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RAMPART CAVE COPROLITE AND ECOLOGY OF THE SHASTA GROUND SLOTH*

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ABSTRACT. The shasta ground sloth *Nothrotherium shastense* inhabited Rampart Cave in the Grand Canyon of the Colorado River, Arizona for at least 25,000 years. During this interval occupation was probably discontinuous; radiocarbon dates of the dung from the surface of the cave are on the order of 10,000 years, from the 18-inch level 12,000 years, and from the 54-inch level older than 35,000 years. Dung samples collected at 6-inch intervals to a depth of 60 inches proved rich in well-preserved pollen. Within each level there is great variation in pollen content. In part this reflects seasonal change in flowering time of various plants growing adjacent to the cave. An increase in *Artemisia, Pinus, Betula,* Cupressaceae, and other montane trees and shrubs reveals that levels 18 through 48 represent a time of cooler or wetter climate with Upper Sonoran vegetation displaced downward 2000 to 4000 feet.

These samples were analyzed spectrographically for trace element content. On theoretical grounds the abundance of manganese proves a promising index of climatic change; when compared with the pollen evidence, there is a reasonably good fit between high manganese values and periods of greater moisture. These correspond to the Wisconsin glacial age.

Cobalt is very rare and copper is abundant in dung from all levels. There is no indication that a change in abundance of these triggered ground sloth extinction, as claimed by Salmi (1955).

Nothrotherium excelled as a browser in the arid Southwest. Some of its preferred food plants, as creosote bush, yucca, snakeweed, and cactus, are not harvested systematically by existing large desert herbivores. The ecological niche of *Nothrotherium* remains unfilled. Its extinction defies an obvious environmental explanation either in terms of trace element deficiency, competition, or climatic change. The cause of extinction must lie elsewhere.

INTRODUCTION

In 1936 a rich cave deposit of Late Pleistocene fossils and dung, notably of the ground sloth *Nothrotherium shastense* Sinclair, was discovered by a National Park Service employee, Willis Evans. The locality, named Rampart Cave, lies in the Lower Granite Gorge of the Grand Canyon, Arizona about four miles upstream from Pierce's Ferry (fig. 1). The cave opens near the base of the Muav limestone (Upper Cambrian) at an altitude of 1750 feet, approximately 4000 feet below the rim of the canyon and 750 feet above the Colorado River. Soon after discovery the U. S. National Park Service closed the cave mouth with a gate, preventing entry of unauthorized persons. Except for test pits and a trench, the fossil and dung deposit, five to six feet in depth, is preserved largely intact.

There are two important paleontological reports on Rampart Cave. Laudermilk and Munz (1938) identified plant material, including some pollen and spores, from the sloth dung. Wilson (1942) described a vertebrate fauna of at least ten genera in addition to the sloth. Our contribution concerns radiocarbon dating (Shutler at Lamont), pollen analysis (Martin), trace element studies (Sabels), and extinction theory. Our study is based on a 60-inch dung profile collected by Shutler in June of 1956. Exact location of the profile is shown on the cave floor plan (fig. 1).

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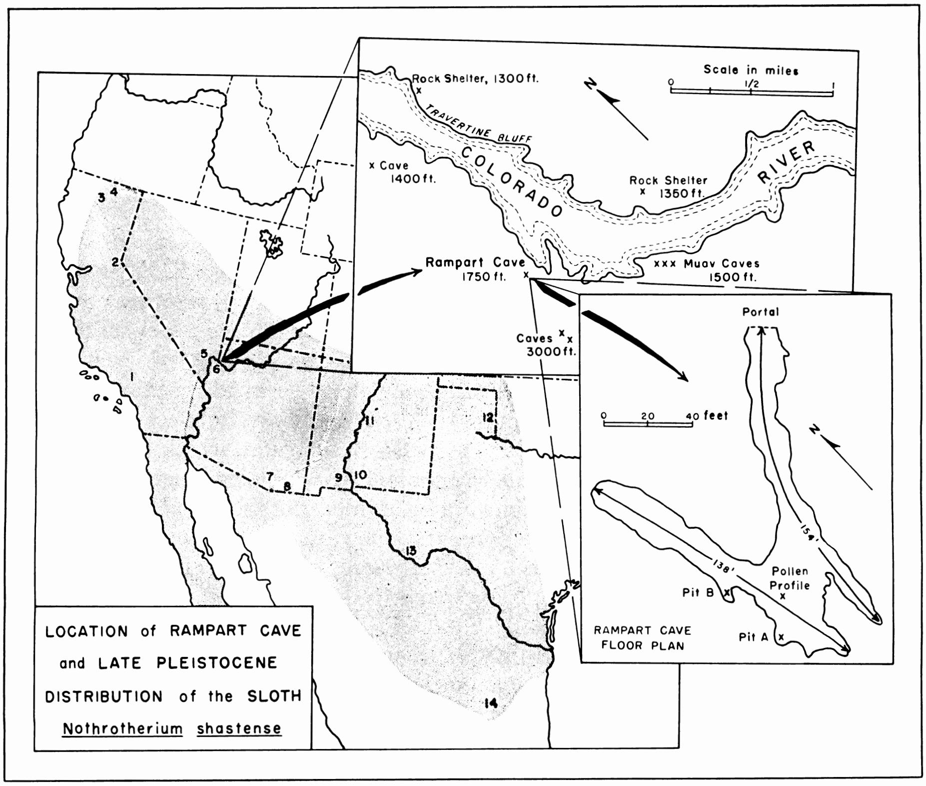

Fig. 1. Location of Rampart Cave and Late Pleistocene distribution of *Nothrotherium shastense*. Fossil remains have appeared at the following locations—California: 1. Rancho La Brea, 2. Hawver Cave, 3. Samwel Cave, 4. Potter Creek Cave. Nevada: 5. Gypsum Cave. Arizona: 6. Rampart and Muav Caves, 7. Ventana Cave, 8. Pyatt Cave. New Mexico: 9. Aden Crater, 10. Conkling Cave and Shelter Cave, 11. Sandia Cave. Texas: 12. Wheeler County, 13. Brewster County. Mexico, Nuevo Léon: 14. San Josecito Cave. Not shown is a record from Klamath County, Oregon.

Hibbard (personal communication) reports an Early Pleistocene record of *Nothrotherium* from below Pearlette Ash in Knox County, Texas.

