Pleistocene Dung and the Extinct Herbivores of the Colorado Plateau, Southwestern USA

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SAMENVATTING

De auteur beschrijft hoe en welke informatie verkregen kan worden van fossiele mest van grote herbivoren.
Op grond van de morfologie en de grote van de fractie (drooggewicht in gr.) en soms op haarinhoud, kan van fossiele mest bepaald worden van welke herbivoor het afkomstig is.
Bovendien kan uit de inhoud ervan conclusies getrokken worden over :de vegetatie, het dieet van het dier, het seizoen, de ouderdom van het fossiel d.m.v. koolstofisotoop-datering, eventuele veranderingen in het dieet, mogelijke oorzaak van uitsterven, de sexe van het dier dat de mest heeft achtergelaten en veranderingen in het milieu.
Er wordt een overzicht gegeven van locaties (grotten) op het Colorado Plateau waar mest is gevonden van *Bison sp.*, *Mammuthus sp.*, *Nothrotheriops shastensis* (grondluiaard) en *Oreamnos harringtoni* (uitgestorven berggeit).
De volgende conclusies worden getrokken over de dieetsamenstelling van de hiervoor genoemde soorten van het Colorado Plateau:
de mammoet: verschillende plantensoorten, maar overwegend (1/3 deel van de totale mestinhoud) grassen;
de uitgestorven berggeit: vnl. grassen en ook jonge scheuten;
de grondluiaard: vnl. jonge scheuten en daarbij ook grassen;
de bizon: merendeels grassen en daarbij jonge scheuten.

The vertebrate paleontologist is typically concerned with a plethora of isolated skeletal remains from which to reconstruct extinct species or faunal communities. If lucky, the paleontologist will happen along an articulated skeleton (THEWISSEN and FRANZEN, 1987), which permits an unusually detailed osteological examination of a particular species. The paleontologist will be able to describe the skeleton of an extinct animal fairly well, but more often than not diet is at best hypothesized, based on tooth morphology, and the local plant community is inferred from an associated pollen reconstruction.

Water, the provider of life, is also the promotor of decay. Invariably the taphnonomic situation of an animal carcass is such that stomach contents, skin, muscle, organs, and hair/keratin decay away relatively quickly. Even in arid regions of the desert Southwest, USA or the Arctic, provide enough moisture to permit slow but certain decay of non-skeletal remains - unless protected. Two environmental situations typically allow for soft-tissue preservation:

1) regions of the Holarctic permafrost (POPOV, 1948; VERESHCHAGIN, 1977; VERESHCHAGIN and NIKOLAEV, 1982), and
2) the xeric cave deposits of deserts (EAMES, 1930; MARTIN *et al*, 1961).

Although a wide variety of extinct megaherbivores are known from skeletal remaines (ANDERSON, 1984; KURTéN and ANDERSON, 1980), only a few are recorded by preserved dung and hair specimens. Here we review of the late Pleistocene (Rancholabrean land mammal age) dry cave localities of the Colorado Plateau, Southwestern USA, that contain preserved dung deposits, and the variety of analyses that can be performed on the unique remains. Because the study of glacial-age dung remains is in its infancy in North America, we will examine only four of the best known species: *Mammuthus* (Proboscidea, mammoth), *Nothrotheriops shastensis* (Xenarthra Megalonychidae, Shasta ground sloth), *Bison* (Artiodactyla, Bovidae Bovini, bison), and *Oreamnos harringtoni* (Artiodactyla: Bovidae: Rupicaprini, Harrington's mountain goat).

Use of preserved dung for reconstrucution of diet and environments began in the arid Southwest when EAMES (1930) examined dung of extinct Shasta ground sloth from New Mexico, and LAUDERMILK and MUNZ identified macrobotanical fragments from similar dung from Gypsum Cave, Nevada (1934), and Rampart and Muav caves, Arizona (1938; LAUDERMILK, 1949).

MARTIN *et al* (1961) later identified pollen from Shasta ground sloth dung in Rampart

Cave (western Grand Cannyon, southwestern-most Colorado Plateau; fig. 1). IBERALL (1972; now, ROBBINS *et al.*, 1984) went a step further in paleoecological reconstructions when she used microhistological analyses (plant cuticle and other remains) to identity the diet of the extinct Harrington's mountain goat form Stanton's Cave (northern end of Colorado River in the Grand Canyon, Arizona). HANSEN (1978) used the same technique to re-examine the Shasta ground sloth dung from Rampart and Muav caves. Long (LONG and MARTIN, 1974; LONG *et al.*, 1974) was the first to use multiple radiocarbon dating (beta particle technique) to locate the last use of Rampart Cave by the ground sloth. Analysis of dried dung on the greater Colorado Plateau began in earnest when HANSEN (1980) provided the identifications from the fragmented remains in Cowboy Cave, Utah (northern-most locality on fig. 1). It was this study that heralded a new era of dietary and faunal community studies in this arid region.

Analyses

Although a variety of analyses are currently conducted on preserved dung remains, it should be remembered that the study, in its fullest spectrum, is just beginning. The use of dung as a tool for the paleontologist is endless. Besides indicating that a particular animal inhabited the area of the deposit, dung of extinct megafauna can be used:
1) to determine some of the local plant community components,
2) to directly reconstruct the diet
3) to identify the season(s) of occupation
4) as a direct means to radiometrically date the species
5) to possibly determine the time of demise. the species
6) to define possible changes in diet through time, up to the time of extinction
7) to examine possible causes of extinction
8) to identify the sex of species leaving the deposit
9) to identify environmental changes - to name but a few uses. The major items will be discussed here.

