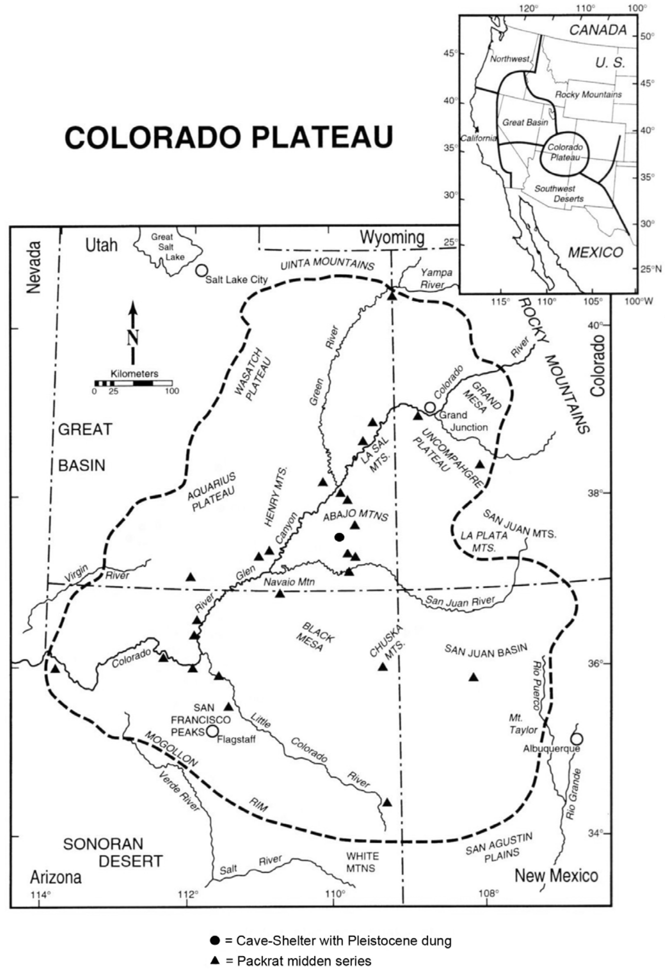

FIGURE 1. Map of the Colorado Plateau locating caves and rock shelters with dry-preserved dung of Late Pleistocene and Holocene age (numbers for localities described in Table 1). Black triangles represent major packrat midden localities not discussed in detail here, all of which contain dung of *Neotoma*, some with dung of other species such as lagomorphs and other rodents.

development of limestone caves and sandstone rock shelters and crevices. Fossil faunal and floral remains can be found preserved in a variety of taphonomic scenarios including lake and marsh deposits, fluvial sediments, and cave environments (see Behrensmeyer et al., 1992). Dung produced by herbivores and carnivores typically decays due mainly to insect and bacterial degradation enhanced in wet/humid environments. The arid climate that has occurred on the CP for the past +40,000 years coupled with dry caves and rock shelters has permitted an unusual taphonomic scenario of dry-preservation via desiccation. Animals that use these chambers, whether as a den, lair, refuge, nest, birthing sanctum, or roost, and either died or left organic vestiges, often dung, in the cave have an improved opportunity for these remains to be preserved. Because of this, the dry deposits in cave and rock shelters of the CP provide an unusual abundance and diversity of animal dung that is rarely preserved elsewhere.

Although we review here the dung remains from only the CP caves and rock shelters, similar and fewer deposits are known from elsewhere in the Southwest, including the Mojave Desert (Gypsum Cave, Nevada), the Guadalupe Mountains (Sloth Caves, Texas), and in New Mexico (Aden Crater, Shelter Cave). Pleistocene- and early-Holocene-age dung can be located in almost any shelter that provides a rock structure that a) minimizes the impact of fluctuations in temperatures, b) minimizes the outside climate and environment on the inside deposits, and c) there is a dry to hyper-arid internal environment. Some of the first literature about Late Pleistocene dung deposits in North America includes the reports about *Nothrotheriops shastensis* (Nothrotheriidae) dung from the dry Gypsum Cave, immediately west of the CP adjacent to Las Vegas, Nevada at the southern extremity of the Great Basin Desert (Laudermilk and Munz, 1934).