Similar fossil remains of ground sloths, often including dung and certain soft parts, have been reported in caves in New Mexico (Lull, 1930), Nevada (Harrington, 1933), Tennessee (Mercer, 1897), and southern Patagonia, South America (summary in Rusconi, 1949). Through study of such deposits it may be possible to gain fresh insight concerning the ecology of gravigrade sloths. As Salmi and others have realized, dung deposits may provide clues to the cause of sloth extinction.

ACKNOWLEDGMENTS

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DESCRIPTION AND AGE OF THE DUNG

Eleven samples were collected in Rampart Cave at 6-inch intervals from the bottom to the top of a freshly cleaned face of an open trench. Except the deepest (60-inch level) all are dung samples, containing coarse plant fragments and fibers. Level 60 comprises a whitish powder containing black organic particles including pollen. It resembled the combustion products of levels 12, 18, and 24 and appears to be a product of slow natural decay of organic matter.

Three types of dung were recognized: (1) coarse, loose, light-colored plant fragments, often in lumps of two to three inches in diameter, which we assume represent the feces of *Nothrotherium.* Presumably these are fragments of dung masses; they match the description of Laudermilk and Munz (1938); (2) small, oval fecal pellets of a rodent, probably the cave rat, *Neotoma*; and (3) larger, lozenge-shaped dung balls of an herbivore, apparently an artiodactyl and possibly *Ovis* or *Oreamnos*, both found as fossils in the cave (Wilson, 1942).

Seven of the samples constitute sloth dung exclusively; cave rat scats were included in sloth dung from the surface and 30-inch levels. Level 36 is composed entirely of coarse plant material, cave rat and artiodactyl scats, seemingly the midden of a cave rat. Plant material in level 36 included three juniper twigs and a seed of juniper (*Juniperus*), spines of various shrubs and broken areoles of cacti, especially *Echinocactus* (determined by C. T. Mason and R. Hevly, University of Arizona Herbarium). It is possible that sloths did not inhabit the cave at this time. The maximum rate of fecal deposition, computed from the radiocarbon dates (see below), adds to the probability that sloth occupation in lower levels was not continuous.

TABLE 1

Radiocarbon dates from sloth caves

	Locality	Laboratory number	Sloth Dung Yr. B. P.	Humic Acid Yr. B. P.	Stratum
1.	Rampart Cave, Arizona	L-473A	10,050 ± 350	10,020 ± 350	Surface
2.	"	L-473C	12,050 ± 400	11,950 ± 300	18″
3.	"	L-473D	>35,500	>32,600	54″
4.	Gypsum Cave, Nevada	C-222	8,527 ± 250		2′ 6″
5.	"	C-221	10,455 ± 340		6′ 4″
6.	Palli Aike Cave, Chile	C-485	8,639 ± 450		?
7.	Mylodon Cave, Chile	C-484	10,832 ± 400		Layer C

Radiocarbon dates of dung samples from the surface, 18-inch depth, and 54-inch depth are shown in table 1. The age obtained for level 18, 12,000 years, suggests an Older Dryas (Port Huron) correlation. The date of the surface sample, 10,000 years, is older than the minimum age of dung reported from adjacent Gypsum Cave in Nevada (8500 years). Perhaps *Nothrotherium* survived slightly longer at that locality.

The sample from the 54-inch level exceeded the sensitivity of Lamont Laboratory's gas counter and is at least 35,500 years old. The time span from surface to level 54 is thus *at least* 25,000 years and embraces the last glacial maximum of the Wisconsin age.

The radiocarbon dates can be used to estimate the average rate of fecal deposition. From the map in Laudermilk and Munz (1938), we estimate the area of the cave floor at 4875 square feet. If the top 18 inches of dung accumulated in 2000 years, the average annual rate would be 0.00075 feet, or 0.24 mm. Assuming an equal rate of deposition over the entire cave floor, this figure would require an average increment of about 3 2/3 cubic feet per year.

Deposition in the lower 36 inches was even slower. Since the 54-inch stratum is at least 35,000 years old, the average rate of deposition between levels 54 and 18 was at most 0.00013 feet (0.004 mm) per year, or an average annual volumetric increment of 0.6 cubic feet. The annual dung accumulation of a single animal must have exceeded this value greatly. Did the sloth occupy the cave only in the winter and move to higher altitudes to escape the summer heat? Low frequency of chenopod-amaranth pollen points to such a possibility. Was habitation erratic with several hundreds or even thousands of years intervening between periods of occupation? Or did sloths favor middens outside the cave and rarely eliminate within it? These details of sloth life history remain unknown; our main conclusion here is that dung accumulation within the cave was not continuous.