Analysis of dried dung is divided into three steps:
1) identification of the producing species
2) determination of the contents (a large and varied category)
3) paleoenvironmental and paleoecological reconstructions. The first step of identification is the most critical analysis. Published accounts and comparative collections of dung are rare. See MEAD and AGENBROAD (submitted 1988) for a more detailed field and laboratory guide to extinct and modern herbivore dung of North America MURIE (1954) provides the best overall field guide to dung identification of living North American mammals (an equally good field guide to dung identification of Australian native and introduced animals is provided by MORRISON, 1981; an excellent book to observe how a dung guide is to be used).

Identification

Two analyses (morphology and size fraction; and sometimes a third, hair content) are used to identify the species of the herbivore which produced the dung. Herbivores consume large quantities of vegetation and much of the bulk is expelled as waste. Consequently, the dung is deposited as one large mass, or as a large number of fecal pellets which are reasonably regular in size and shape, sometimes distinctly so. The dung, when broken open, can be seen to be composed of evenly cut twigs or chaff-like vegetation. The size of the contents is often indicative of a type or group of animals. Overall morphology of a particular species of dung can change somewhat with the moisture content of the ingested vegetation.

Proboscideans in general produce an extremely big bolus, larger than other dung masses produced by other herbivores. Mammoth dung (fig. 2) is approximately 230 by 170 by 85 mm in size (DAVIS *et al*, 1984; MEAD *et al.*, 1986c), full of graze remnants, and is identical in size and content to those boluses of the living elephants, Loxodonta and Elephas (WING and BUSS, 1970). Although the large size is a certain identifying character, often the boluses are trampled into smaller fragments (HANSEN, 1980) leaving the identification to the size fraction analysis. Fractional analysis of the dung contents is expressed as dry weight in grams or percent of dry weight according to size (<0.25, 0.25 - 0.5, 0.5-1.0, 1.0-2.0,>2.0 mm (fig.3). Lenghts and widths of grass stems and twigs in modern elephant dung measure up to 70.0 by 5.0 mm, similar to the 60.0 by 4.5 mm observed in the mammoth dung from Bechan Cave, Utah.

The Shasta ground sloth is a browser and produces dung boluses as linear-connected thick plates (MARTIN *et al.*, 1961; MARTIN 1975; fig.4). In addition to the distinctive shape, the twig contents are all clipped short (HANSEN, 1980; SPAULDING and MARTIN, 1979). Size fractional analysis illu-