Dry-preserved dung from caves and rock shelters on the CP is largely restricted to that produced by mammals, especially the herbivores. Dung from birds (discounting stomach regurgitation pellets from diurnal and nocturnal raptors and vultures) is largely not described (but is known) from the CP and is not reviewed here. Exceptions include the tremendous work on condor roosts and nests from caves in the Grand Canyon (Emslie, 1987, 1988), and the rarely-studied owl roosts (Bell and Glennon, 2003). Analysis of dung from squamates and turtles is essentially unknown in the literature on the CP, although dung of the vegetarian chuckwalla lizard, *Sauromalus*, is known to occur in Rampart Cave, Grand Canyon.

The most common dung found preserved in dry caves and rock shelters on the CP belongs to the packrat, *Neotoma*, which has the strange habit of collecting a variety of plant and animal remains for food, nest construction (typically plants), and predator deterrence (cactus spines, scent puzzlement items: typically dung, regurgitation pellets, small carcasses, and skeletal remains) (Finley, 1958, 1990; Vaughan, 1990; Spaulding et al., 1990; Mead, 2005). The packrat periodically ‘cleans’ the nest and den of its own fecal pellets, pushing them outside of its tunnels onto the ever-growing accumulation of organic remains. Over time this debris pile creates a midden (much like mine tailings), often cemented together with packrat urine. In dry caves, crevices, and rock shelters these middens harbor an enormous diversity of plant and animal remains all collected typically within 100 m of the deposit. Plant macrobotanical remains have been instrumental for the reconstruction of the Late Pleistocene climate and plant and animal communities in the Arid Southwest (see various chapters in Betancourt et al., 1990).

Because the packrat midden record is voluminous, we will not refer to all fossil middens on the CP even though each cemented deposit contains thousands of *Neotoma* dung pellets (Table 1). We will refer to particular middens only if they also record dung from another species of particular interest. For example, *Neotoma* middens in the Great Basin and Mojave deserts west and north of the CP are the only repository known for the BB-sized circular pellets of the Rancholabrean-age boreal-montane lagomorph, pika (*Ochotona* sp.; Ochotonidae) (Mead and Spaulding 1995). Diet of *Neotoma* is reconstructed largely from the

TABLE 1. List of caves and alcoves on the Colorado Plateau that contain dry-preserved dung of Late Pleistocene and Holocene age. *Neotoma* middens containing plant remains and packrat dung not listed here by name but clusters of middens published upon show as a triangle on map in Figure 1. Raptor bird regurgitation pellets not listed. *Neotoma* dung listed here refers to either a packrat midden in the cave or isolated dung on the surface or within profile of the deposit. Map numbers for localities refer to numbers in Figure 1. **Abbreviations: Ba**, *Bassariscus astutus*; **Bi**, *Bison* sp.; **Ca**, cf. camelid; **Eu**, *Euceratherium collinum*; **Eq**, *Equus*; **Ez**, *Erethizon dorsatum*; **Fe**, large felid; **Le**, cf. *Lepus*; **Ma**, *Mammuthus* sp.; **Ne**, *Neotoma* spp.; **Ns**, *Nothrotheriops shastensis*; **Oh**, *Oreamnos harringtoni*; **Oc**, *Ovis canadensis*; **Sy**, cf. *Sylvilagus*; **Uk**, unknown small rodents and other artiodactyls, spp.; **Vp**, Vespertilionidae and possibly other species, bat dung, likely of a few different species; *, *Desmodus* (vampire) skeletons known from Rampart Cave.