POLLEN ANALYSIS

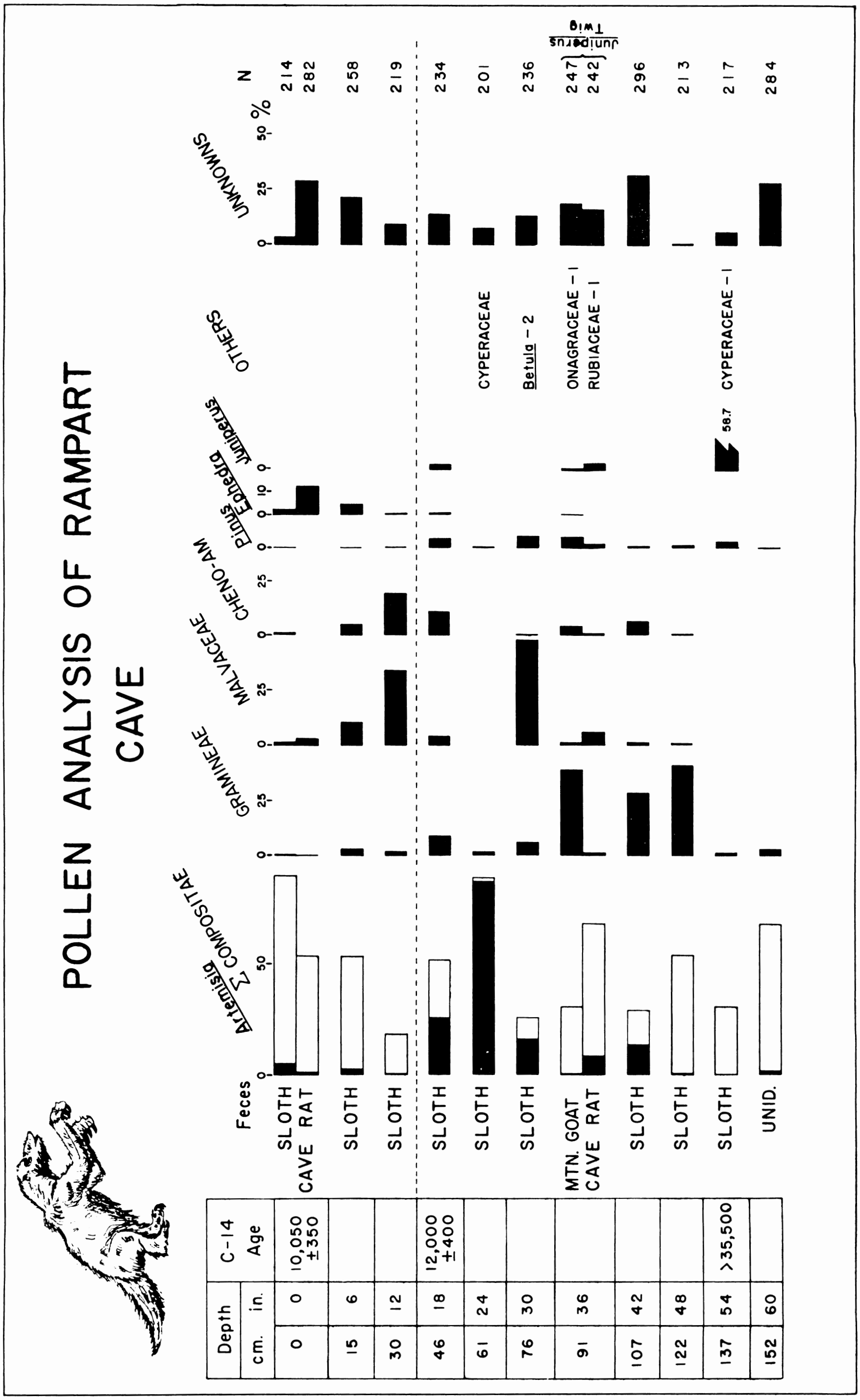
Procedure and Theory

Organic material from each level was analyzed for pollen and spores. Hydrofluoric acid extraction served to remove the small amount of inorganic material present in the dung; screening, acetolysis, and heating in 5% KOH solution were employed to concentrate the plant microfossils. A few rodent and artiodactyl scats were analyzed separately (fig. 2). Amorphous organic material from the floor of the cave (level 60) could not be identified as to source. Abundant, well-preserved pollen was recovered, and a 200-grain count, exclusive of unknowns, was made at each level.

In three respects the final pollen profile differs from those of water-laid sediments. The frequency of unknowns is high (1 to 32%), zoögamous types are common, and there is great variation between adjacent strata.

An abundance of unknowns can be attributed to our unfamiliarity with zoögamous pollen types. The latter reflect the feeding habits of the sloth which ingested animal-pollinated flowers. Their pollen is not released in quantity into the atmosphere and is not abundant in most water-laid sediment.

The matter of internal variation between strata invited additional study. Except perhaps in the case of levels 0 and 6, variation between adjacent levels


POLLEN ANALYSIS OF RAMPART CAVE
Depth
cm.
in.
C-14 Age
Feces
Artemisia
Σ COMPOSITAE
GRAMINEAE
MALVACEAE
CHENO-AM
Pinus
Ephedra
Juniperus
OTHERS
UNKNOWNS
N
0
25
50
10
%
0
0
10,050 ±350
SLOTH
CAVE RAT
214
282
15
6
SLOTH
258
30
12
SLOTH
219
46
18
12,000 ±400
SLOTH
234
61
24
SLOTH
CYPERACEAE
201
76
30
SLOTH
Betula - 2
236
91
36
MTN. GOAT
CAVE RAT
ONAGRACEAE - 1
RUBIACEAE - 1
247
242
Juniperus Twig
107
42
SLOTH
296
122
48
SLOTH
213
137
54
>35,500
SLOTH
58.7
CYPERACEAE - 1
217
152
60
UNID.
284

exceeds that to be expected by chance alone. It seems unnecessary to search farther than the feeding habits of the sloth for at least one obvious explanation. Unlike lake or marsh sediments, a fecal sample represents the integration of a fairly short period of flowering time, perhaps no more than a month. It should contain high percentages of whatever flowering plants were being ingested by the sloth and should vary drastically from season to season.

Unlike the zoögamous mallows and creosote, high percentages of anemogamous sagebrush and juniper do not necessarily reflect the dietary habit of the sloth. These plants produce pollen in sufficient quantity to dust all the vegetation in their vicinity, and the sloth might ingest their pollen in abundance without feeding on the plants themselves.

To learn more regarding internal variation, we analyzed replicate counts of five levels (fig. 3). The original count (subsample 1 in fig. 3) was made in July 1958 and used in constructing our pollen diagram.

In January 1959 a second count was made of residue from levels 6, 18, 24, 30, and 54. With the exception of a slight alteration in grass and *Ephedra* percentages, there was no difference between subsamples 1 and 2 which might not be attributed to chance.