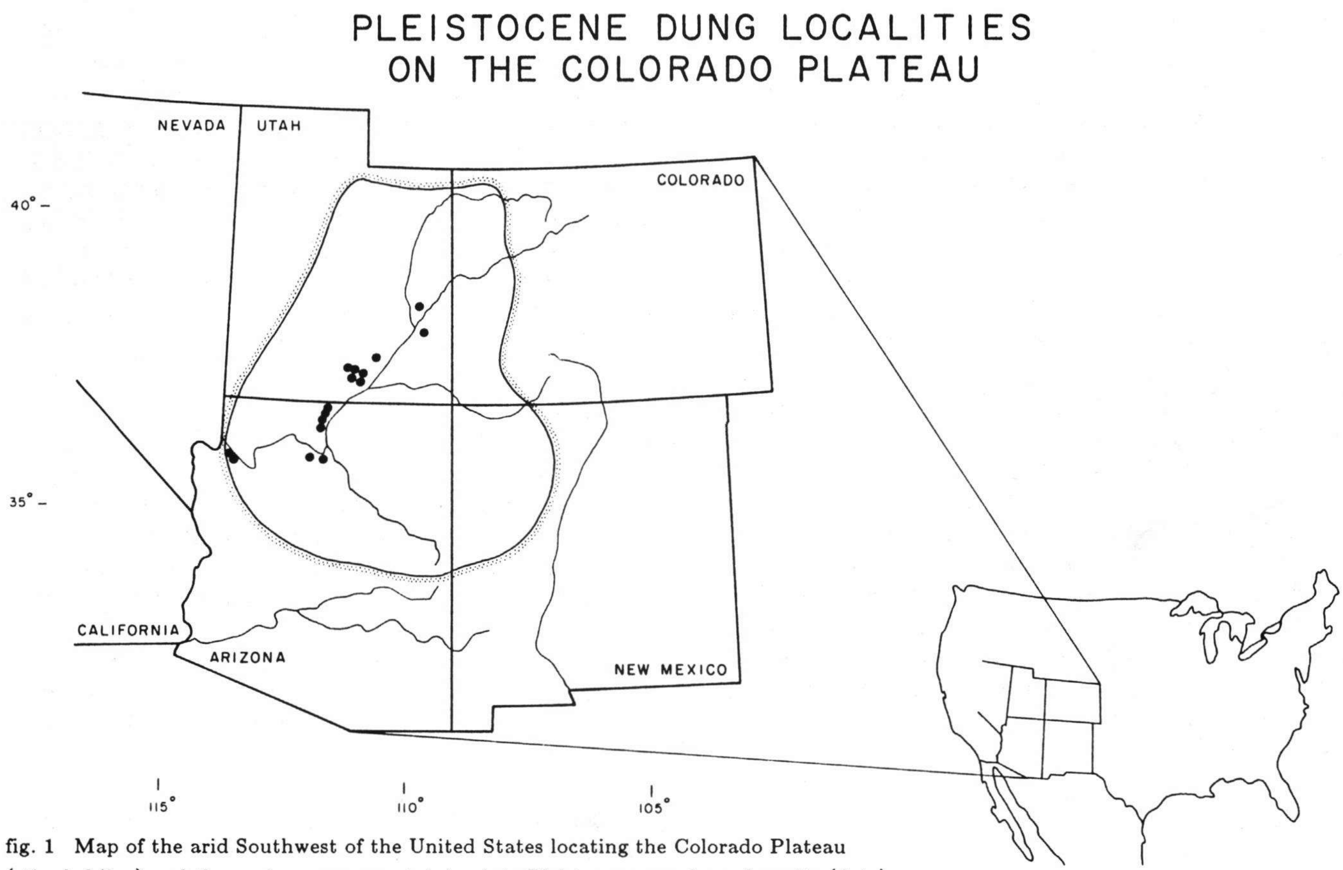

fig. 1 Map of the arid Southwest of the United States locating the Colorado Plateau (stippled line) and the various caves containing late Pleistocene age dung deposits (dots).

fig. 2 A single bolus of *Mammuthus* from Bechan Cave, Utah. Note the coprophagus insect holes made when the dung was still wet.

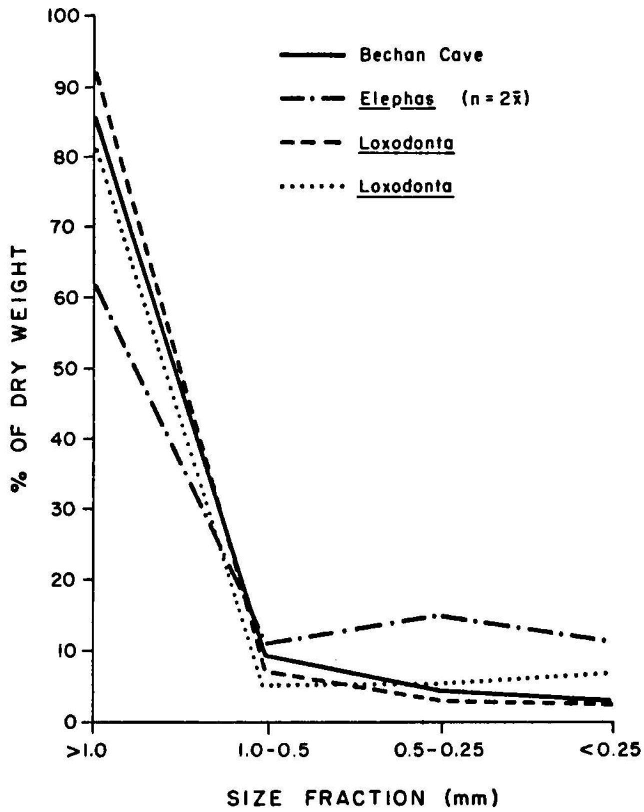

fig. 3 Size fractional analysis of various proboscidean dung.

strates that Equus (horse) dung can be similar to that of the Shasta ground sloth (fig. 5). However, the size (width and length) of the largest twigs of Nothrotheriops and Mylodon (mylodont ground sloth, Chilean sample) is usually much shorter than that of Equus, even when the horse eats woody shrubs (fig. 6). Shasta ground sloth was the first species of a North American extinct megafauna to have a directly reconstructed diet (MARTIN *et al.*, 1985; THOMPSON *et al*, 1980).

Artiodactyls produce a variety of dung morphologies. Bison dung will change from basically circular plates aligned in a row when dry food is eaten, to the typical amorphous pile ("chip") of waste when green or wet vegetation is consumed (fig. 7). In conjunction with the distinctive shape, the size fraction of the contents permit identification. Although graze versus browse ingestion will change the coar seness of the contents, the overall fractional components and morphology remain approximately the same.

Most artiodactyls produce relatively small dung pellets. COE and CARR (1983) determined that with African artiodactyls there is a

fig. 4 Two views of *Nothrotherops* dung from Pampart Cave, Arizona. left view illustrating the positioning of dung plates. Right view showing the morphology of the contents.

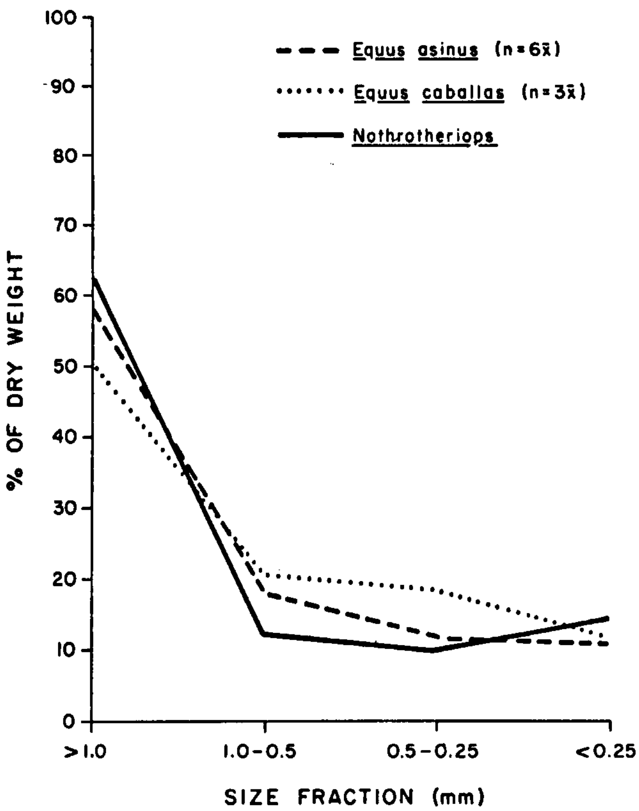

fig. 5 Size fractional analysis of dung from *Nothrotheriops* and *Equus*.