Dung Locality / Taxon	Map Number	Ba	Bi	Ca	Eq	Eu	Ez	Fe	Le	Ma	Ne	Ns	Oh	Oc	Sy	Uk	Vp
Bat Cave	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X
Bear Ladder Shelter	2	-	-	-	-	-	-	-	-	-	X	-	X	-	-	X	-
Bechan Cave	3	-	-	-	?	X	-	-	X	X	X	X	X	X	X	X	-
BF Alcove	4	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-
Bida Cave	5	-	-	-	-	-	-	-	-	-	X	-	X	X	-	-	-
Chuar Cave	6	-	-	-	-	-	-	-	-	-	X	-	X	-	-	-	-
Cottonwood Alcove	7	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-
Cowboy Cave	8	-	X	-	?	X	-	-	-	X	X	X	-	-	-	X	-
Crescendo Cave	9	-	-	-	-	-	-	-	-	-	X	-	X	-	-	-	-
Disappearing Cave	10	-	-	-	-	-	-	-	-	-	X	-	X	-	-	-	-
Grobot Grotto	11	-	X	-	-	X	-	-	-	X	X	-	X	?	-	X	-
Hooper’s Hollow	12	-	X	-	-	X	-	-	-	-	X	-	?	X	-	X	-
Kaetan Cave	13	-	-	-	-	-	-	-	-	-	X	-	X	-	-	-	X
Mammoth Alcove	14	-	X	-	-	-	-	-	-	X	X	-	-	X	-	X	-
Muav Caves	15	-	-	-	-	-	-	-	-	-	X	X	-	-	-	X	-
Oak Haven	16	-	X	-	-	X	-	-	-	X	X	-	-	-	-	X	-
Oakleaf Alcove	17	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-
Rampart Cave	18	X	-	-	X	-	-	X	X	-	X	X	X	X	X	X	X*
Rebound Cave	19	-	-	-	-	-	-	-	-	-	X	-	X	-	-	-	-
Sandblast Cave	20	-	X	-	-	-	-	-	-	-	X	-	X	-	-	-	-
Shrine Cave	21	-	-	-	-	-	-	-	-	-	X	-	X	-	-	-	-
Shrub-ox Alcove	22	-	X	-	-	X	-	-	-	X	X	-	X	X	-	X	-
Stanton’s Cave	23	X	X	-	X	-	-	-	-	-	X	-	X	X	X	-	?
Stevens Cave	24	-	-	-	-	-	-	-	-	-	X	-	X	-	-	-	-
Three Springs Cave	25	-	-	-	-	-	-	-	-	-	X	-	X	-	-	-	-
Vulture Cave	26	X	-	-	-	-	X	-	-	-	X	-	-	-	-	X	-
Wither’s Wallow	27	-	X		-	-	-	-		X	-	-	-	X	-	X	-

macrobotanical remains found in the middens. Few studies have examined the pollen and microhistological remains from *Neotoma* dung (see references in Anderson and Van Devender, 1995; Mead and Spaulding, 1995 for data west and south of the CP).

DUNG

Identification

The producer of dung recovered from dry caves can be difficult to identify. The identification of dung has been made, or attempted, via overall morphology, morphology with size and mass data, size fraction analysis of dung contents, bile acid analysis, and molecular analyses. Overall morphology has produced the most reliable results; however, this simple technique requires a large and diverse comparative collection of modern and known-fossil taxa. Such comparative collections are exceedingly rare, especially one with a world-wide scope. Paul S. Martin began such a collection at the University of Arizona (Tucson) in the late 1950s. In the 1970s the collection greatly expanded with prolific sampling by a few of Martin's students (largely JIM, W. G. Spaulding, and T. R. Van Devender). The Martin dung collection transferred to Mead at Northern Arizona University in the 1980s who continued to enhance the collection while working on the many Late Pleistocene dung deposits of the CP (many of which are curated in National Park Service museum collections). In 2008 the extensive, mainly modern, dung comparative collection was moved to East Tennessee State University where it is now housed and curated into the Department of Geosciences, Laboratory of Vertebrate Paleontology collections, and where it continues to grow with additional acquisitions.

Eames (1930) and Lull (1930) published the first detailed description of dung from an extinct animal in the Southwest. Remains from Aden Crater, New Mexico, preserved dried dung of a previously unknown morphology to be directly associated with a dried carcass of the extinct ground sloth, *Nothrotheriops shastensis*. Soon additional examples of the association of dung with sloth bones were found in Gypsum Cave (Nevada) and Rampart Cave, Grand Canyon, Arizona (Laudermilk and Munz, 1934, 1938). Spaulding and Martin (1979) examined size fractions of the macrobotanical contents of the dung of *Nothrotheriops shastensis* and various ungulates and were able to further differentiate types of dung. The short and clipped woody botanical remains indicate that the Shasta ground sloth was a browser (Fig. 2).

Size fraction analysis and mass of other morphologically distinct dung pellets were used to differentiate the dung pellets of the extinct mountain goat, *Oreamnos harringtoni* from extant bighorn, *Ovis canadensis* and other bovids and cervids (Robbins et al., 1984; Mead, O'Rourke et al., 1986). Hansen (1980) utilized gross morphology to identify the animal producers at Cowboy Cave, and then proceeded to work on the microhistological remains for dietary reconstructions. Mead, Agenbroad et al. (1986) used a combination of gross morphology and size fraction to identify dung attributed to *Mammuthus* at a number of localities on the CP (Fig. 3). This same approach was used in the identification of dung attributed to the extinct *Euceratherium collinum* (Mead and Agenbroad, 1989; Kropf et al., 2007). Modern and fossil dung of the *Ochotona* (mentioned previously) was analyzed using gross morphology to differentiate it from the pellets produced by the cottontail rabbit, *Sylvilagus* (including the small pygmy rabbit, *Brachylagus*) and the large hare, *Lepus* (Mead and Spaulding, 1995). These same techniques were used on the lagomorphs from deposits on the CP.