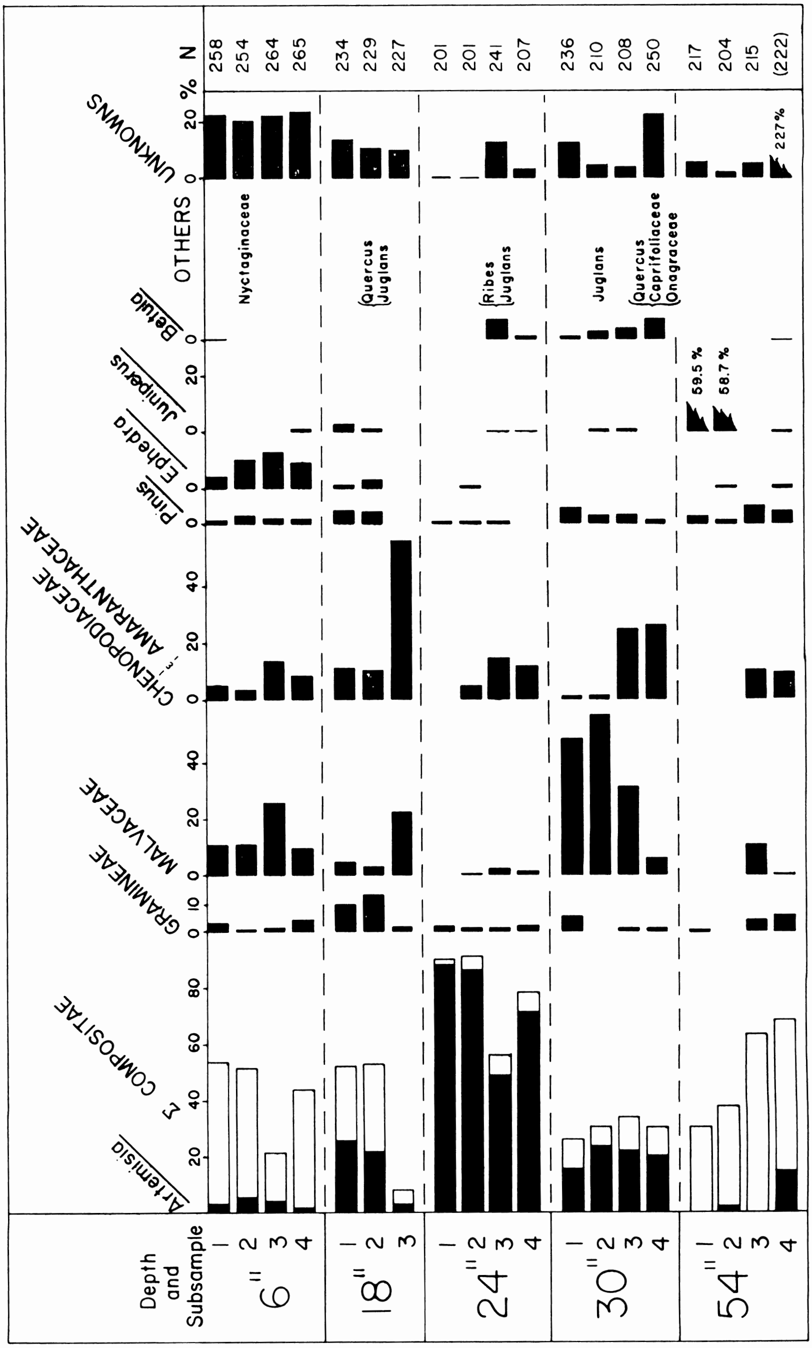
The original sample bags of levels 6, 24, 30, and 54 were then removed from storage and a third and fourth subsample were extracted. In this case we failed to recover our original percentages (see subsample counts 3 and 4 in fig. 3). Applying the confidence interval tables for binomial distribution with n equal to 250 (Snedecor, 1956, p. 5), the probability that the difference between original and rerun samples is due to chance alone is less than 1% in each case. In level 54 the frequency of Cupressaceae dropped from 59% to zero.

To summarize, we find a high variation, both between levels and between dung subsamples within a single level. This can be explained most easily in terms of the seasonal progression in flowering of different plants eaten by the sloth. Admittedly the high subsample variation makes climatic interpretation of the pollen diagram less secure than one might wish. Only by considering all possible climatic indicators within the sequence is it possible to claim reasonable evidence of change.

Climatic Indicators

At 1750 feet altitude Rampart Cave lies in the Lower Sonoran zone. Among 56 plants identified during their visit to the cave in June 1937, Laudermilk and Munz listed the following shrubs: creosote, barrel cactus, catclaw acacia, ocotillo, burro weed, and incienso. Presumably these are the dominant feature of the landscape. Pollen of various plant taxa that do not occur at this elevation today appear in certain dung levels: a) sagebrush (*Artemisia*); b) pine (*Pinus*, mainly small pollen grains of the piñon type); c) birch (*Betula*); d) cypress-type (family Cupressaceae, probably *Juniperus*); e) rare occurrences of fir (*Abies*), alder (*Alnus*), walnut (*Juglans*), hornbeam (*Ostrya*), currant (*Ribes*), and honeysuckle (*Lonicera* or *Symphoricarpos*). We will discuss them in turn.

Fig. 2. Pollen profile of Rampart Cave. Cheno-Am = Chenopodiaceae plus Amaranthaceae. *Artemisia* (black bar) enclosed within sum of Compositae (open bar).


Depth and Subsample
6"
18"
24"
30"
54"
1 2 3 4
1 2 3
1 2 3 4
1 2 3 4
1 2 3 4
Artemisia
COMPOSITAE
20 40 60 80
GRAMINEAE
0 10
MALVACEAE
0 20 40
CHENOPODIACEAE, AMARANTHACEAE
0 20 40
Pinus
0
Ephedra
0
Juniperus
0 20
Betula
0
OTHERS
Nyctaginaceae
Quercus
Juglans
Ribes
Juglans
Juglans
Quercus
Caprifoliaceae
Onagraceae
59.5 %
58.7 %
UNKNOWNS
0 20 %
227 %
N
258
254
264
265
234
229
227
201
201
241
207
236
210
208
250
217
204
215
(222)

(*a*) *Artemisia* (*fig. 4*).—Although sagebrush is wind pollinated, and may drift down into lower Granite Gorge at present, it is so abundant in certain levels that its past growth at 1750 feet seems certain. In level 24, 88 percent suggests that it was then browsed by the sloth as it is now by sheep. Identification to genus is reasonably secure; the long colpi, thick exine with columellae, and minute spines immediately distinguish *Artemisia* from *Franseria* and other anemophilous Compositae. Subgeneric identification was not attempted. There are 14 species in Arizona, ranging from 2500 to 9000 feet (Kearney and Peebles, 1951). In Arizona none of the shrubby artemisias are reported below 4000 feet. They are typical of cool desert, grassland, and woodland, including subalpine openings. Laudermilk and Munz reported only *Franseria* among the anemophilous Compositae seen near Rampart and Muav Caves.

(*b*) *Pinus*.—As shown in figure 2 pine pollen appears slightly more abundant in levels 18, 30, 36A, and 54. In the original 200-grain count the percentages varied from 0.1 to 5.8, a fluctuation that might be attributed to chance alone. To test this possibility pine frequency was recorded in a thousand-grain scan with the following results: level 0 (sloth)—1; level 0 (rat)—0; level 6—6; level 12—8; level 18—25; level 24—3; level 30—30; level 36 (mountain goat)—48; level 42—7; level 48—6; level 54—20; level 60—4. On this basis the increase in pine in levels 18, 30, and 36A cannot be attributed to sampling variation.

Admittedly this provides no more than a clue to the possible history of pine in the Grand Canyon. Frequencies of 5% pine pollen have been recovered in cattle tanks of the desert grassland in southern Arizona, roughly ten miles distant from the nearest isolated montane pine populations. Piñon-juniper woodland occurs near both north and south rims of Lower Granite Gorge, and Nichol (1952) maps isolated yellow pine stands within 40 miles of Rampart Cave. Small amounts of conifer pollen may be wind-transported into the area at present.