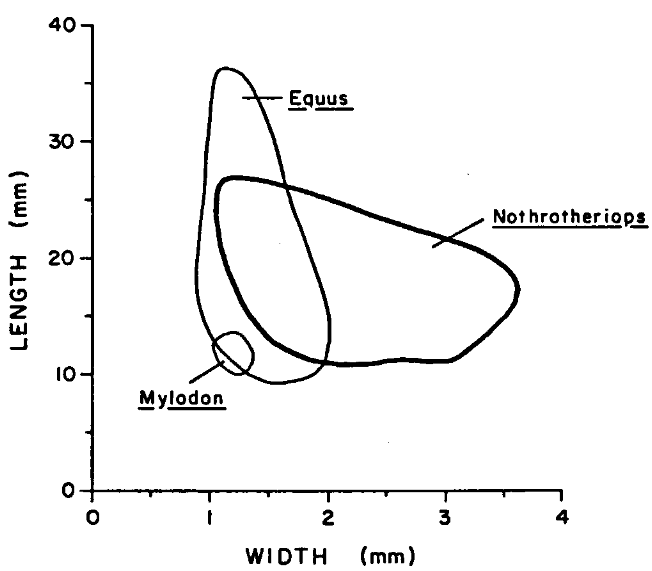

fig. 6 Width and length (mm) of the largest twigs in dung of *Nothrotheriops, Myolodin* and *Equus*.

steady increase in pellet with unit body weight gain. Whether this is true for all pallet-producing ruminants is vet to be termined. MEAD et al. (1986b) used a ratio of the length and width of each pallet in comparison to the pellet weight to distinguish the dung from a number of living and extinct North American artiodactyls (fig. 8).

Dung of Harrington's mountain goat from the Grand Canyon was found to be, at adult size, much larger and more cuboid in shape in comparison to the living mountain goat (O. americanus), bighorn sheep (Ovis canadensis), deer (Odocoileus spp.), and pronghorn (Antilocapridae: Antilocapra americana). Dung from the American moose (Alces alces) and the muskox (Ovibovini, extinct and living genera) were found to be much larger than those of Oreamnos. Only the living wapiti (Cervus elaphus) produces (occasionally) dung similar in size to that of the extinct mountain goat, however, the pellets are never as cuboid as those that can be attained by O. harringtoni (fig. 8). The Grand Canyon fossils, when found in direct association with skeletal remains, are always with Oreamnos harringtoni, never with any other artiodactyl genus. Most of the deposits are in remote caves on cliffs, requiring entrance by the best of agile climbers (MEAD *et al.*, 1986b). Many, but not all, of the living large-pellet producers can be separated by dung morphology (at adult size)(fig.8). The small producers present some problems, however, difficulty arises with the potential introduction of extinct pellet-producing forms (e.g. Navahoceros, ectinct mountain deer; Kurtèn 1975). Fractional size of the dung contents usually is the same size, although the type of forage will greatly determine the overall size and shape. Richard Hansen (Colorado State University; pers.comm.) has indicated that the cuboid dung from the Grand Canyon caves are best identified, in his view, as *Cervus*; the extinct mountain goat, which is 30 % smaller in stature than the living species, should not (COE and CARR, 1983) produce pellets twice as heavy as those of *O. americanus*.

Hair is often found incorporated in the dung of herbivores, being included with the ingestion of food by hide licking. Although hair identification of extinct fauna is at very preliminary stages in North America, some haires have been identified (HANSEN, 1980; MEAD, 1983). Hairs of mammoth have been identified from southwestern dung mats (AGENBROAD and MEAD, 1987; HANSEN, 1980) and from frozen carcasses in Siberia (SOKOLOV and SUMINA, 1982).

Contents

After identifying the species of animal represented by the dung, the most important analysis is the precise dating of the remains. Dung can be dated either indirectly (by its association with other dated remains) or directly. MELTZER and MEAD (1985) have indicated that the most reliable radiometric determination for the extinction process in North America is the direct radiocarbon dating of the concerned species. Once the dung has been identified to species, there is probably no better and no more direct remain to date then the dung (and/or keratin).

The fact that the material is preserved indicates that virtually no natural contamination exsists (usually contamination enters organic specimens via percolating water). Potentially minor contaminants that might pose a problem, if present, are easily removed during normal sample preteatment (e.g. hydrochololoric acid washes).

A directly radiocarbon dated and identified dung remain is a potentially powerful paleo-ecological tool. The examination of trace elements was one of the first analyses extracted form dung, unfortunatly little paleoecological information has so far been gained from these experiments (CLARK *et al.*, 1974; MARTIN *et al.*, 1961; PROVOTOROVA and RYABIKOV, 1982).