Chronology

Percolating water allows both microbial decay and the introduction of water-soluble contaminants into organic remains. One of the reasons that dung of extinct species is of high paleoecological value is that the mere existence of the well-preserved dung indicates that it has not been wet and hence contaminated since production. Meltzer and Mead (1983, 1985) and Mead and Meltzer (1984) developed a method (rating system) to access the radiocarbon dates produced on and for extinct species of megafauna of North America. Dry-preserved dung, once accurately identified to the producing taxon, yields some of the highest quality radiocarbon dates.

Dung was used to critically examine the timing for extinction of *Nothrotheriops shastensis* (Long and Martin, 1974; Long et al., 1974). Dry-preserved dung and keratinous horn sheaths belonging to *Oreamnos harringtoni* were used to develop the timing of extinction for this mountain goat in the Grand Canyon (Mead, Martin et al., 1986). Besides skeletal remains, dung identified as *Mammuthus* sp. was used to determine its time of extinction on the CP (Agenbroad and Mead, 1989; Mead, Agenbroad et al., 1986). Utilizing dung, the youngest radiocarbon age for various extinct megaherbivores on the CP was determined: *Euceratherium collinum* 11,630 yr B.P.; *Oreamnos harringtoni* 11,160 yr B.P. (weighted average); *Mammuthus* sp. 11,820 yr B.P.; and *Nothrotheriops shastensis* 11,016 yr B.P. (weighted average) (Mead and Agenbroad, 1992).

Diet Reconstruction

When direct observation of a species feeding is not possible, the best and most detailed description of diet from an animal, whether modern or fossil, comes from analysis of its dung. Reconstructions of the diet of extinct mammals utilizing macrobotanical remains in dung began in many ways with the pioneering work by Laudermilk and Munz (1934, 1938) on the *Nothrotheriops shastensis* dung from Rampart, Muav, and Gypsum caves. Analysis of the diet of extinct megaherbivores through the examination of dung really moved to the forefront of paleoecology with the influential analyses by Paul S. Martin, a research approach some of his students and colleagues have continued to this day. Martin et al. (1961) looked at both pollen and macrobotanical fossils recovered from the dung preserved in stratigraphic position within the profile exposed in Rampart Cave (along with remains found elsewhere in the Southwest: Aden Crater and Gypsum Cave). Continued analysis of the diet of *Nothrotheriops shastensis* has occurred with the work of Spaulding and Martin (1979; from caves in the Guadalupe Mountains off of the CP), Hansen (1978; Rampart and Muav caves, Grand Canyon), Thompson et al. (1980; from Shelter Cave, New Mexico off of the CP), Hansen (1980; Cowboy Cave, Utah), and Mead and Agenbroad (1989; Bechan Cave, Utah). Dietary reconstructions of the extinct *Oreamnos harringtoni* were produced by analyzing dung from selected caves on the CP (Mead, O'Rourke et al., 1986; Mead et al., 1987). In addition, microhistological analysis was used to preliminarily assess the diets of *Bison* (Mead and Agenbroad, 1989), *Euceratherium* (Kropf et al., 2007), and a variety of lagomorphs (personal data unpublished).

Dietary reconstructions based on dry-preserved dung from deposits on the CP are poorly known for mammalian carnivores. Holocene dung pellets consisting of small herpetofaunal remains were recovered from ringtail (*Bassariscus astutus*) dung recovered from a den in Vulture Cave, Grand Canyon (Mead and Van Devender, 1981). While carnivore dung is rare in deposits on the CP, interesting information should materialize with the analysis of dung of a large felid preserved in Rampart Cave (JIM data).

Analysis of bat dung for diet and isotopic signatures from the CP is uncommon, known only from Bat Cave, Grand Canyon (Wurster et al., 2008, 2010). Although well-defined dung micro-layers are known from sections of the Shasta ground sloth dung profile in Rampart Cave, these have gone largely unstudied (Long and Martin, 1974). Carbon and nitrogen content analysis of megamammal dung have also received little attention (Clark et al., 1974). Carbon isotopes from *Neotoma* dung was examined by Cole and Arundel (2005). Parasites from fossil dung are almost unheard of on remains from the CP except for the report on those identified from *Nothrotheriops shastensis* recovered from Rampart Cave (Schmidt et al., 1992).