Conversely, piñon trees might have grown at the mouth of Rampart Cave and be entirely under-represented, if none of the dung samples were dropped during the season when the animals would have ingested pine pollen.

Taken by itself we would not draw climatic inference on the slight frequency change in pine pollen. Nevertheless there is a relationship between pine abundance and that of other cool climate indicators.

(*c*) *Betula* (*fig. 4*).—Two birch grains were observed in the first count of level 30 (subsample 1 of fig. 3). Six were observed in the recount (subsample 2) and eight in the sample rerun (subsample 3). Although none were noted in the original count of level 24, a total of 18 were found in the sample rerun (subsample 3) from that level. One was found outside the counted por-

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Fig. 3. Subsample variation in pollen count of certain dung levels. The large numbers indicate depth of sample; small numbers represent individual replicate counts within that sample (see text). 227 percent "unknowns" in level 54 are mainly of *Larrea* (creosote bush).

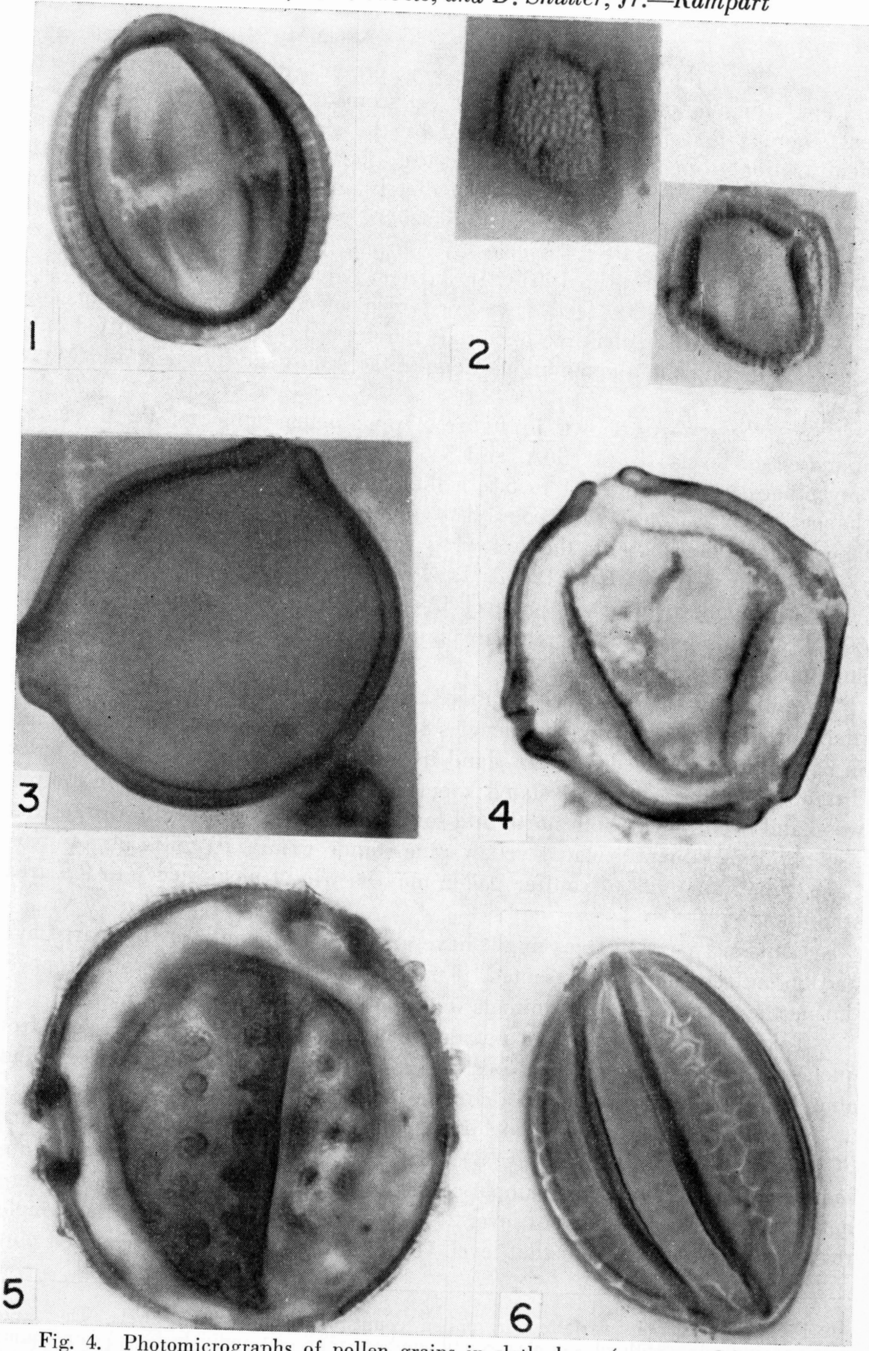


Fig. 4. Photomicrographs of pollen grains in sloth dung (not to scale): 1. *Artemisia*; 2. *Larrea* (1250x), high and mid focus; 3, 4. *Betula*; 5. Malvaceae, *Sphaeralcea* type; 6. *Ephedra, nevadensis* type.

tion of the slide from level 6. Although it is possible that a few *Ostrya* were included in the birch count, most grains showed an unmistakable *Betula* pore structure.

The small but appreciable percentages of birch, higher than one might expect as a result of wind transport alone, imply that birch trees grew near Rampart Cave in the Late Pleistocene. In Arizona Kearney and Peebles (1951) describe the present distribution of water birch (*Betula fontinalis*) as including the North Rim of the Grand Canyon between 7000 and 8000 feet, mostly along streams and often forming thickets. Little (1950) locates it within piñon-juniper woodland and ponderosa pine forest zones, 5000 to 8000 feet altitude. The fossil pollen record is a substantial indication of climatic change.

(*d*) *Cupressaceae, probably Juniperus.*—Pollen of the cypress family was present but very scarce in levels 18, 30, and 36. It dominated the original count and recount of level 54, but was absent in the sample reruns (subsamples 3 and 4). The assignment of all cypress-type pollen to the genus *Juniperus* can be defended in the absence of *Cupressus* from the Grand Canyon and the present distribution of juniper throughout the area at 3000 feet and above.