The contents of dung are described by examimining the macrobotanical, palynological, and microhistological remains. Macrobotanical remains are those plant remains large enough to be identified to species using a dissecting microscope. Invariably seeds, woody twigs, and leaves will be passed relatively unaltered through the digestion tract, especially in non-ruminants such as with the mammoth, horse, and ground sloth (DAVIS *et al.*, 1984, 1985; LAUDERMILK and MUNZ, 1934, 1938). Macrobotanical identification is probably the most common dietary analysis of Siberian mammoth dung (GORLOVA, 1982; KUPRIYANOVA, 1957; SOLONEVICH and VIKHIREVA-VASILKOVA, 1977; UKRAINTSEVA, 1981, 1985; UKRAINTSEVA et al., 1978).

Ruminants, however, finely chew the vegetation so that macrobotanical analysis of dung pellets is rarely useful. For these dung, in addition to those taxa just mentioned, microhistological remains and pollen are extracted for ecological information MARTIN *et al.* (1961) and SPAULDING and MARTIN (1979) used the pollen data preserved in the dung of the Shasta ground sloth to reconstruct the diet and local plant community (see also MARKGRAF, 1985, for Mylodon from South America) THOMPSON *et al.* (1980) found that pollen in Shasta ground sloth dung does not accurately reflect the

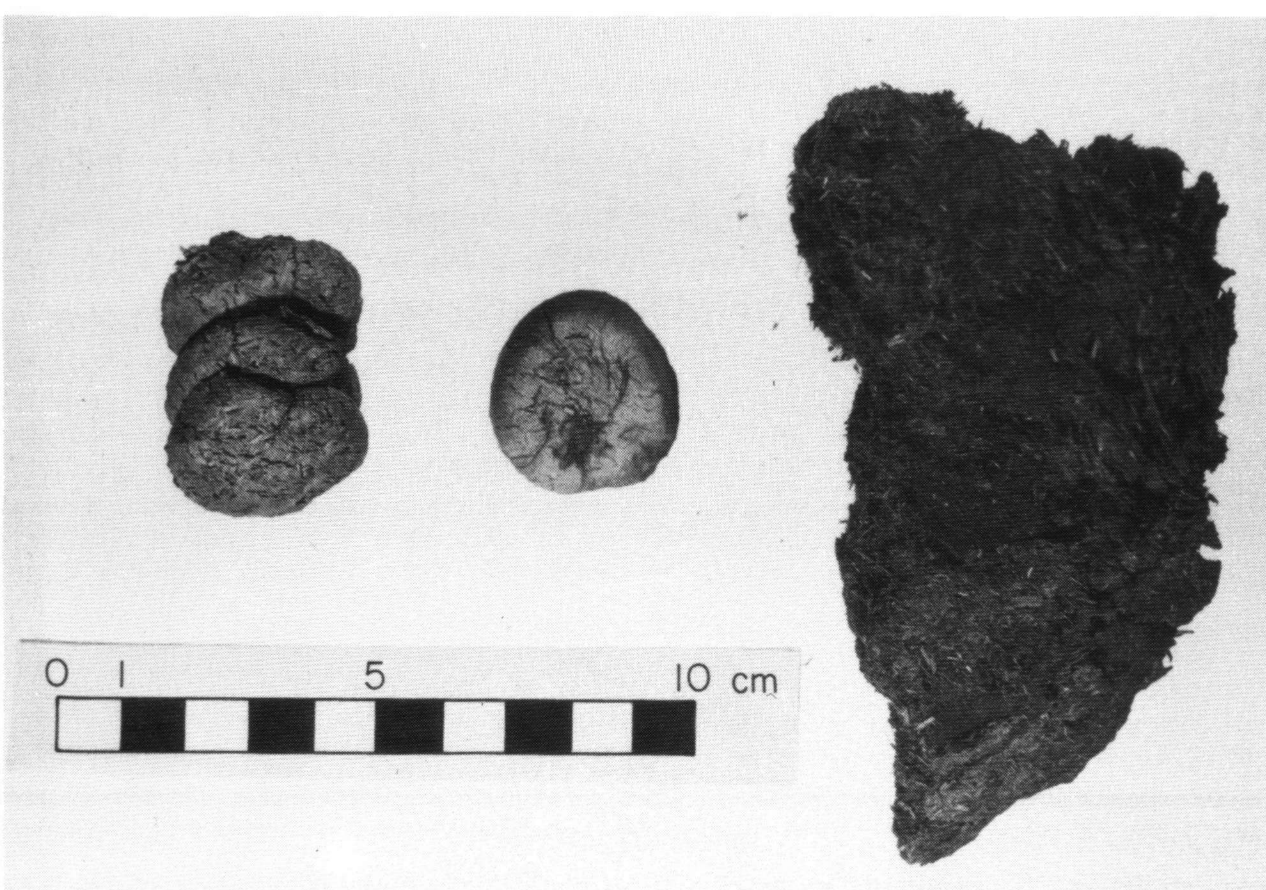

fig. 7 Two morphological types of *Bison* dung. Left view of round plates. Right view a fragment of a large "chip". Note that fractional sizes are the same.

actual total ingested dietary vegetation HANSEN (1978, 1980) pioneered the use of microhistology for obtaining the diet of extinct megafauna in North America. THOMPSON *et al.* (1980) were the first to demonstrate that both pollen and microhistological data should be gathered from dung, because they are recording different sets of data, each important to paleoecological interpretations. O'ROUKE and MEAD (1985), MEAD *et al* (1986b), and MEAD *et al* (1987) used pollen and microhistological remains for reconstructing the diet and season of diet for Harrington's mountain goat.