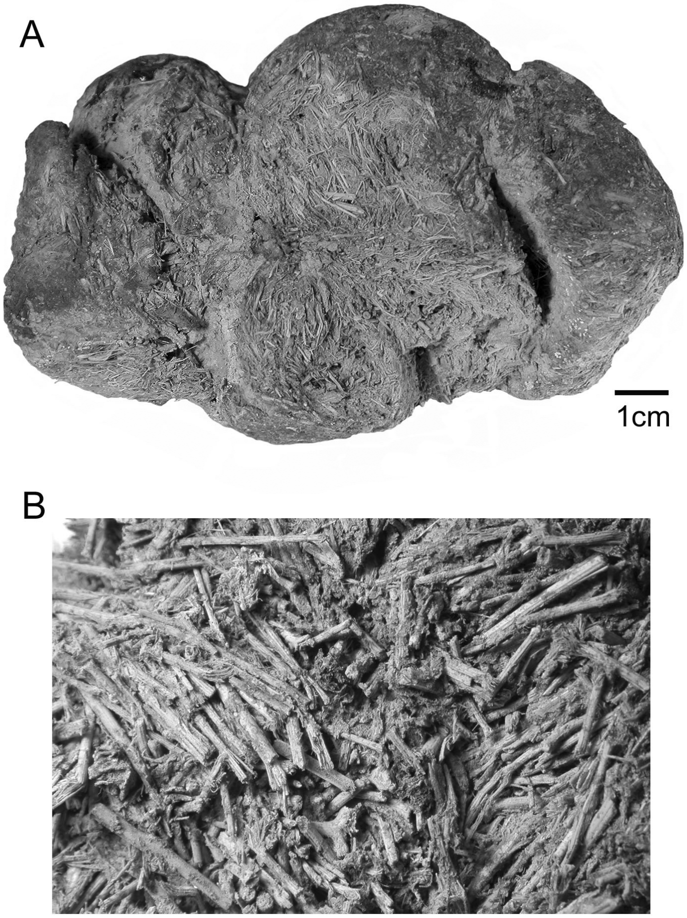

FIGURE 2. Dung of *Nothrotheriops shastensis* from Rampart Cave, Grand Canyon, Arizona. **A**, Overall morphology; **B**, close-up showing the browse and short, clipped woody vegetation. The brown outer surface includes bile acids that record DNA and other biochemical data that has yet to be fully assessed.

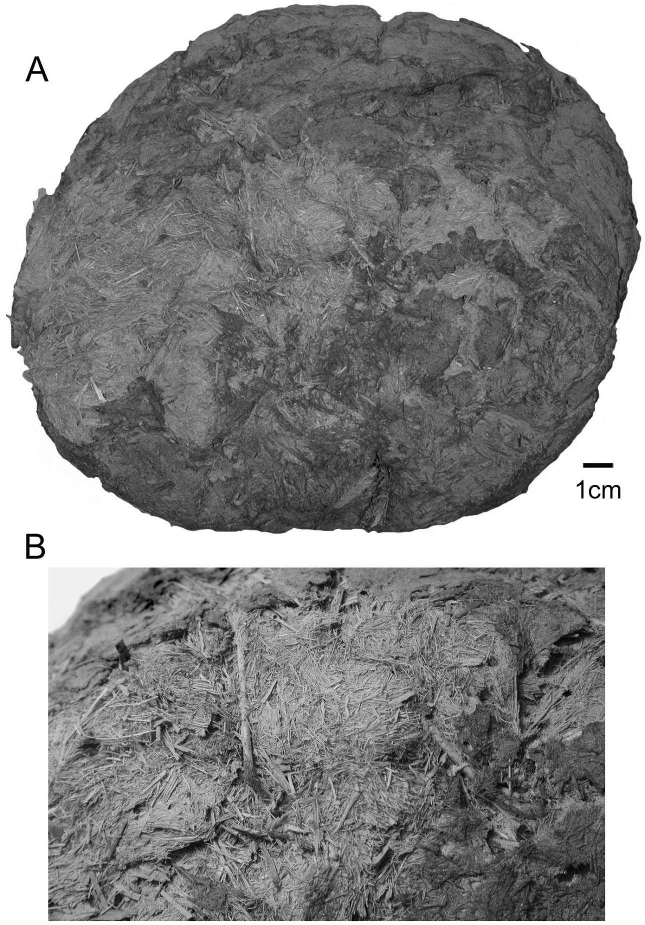

FIGURE 3. Dung of *Mammuthus* sp. from Bechan Cave, Utah. **A**, Overall morphology; **B**, close-up showing the graze species, the large number of the long plant fragments illustrates the poor chewing abilities of mammoths. The brown outer surface includes bile acids that record DNA and other biochemical data that has yet to be fully assessed. Note the few circular holes made by insects when the dung was fresh and still wet; decay ceased upon desiccation.