Several twigs and a seed found in the pack rat midden of the 36-inch level constitute rather sound evidence that juniper grew at the level of the cave, at least 1300 feet below their present lower limit.

Juniper pollen is shed in winter in southern Arizona, and its abundance in level 54 probably indicates winter residence of the sloth at that time.

(*e*) *Rare occurrences.*—The following pollen types of possible climatic significance appeared rarely. None were seen in the original sample series used in constructing the pollen diagram: *Abies*, fir, level 30; *Alnus*, alder, level 54; *Ribes*, currant, level 24; *Symphoricarpos* or *Lonicera* (Caprifoliaceae), level 30; *Quercus*, oak, level 18; *Juglans*, walnut, levels 18 and 24.

All of these plants grow at elevations considerably above Rampart Cave, and presumably very little of their pollen wafts into Lower Granite Gorge at present. Although the possibility of accidental wind transport cannot be eliminated, it is notable that none of these rare indicators occurred outside of levels 18 through 54. In the case of zoögamous *Ribes* and *Lonicera-Symphoricarpos*, wind transportation is highly improbable, and it is more likely that the sloth included currants and honeysuckle in his diet. The lower altitudinal limit of *Ribes* in northern Arizona is 4000 feet (Kearney and Peebles, 1951).

In general the pollen record suggests a maximum vertical shift of 2000 to 4000 feet (600 to 1200 meters) in the vegetation gradient during the late Pleistocene. We attempted to seek additional evidence for this change in the biogeochemical nature of the dung.

TRACE ELEMENT ANALYSIS

A midden in the weathering zone is a geochemical anomaly undergoing dissipation. The same is true for dung deposits in wet caves. Dry caves unaffected by weathering preserve the original deposition pattern of trace elements in coprolite, regardless of the solubility of the mineral assemblages within the individual strata. The degree of preservation of the trace element pattern in dung will vary, depending on the nature of the animal's feces and its excreting habits. Urine excretion will simulate weathering. *Nothrotherium* was probably an animal of high water economy. It may have existed largely on metabolic water, a conclusion based on studies of living sloths (see later discussion).

Processing of Samples

The composition varies from dust to coherent dung balls containing sizeable plant remnants. Therefore, great care must be taken in the preparation of representative samples.

They were processed as follows: a. quartering (homogenizing); b. pulverizing of the last fraction; c. combustion at 500°C. in a closed platinum crucible; d. pulverizing and quartering of the ash; e. mixing with spectrographic grade graphite powder, ratio 1:3; f. arc exposure until volatilization is complete.

Samples reacted differently when ignited in the platinum crucible. Some gave off ammonia and sulfur (see fig. 5). The sulfur condensed at the cooler parts of the crucible. When exposed without admixed graphite for one minute, at nine amperes current and 5 mm electrode distance, these samples did not arc to completion. Instead they left a glass bead residue. During this interval the excitation voltage remained low, 25 volts. Those samples which formed no bead and arced to completion were characterized, after a brief initial low-voltage interval, by an excitation voltage of 50. Variation in ionization potential of different chemical elements and their influence on arc temperature account for this effect. As a consequence, if there is an abundance of alkali metals present, the arc temperature stays low and most other elements fail to volatilize. In this case complete arcing requires admixture of graphite powder. Behavior of samples upon burning and arcing is shown in figure 5.

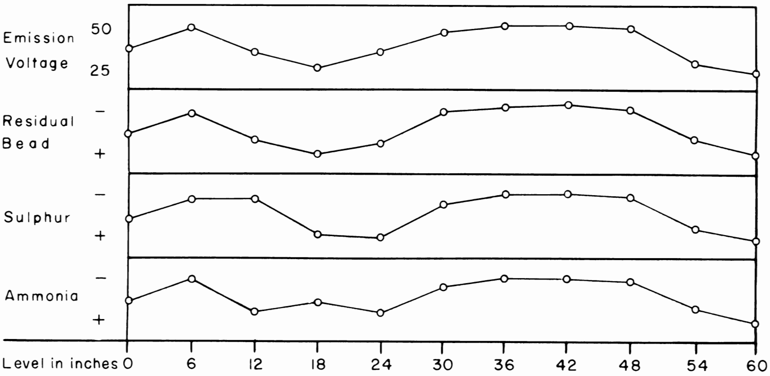


Fig. 5. Qualitative observations of sloth dung samples during spectrographic processing (see text).

Results and Interpretation of Emission Spectrography

Semiquantitative interpretation of the abundance of elements by densitometry leads to a comparison of the relative abundance of every element in different samples. Among the elements Na, K, Mn, Cu, Mg, Ca, Sr, Al, Si, Pb, Ti, V, Fe, Ni, Sn, Co, Zn, Ag, P, and Cr, the first three seemed to be of greatest significance as climatic indicators under the conditions at Rampart Cave.

The results of the emission spectrographic study appear in figures 5 and 7. The data were reproduced in three successive runs. A discussion of certain elements and their climatic or metabolic interpretation is given below.

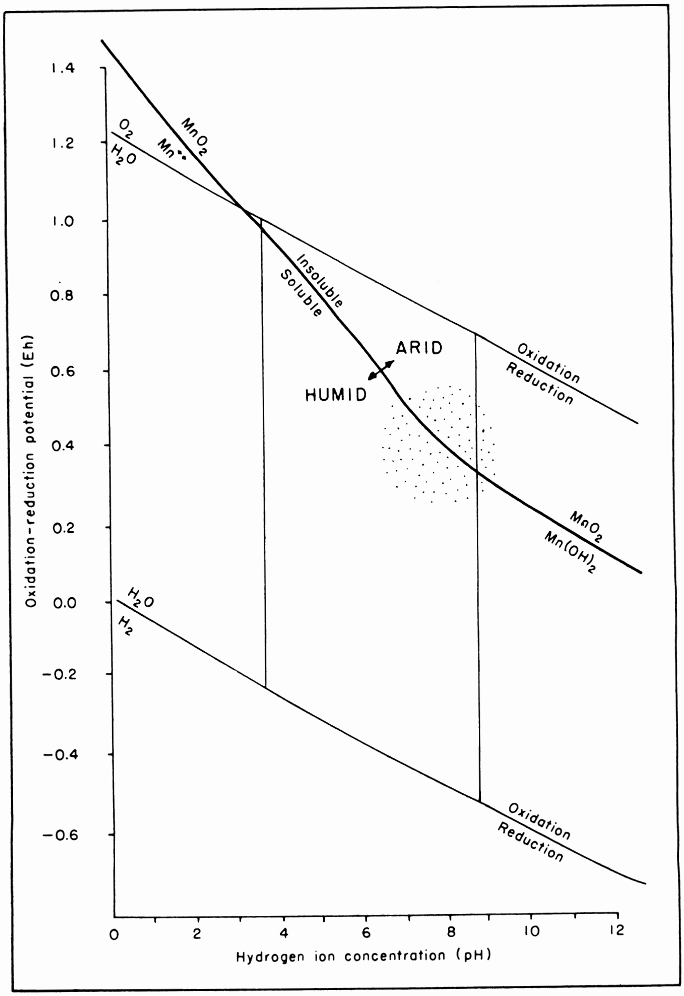
Copper.—Copper was present in all samples. If 1.0 is taken as the density of absolute darkness, the density of the Cu lines varies between 0.28 and 0.50. There was no obvious trend relating time and abundance of copper. Considering that a marked intensification of the observed lines 3248 Å and 3374 Å must take into account matrix effects (Webb and Fearon, 1937), the absolute abundance is estimated to have been in order of magnitude of 100 parts per million at any time. Presumably *Nothrotherium* did not suffer Cu deficiency.