Recontructions

As one might assume, the best reconstructions are those that use multiple lines of evidence for a conclusion or a set of conclusions. It is not the scope of this paper to review all the conclusions and reconstructions arrived form dung analyses, however, some of the more important findings from the Colorado Plateau will be examined, especially using the microhistological data.

Table 1 lists the localities containing dung of *Bison* sp., *Mammuthus* sp. (cf. *M.columbi*), *Nothrotheriops shastensis*, and *Oreamnos harringtoni* recovered from deposits on the Colorado Plateau (fig. 1). Dung has been directly radiocarbon dated back to >40.000 yr B.P. (years before present) for a number of species. Radiocarbon dating of dung indicates that the Shasta ground sloth became extinct by 11,018 ± 50 yr B.P., a weighted average of dates (MARTIN *et al.*, 1985). Similar analysis of dung and keratin (horn sheath) remains of Harrington s mountain goat indicates an extinction finale by 11,160 ± 125 yr B.P. (MEAD *et al.*, 1986a). An equivalent analysis using mammoth dung is in progress, although preliminary examination form just Bechan Cave indicates that the elephant of the Colorado Plateau may have left or been exterminated slightly earlier (12,490 ± 40 yr B.P., weighted average of 13 tandem accelerator mass spectrometer samples; MARTIN, 1987))(this does not take sampling bias into consideration).

With continued direct radiocarbon dating of all identified dung species, it should be possible to determine when these mammals became extinct on, or at least extirpated from, the Colorado Plateau.

Mammoths on the Colorado Plateau are found to have eaten a variety of plants (Table 2), although most of the diet seems to be graze species. Nearly one-third of the encountered macrofossils form Bechan Cave mammoth dung are sedge (*Carex*); 95% of the contents from dung recovered from Cowboy were *Sporobolus* grass (Table 2).

Table 3 reports the large variety of plants eaten by the extinct mountain goat. Both graze and browse were important in the diet, and differed by season and location relative to the Colorado River (MEAD *et al.*, 1986b, ROBBINS *et al.* 1984). Table 4 lists the plants eaten by the shasta ground sloth. Although it was mainly a browser, the dung samples from Muav Caves, near a spring, indicate that graze items occasionally were important to the diet, possibly during spring growth. The diet of the bison is just beginning to be established for the Colorado Plateau (Table 5). Although it appears to use predominantly graze, the bison obviously will eat certain browse species.

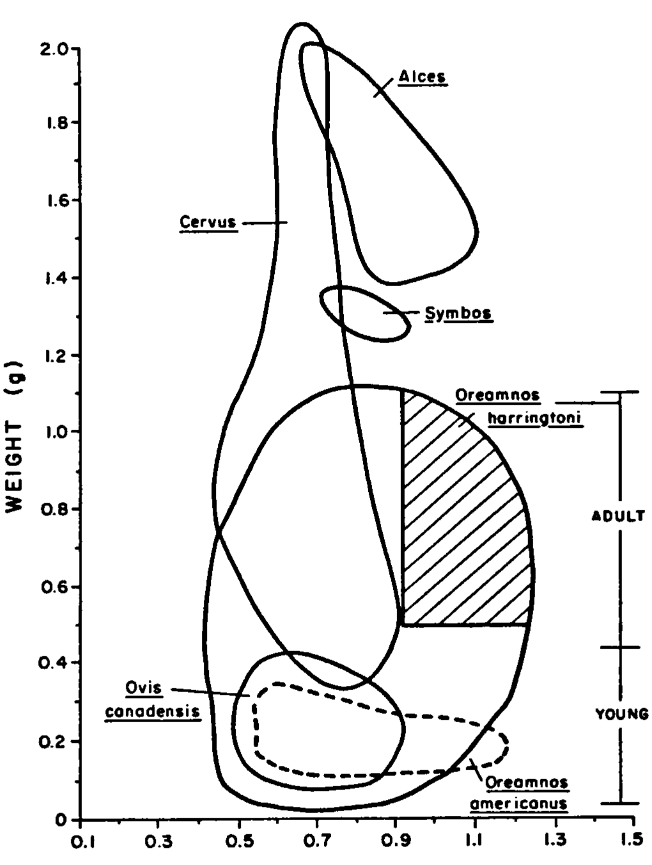

fig. 8 Dung pellets of adult ruminants can otften be segregated by a ratio of weight to width:length. Hachured area represents unquestionable adult *Oreamnus harringtoni* dung.