Climate Change Responses

A study by Smith et al. (1995) concluded that dung pellet width and body size in modern *Neotoma* are closely correlated. Although they examined only three species of packrat (*N. cinerea*, *N. lepida*, and *N. albigula*) the authors felt that body size tracked changes in environmental temperatures through time (Smith and Betancourt, 1998). To avoid the potential complication of changes in *Neotoma* species through time, they examined only localities inhabited at present and in the past by *N. cinerea* (the largest of the packrats). It is not clear how they ultimately determined which species inhabited the ancient middens and how they decided that only *N. cinerea* was the nest-builder. The results by these authors and their basic assumption of the project seemed biased toward *N. cinerea* and did not really take into account smaller species of packrat that could be in a midden that also contained the larger *N. cinerea* ("Pellets with widths less than 4.0 mm (~90 grams) were discarded because of a large increase in measurement error that arose at these size classes" Smith and Betancourt 1998:2; see also Smith and Betancourt, 2006; Smith et al., 1995, 2009). Typically packrat middens can be utilized by a number of species over time (e.g., see Mead and Phillips, 1981). Nevertheless, the potential usefulness of the paradigm seems positive, important, and definitely needs further examination.

Biochemical/Molecular

The dry-preserved dung from extinct and extant species has proven to be an excellent resource for various biochemical and molecular analyses. Early-on Nuclear Magnetic Resonance (NMR) analysis was employed with the hope of utilizing the preserved organic compounds to provide another way to chemically identify the dung producer. Unfortunately the NMR spectral pattern from dung bile was not consistent enough to provide a reliable signature for species identification (de Ropp et al., 1998). Of particular value has been the recovery of aDNA from the dung of extinct species. This new approach has not only provided an independent means to confirm the producer of the dung (Poinar et al., 1998) but equally important has lead to a finer resolution of the plant species in herbivore diet not previously revealed by macrobotanical or microhistological methods (Hofreiter et al., 2000).

The application of different types of molecular analyses to dry-preserved dung has been instrumental in providing a better understanding of the paleoecology of a variety of extinct megamammals (Hofreiter et al., 2003), including *Euceratherium* (Campos, Sher et al. 2010), *Nothrotheriops* (Poinar et al., 1998; Hofreiter et al., 2000), and *Oreamnos harringtoni* (Campos, Willerslev et al., 2010). While still a relatively new approach, preliminary results in this developing new area of research utilizing preserved dung have been extremely promising.

CONCLUSIONS

Dry-preserved dung is common in most caves and rock shelters on the Colorado Plateau due to the arid climate of the region and the extremely dry inside environment. Most of these localities on the CP are managed by the National Park Service and the Bureau of Land Management. The study of desiccated dung from these dry caves on the arid CP has proven to be instrumental in both determining the time of extinction of individual species as well as reconstructing the diet for many species of Late Pleistocene herbivores. Dietary reconstructions have also further refined our knowledge of the local plant community that existed in the area when the animal was alive. Although a lot of information has been retrieved from dry dung, much more data is surely to appear as these non-renewable fossil resources are examined with new techniques aligned with new questions. For this reason alone, dung localities should be located, their contents evaluated, samples taken and conserved, and the shelters preserved.

ACKNOWLEDGMENTS

We appreciate most of all the development of the dung collection by Paul S. Martin now housed at ETSU. Paul truly catalyzed the use of dry-preserved dung found throughout the Arid Southwest for paleoecological studies. JIM appreciates the dung samples (and the implied humor) sent to him by many colleagues over the years to include into the growing comparative collection curated by SLS. Zoos and game managers around the world have helped to greatly expand the collection; more is needed. Emilee Mead helped in the early decades of the collection enhancement and disseminating the results of research. Rachel Maddow helped greatly in getting the attention of the public to the studying and collecting of ancient dung. We appreciate the editing suggestions and discussions provided by H. Greg McDonald and Gary Morgan.

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