Cobalt.—The sensitivity limit of the instrument for Co lies in the order of magnitude of 10 parts per million. In no sample examined did the abundance of cobalt exceed this limit, so that no further statement concerning its abundance can be made. The range critical for deficiency diseases for ruminants lies between 1 and 10 parts per million in the food material (Underwood, 1956). As the sensitivity of the instrument used by Salmi is 1 part per million (1955, p. 318), and metabolic extraction of 10 to 90% of the food cobalt is quite reasonable (see discussion below), one is unable to establish whether or not *Mylodon* in South America or *Nothrotherium* in Arizona were eliminating minute amounts of cobalt. More sensitive techniques must be applied to decide this question.

Sodium and potassium.—Given arid conditions and a suitable topography, surface salts accumulate, forming alkali soils. The same compounds form from humid soil solutions, but they are removed in ground water and cannot accumulate. It follows that abundance of alkali in soils, plant tissue, and feces should be taken as an indication of prevalent dry (arid) climate. The bead effect can be used as a quick climatic indicator.

Manganese.—The chemical behavior of manganese depends upon two processes, which individually lead to opposite results. These processes consist of leaching of divalent manganese in solution, mainly as the bicarbonate, and precipitation of very insoluble hydroxides and oxides of trivalent or quadrivalent manganese. In contrast to other elements (V, Cr), the lowest state of oxidation (low Eh values) gives the most mobile ions, while higher oxidation states (high Eh values) are connected with a fixation of the element (fig. 6). What happens to the element will therefore depend on the access and amount of oxygen.

The pH of circulating waters is also of great importance in the geochemistry of manganese. Availability in general decreases with increasing pH. Manganese shortage seems to occur in two very different ranges of soil pH. The one range is in extremely acid soils, with pH less than 4 (Everglades, Florida), where nearly all the manganese has been removed by leaching of the manganous ions which have been made soluble by the acid conditions. The other range of manganese shortage is above pH 7. On such soils plant uptake is very low, although chemical analyses of soils show ample total manganese. The cause of the manganese shortage is its presence in very insoluble higher oxides like pyrolusite, MnO_2 (fig. 6). In an arid climate we assume that the environment of the lower Grand Canyon was alkaline, with pH above 7. No, or very little, soluble manganese would be expected. Under humid conditions, slight acidity of the environment and reducing factors (decaying plants) will provide greater abundance of divalent manganese ions. Transitions between arid and humid climates seem to coincide with transitions between insoluble and highly soluble manganese compounds in the stability diagram (fig. 6). This mechanism, if effective, will supply sufficient manganese to plants living under humid and semihumid conditions but will cause shortage in plants of arid to semiarid environments.



Stability fields of Mn ions (After K. Krauskopf)

Fig. 6. Stability field of manganese compounds, modified after Krauskopf. Rampart Cave environments fall into the shaded circle.

The next step is animal ingestion. Fortunately, manganese is hardly affected by metabolic processes (Underwood, 1956) and resists digestive absorption. The last link between the past climate and the present study is the dry dung deposit in Rampart Cave.

In this fashion we propose to distinguish relatively humid and relatively arid periods. This hypothesis was tested by comparison with the behavior of other elements and by comparison with the change in climatic indicators encountered in pollen analysis.[1]

CLIMATIC CHANGE

Despite uncertainties in means of pollen dispersal and the formidable internal variation in our pollen diagram, it is possible to recognize three pollen zones: (a) a warm-dry interval from the surface to level 12: (b) a cool-moist interval from level 18 to 54; (c) a warm-dry time represented by level 60 and in certain subsamples of level 54. Zones (a) and (c) may have been equivalent in climate; they share a common feature, dominance of zoögamous Compositae. Subsample 4 of level 54 is dominated by pollen of the desert shrub *Larrea*, also present in lower frequency in levels 6 (0.4%), 12 (16.4%), and 18 (0.4%).

During the period represented by zone (b) there was sufficient ecological displacement to bring a juniper-sagebrush savanna, locally with birch, down to 1700 feet. In terms of life zones this represents an Upper Sonoran environment roughly 2000 to 4000 feet below its present lower altitudinal limit in the Grand Canyon.

A semiquantitative comparison of climate as recorded by manganese abundance and pollen composition is shown in figure 7. On grounds of its solubility characteristics, explained above, the manganese ion was selected as the most promising biogeochemical indicator of climatic change. Admittedly, both pollen and manganese curves incorporate certain uncontrollable sources

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[1] Recent quantitative determinations by Sabels at the spectrographic laboratory of the Department of Geology, University of California at Los Angeles, refine our qualitative data presented above. The following results were obtained on manganese, copper, and cobalt.

With palladium and germanium as internal standards for manganese and copper (Vanselow and Liebig, U. C. Berkeley, 1945), an artificial plant-feces base powder was prepared. Using the intensity ratios Mn 2576/Pd 3461 and Cu 3247,3274/Ge 2754 it was found that the abundance of manganese (in Rampart Cave material) varied between 200 and 1000 ppm. Samples from levels 18, 54, and 60 contained 200 to 300 ppm, those from levels 0, 6, 12, 36, 42, and 48 contained 500 to 700 ppm, those from levels 24 and 30 contained 800 to 1000 ppm manganese.

Copper in excess of 100 ppm was found in samples of the 6-, 12-, 24-, 54-, and 60-inch levels. The copper content of samples 0, 18, 30, and 48 varied between 15 and 40 ppm.