Future directions

It is necessary to locate additional dung deposits and conduct all the above mentioned tests on each species. If a particular deposit contains, for example, three different layers of dung, with bison, mammoth, and mountain goat dung in each layer, then a sample of each dung species should be tested from each of the three layers. Such detailed analyses may begin to unravel the cause of extirpation and extinction and when it may have begun.
The actual number of tests to be conducted on a dung remains is at the mercy of the innovative scientist. We are beginning to examine the biochemistry; Dr. Jerold Lowenstein (University of California) is searching for a way to extract a chemical signature for each species of dung. This technique, if succesful, will enable us to identify the species belonging to the small pellet-producing taxa and double-check identifications already made. We might be able to identify extinct species of deer (*Navahoceros*) and pronghorn (*Stockoceros* and *Tetramervx*), animals which probably produced dung pellets near identical to at least five other artiodactyls.
Researchers at Johns Hopkins University (Maryland) and San Diego Zoological Park (California) are examining the possiblity of determining the sex of the dung producer. With this technique it may be possible to determine if a certain cave was used by one sex or another, in the form of a birthing area. Additional dietary contents (in dung and keratin remains) will be analyzed to see if there was a change in C3/C4 plant consumption during the late glacial. If there was such a change, it will be important to record when it happened, and did it coincide with (cause) extinctions.
We have listed only four species of herbivores known to produce dung which is preserved in dry caves of alcoves on the arid Colorado Plateau of the Southwest. Additional species are preliminarily identified as belonging to Camelidae, Ovibovini, Caprini and Cervidae. It is unusual that dung be preserved at all, therefore, we must look for these paleoecological remains in the unusual deposits. We must continue our research in the permafrost of Siberia and in the caves on the arid Colorado Plateau. We should be seriously examining the acidic, organic-preserving bogs of northeastern Canada and Scandinavia. Caves in the arid lands such ad Mongolia and northwestern China should be evaluated in terms of organic contents. The final determination of the usefulness of dung analyses for paleoecology awaits the future myriad of analytical techniques. We suggest that those researchers working on the frozen carcasses recovered from the permafrost and those working on the dried desert remains begin working together to learn what effect the complexity of changing environments had on the living and extinct megaherbivores of the last glacial.

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Table 1. Limestone and sandstone shelters containing dung of late Rancholabrean age herbivores of the Colorado Plateau, southwestern USA.

Location	*Bison*	*Mammuthus*	*Nothrotheriops shastensis*	*Oreamnos harringtoni*	Unknown large pellet	Radiocarbon years ago[1,2]		Major Reference
ARIZONA								
Disappearing Cave				x		LR		TR
Muav Caves			x			10,650±220 - 11,810±70;	6	1
Rampart Cave			x	x		10,035±250 - >40,000;	19	2,3,18
Sandblast Cave				x		A13,110±680;	1	TR,4
Stanton's Cave				x		>11,000		5,6
Stevens Cave				x		11,880±120 - 14,070±100;	3	TR
Three Springs Cave				x		LR		TR
Tse'an Bida				x		11,850±750 - $24,190^{+4300}_{-2800}$;	5	7,8
Tse'an Kaetan				x		14,220±320 - 30,600±1800;	3	7,8
UTAH								
Bear Ladder Shelter				x		21,330±240 - >39,800;	3	9
Bechan Cave	x	x	x	?	x	11,670±300 - 13,505±580;	19	10-14,19
BF Alcove					x	11,790±190 - 12,130±170;	2	15,16
Cowboy Cave	x	x	x		x	11,020±180 - 13,040±440;	5	17,20
Grobot Grotto	x	x		?	x	15,270±120 - 28,290±2100;	5	15,16
Hooper's Hollow	x			x	x	18,840±350 ;	1	TR,16
Mammoth Alcove	x	x			x	16,630±280 ;	1	TR,16
Oak Haven	x				x	11,690±120 ;	1	TR
Ox Alcove	x	x	x		x	23,100±660 ;	1	TR
Wither's Wallow	x	x				12,010±160 ;	1	TR

TR - this report

1 Martin et al. 1985
2 Martin et al. 1961
3 Long et al. 1973
4 Emslie 1988
5 Robbins et al. 1984
6 Mead et al. 1986a
7 Mead 1981
8 Mead 1981
9 Mead et al. 1987
10 Davis et al. 1984
11 Mead et al. 1986c
12 Agenbroad et al. 1984
13 Davis et al. 1985
14 Mead et al. 1984
15 Mead and Agenbroad 1986
16 Agenbroad and Mead 1987
17 Hansen 1980
18 Hansen 1978
19 Martin 1987
20 Jennings 1980

? - Preliminary information

1 - Dates directly on dung, unless by association (A) with other ages (see reference); maximum/minimum dates provided; number of radiocarbon dates.

2 - The recorded ^{14}C ages are only those concerning the late Pleistocene.

LR - Late Rancholabrean, an assumed age.

Table 2. Diets of the Mammoth on the Colorado Plateau Based on Microhistological and Macrofossil Remains.

References:	Bechan Cave			Cowboy Cave	Grobot Grotto
	TR	1	3	2	TR
Plant Species:					
Graze					
Gramineae		13			
Agropyron				1	
Bromus	2		X		
Carex	94	30	X	T	2
Festuca				T	
Hilaria				T	
Oryzopsis				1	
Phragmites	4		X		89
Sporobolus			X	95	9
Stipa				2	
Equisetum				1	
Browse					
Artemisia		3			
Atriplex		5	X		
Betula		12			
Cactaceae		18			
Chenopodium				T	
Cornus		T			
Picea		T			
Rosa		11			
Sphaeralcea				T	
Symphoricarpos		T			

Table 2 (continued)

References:

TR = this report.

1 = Davis et al., 1985; see also Davis et al., 1984; percentage of macrofossil content.

2 = Hansen, 1980; percentage of relative density.

3 = Martin, 1987.

X = Presence.

T = Trace amount, ≤ 1%.

Table 3. Diets of the Mountain Goat on the Colorado Plateau Based on Microhistological Remains.

	Bear Ladder 2		Tse'an Bida Cave	Tse'an Kaetan Cave	Stevens Cave TR			Stanton's Cave
Reference:	0A	2A	1	1	A	B	C	3
Plant Species:								
Graze								
Agropyron			4	7				
Andropogon								X
Aristida			2		54	9		X
Bouteloua			T					X
Bromus		6	3		6		2	X
Carex		9	4					X
Eleocharis								X
Enneapogan								X
Equisetum		3						X
Festuca			10	13		T		X
Hilaria					9			
Oryzopsis			7	3				
Panicum								X
Phragmites								X
Poa		3	T	2	T			
Schedenardus								X
Sporobolus			19	8	18	T		X
Stipa			T		7			X
Tridens								X

Table 3 (continued)

	Bear Ladder 2		Tse'an Bida Cave	Tse'an Kaetan Cave	Stevens Cave TR			Stanton's Cave
Reference:	0A	2A	1	1	A	B	C	3
Browse								
Acacia			T					
Adiantum								X
Agave								X
Aloysia								X
Antennaria-Cirsium	6							
Arenaria								X
Artemisia								X
Aster								X
Astragalus								X
Atriplex			T	T				X
Baccharis						14	2	
Bark		52				14	2	
Boraginaceae					T			
Cactaceae						3		
Cercocarpus			16	10		T		X
Chrysothamnus								X
Clematis								X
Coldenia								X
Convulvus								X
Cryptantha				T				X
Cympteris			T					
Dyssodia								X

Table 3 (continued)

Reference:	Bear Ladder 2		Tse'an Bida Cave 1	Tse'an Kaetan Cave 1	Stevens Cave TR			Stanton's Cave 3
	0A	2A			A	B	C	
Ephedra								X
Eriogonum								X
Euphorbia								X
Fallugia								X
Galium								X
Glossopetalono			2					
Gutierrezia								X
Hedeoma								X
Juniperus			T	T		54	96	
Laphamia								X
Lesquerella				1 •				X
Lygodesmia								X
Mentezelia								X
Oenothera			T	1	3			X
Opuntia								X
Phlox-Leptodactylon			T	1				
Phoradendron			2			T		X
Physalis								X
Pinus	76	24	4	22				
Populus			T					
Prunus				6				X
Pseudotsuga	16		7	2				

Table 3 (concluded)

Reference:	Bear Ladder 2		Tse'an Bida Cave 1	Tse'an Kaetan Cave 1	Stevens Cave TR			Stanton's Cave 3
	0A	2A			A	B	C	
Rhus			2	5				X
Sarcobatus								X
Sida			2	2				
Solanum						6		
Solidago								X
Sphaeralcea	3		1	11				X
Symphoricarpos			T	T				
Tetradyma								X
Tragia								X
Urtica								X
Yucca			T			9		X

References:

TR = This report; percentage of relative density.

1 = Mead et al., 1986; percentage of relative density; Kaetan:$\bar{x}$ of levels surface to 5; Bida:$\bar{x}$ of all levels.

2 = Mead et al., 1987; percentage relative density.

3 = Robbins et al., 1984; presence (X) 50 levels 25 cm and below.

T = Trace amount, $\leq$ 1%.

Table 4. Diets of the Shasta Ground Sloth Based Only on the Microhistological Remains.

	Muav Caves TR				Rampart Cave	Cowboy Cave	Bechan Cave	Off Colorado Plateau
Reference:	A	B	C	3	1	2	TR	4
Plant Species:								
Graze								
Gramineae								T
Agropyron	10	14						
Aristida	2			T	T			
Bouteloua	2							
Bromus				T				
Carex	6	16	3		T			
Festuca	60	27			T			
Hilaria							2	
Mulenbergia				T				
Oryzopsis						T		
Phragmites		16	50					
Sporobolus	4	2	15			1	46	
Tridens			2		T			
Browse								
Acacia	12	9	5		17	1		
Agave				10				
Amelanchier-type						36		
Artemisia							2	T
Atriplex			3	37	T			
Bumelia								2
Cactaceae				T	1		2	1
Chenopodium-type						T		
Chrysothamnus								1
Forsellesia								T
Fraxinus				T	1			
Garrya								T
Geranium			12					
Juniperus					T			
Oenothera-type			5					
Phacelia				5				
Prosopis				10				
Pseudotsuga						60		
Prunus								T
Ranunculus-type		7	3					
Rosa-type								16
Sphaeralcea	4		2	4	50			3
Tidestromia				1				
Unknown forb		9				3	48	
Yucca				2	T			T

Numbers are percentages of relative density.

References:

TR = This report.

1 = Hansen, 1978; sample A_2 representative; from 40 boluses.

2 = Hansen, 1980.

3 = Long et al., 1974.

4 = Thompson et al., 1980; Shelter Cave, southern New Mexico.

T = Trace amount, $\leq$ 1%.

Table 5. Diets of the Bison on the Colorado Plateau Based on Microhistological Remains.

Reference:	Cowboy Cave 1	Grobot Grotto TR A	Grobot Grotto TR B	Hooper's Hollow TR	Mammoth Alcove TR
Plant Species:					
Graze					
Agropyron	1	2			
Bromus		9	12	T	
Carex	12	3	15		2
Equisetum	2	3	1		
Oryzopsis	4				
Sporobolus	74	74	72	93	47
Stipa	5				
Browse					
Bark		2		3	30
Chenopodium-type	T				
Clematis-type	T				
Chrysothamnus		5			
Ephedra				T	
Lupinus				T	
Moss		2			
Picea					2
Quercus				2	2
Yucca					17

References:

TR = This report; percentage relative chemistry.

1 = Hansen, 1980; percentage relative density.

T = Trace; $\leq$ 1% value.