No cobalt was detected in samples 0, 6, 24, and 30. Faint traces (order of magnitude of one ppm) were found in the 12-, 18-, and 36-inch samples, and measurable traces (order of magnitude of 10 ppm) were seen in the 42- through 60-inch samples. Thus if *Nothrotherium* extinction were to be explained in terms of cobalt deficiency, as measured in the feces, it should have occurred earlier than 12,000 B.P. in the time interval represented by the 30-inch dung strata.

The suitability of manganese abundance studies for paleoclimatic interpretations of cave strata was borne out by more quantitative work on dry and wet caves. Thus the spectrographer can guide tedious pollen studies and costly carbon dating by rapid surveys of cave profiles. This approach is presently being employed by the three authors.

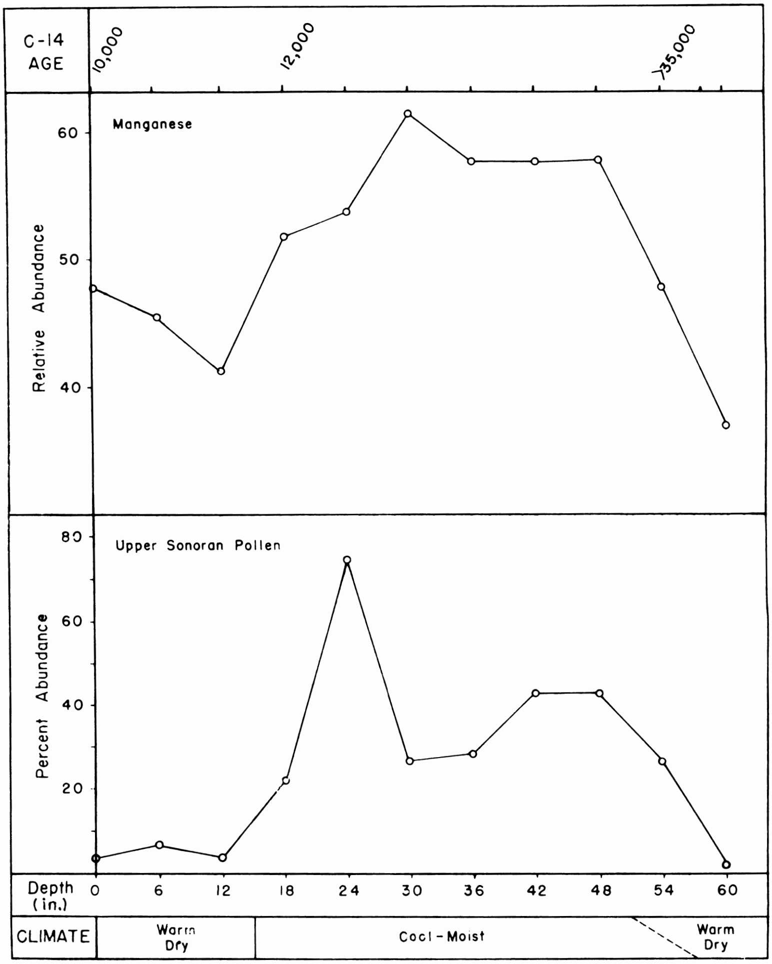

Fig. 7. Abundance of manganese (upper curve) and of Upper Sonoran pollen (lower curve). In each case high values reflect relatively cooler and/or wetter climates; low values reflect drier and/or warmer climates. Radiocarbon age in years before present at the top. The manganese curve was obtained by emission spectrography (see text). For absolute manganese values see footnote in trace element chapter, added in proof. The percent abundance of Upper Sonoran taxa is the sum of *Artemisi*, *Ribes*, Caprifoliaceae, *Juniperus*, *Pinus*, *Betula*, and Gramineae.

of variation. In general the two curves follow each other. Warm-dry conditions occurred at levels 60, 54, 12, 6, and 0; cool-moist conditions occurred from level 48 through 18.

Both curves indicate an arid maximum at level 12; this may represent the Alleröd interval. The manganese curve suggests a slight climatic reversal above level 12, as might be expected if the effect of Upper Dryas-Valders age cooling was felt in the Southwest. Support for such a change is not evident in either the pollen record or in Laudermilk and Munz' study of surface dung.

Possibly here, and elsewhere in the profile, manganese is a more sensitive indicator of climatic change than is pollen composition.

Our present climatic sequence may help to resolve a discrepancy in climatic history as interpreted by Wilson (1942) and Laudermilk and Munz (1938). From their studies of plant remains the latter concluded that " . . . when the ground sloths inhabited Rampart and Muav Caves, the flora and presumably the climate were essentially the same as those of the region today" (p. 278). This agrees with the pollen analysis of superficial layers, which we assume were the source of dung studied by Laudermilk and Munz.

Wilson (1942) commented on the presence of mammals (*Marmota, Oreamnos*) thought to be of boreo-montane distribution. Most of these specimens came from deeper levels of the cave, and thus would fall mainly into pollen zone (b), a period of cooler or wetter conditions. Undated evidence of a past cooler, wetter climate can also be adduced from the quantities of travertine left by former springs and seeps in the vicinity.

Wilson reported a cranium of the Lower Sonoran lizard, the chuckwalla (*Sauromalus*) at a depth of five feet. This is in accord with our evidence of a warm-dry climate during the initial phase of cave filling.

Attempts at more critical comparison between megafossil, microfossil, and biogeochemical evidence must await future excavation. At present we can identify a threefold climatic sequence in the fossil record of Rampart Cave: warm-dry, cool-moist, warm-dry.

EXTINCTION OF GROUND SLOTHS

The cause of disappearance dominates speculation about *Nothrotherium* and other gravigrades. How can this phenomenon be explained?

In studies of *Mylodon* dung from Patagonia, Auer (1954) and, especially, Salmi (1955) adopted biogeochemical and palynological methods in an effort to resolve the problem. Apparent copper and cobalt deficiency led Salmi (p. 332) to conclude that " . . . the resulting deficiency diseases in all probability had a decisive effect later by leading to their complete extinction in all parts of the globe."

Although we have been unable to sustain Salmi's interesting hypothesis, we acknowledge that his pioneering and provocative paper inspired our present studies of sloth dung. Before evaluating our findings with regard to copper and cobalt we will attempt a general scrutiny of the extinction record as it applies to ground sloths. The phenomenon involves basic questions of Pleistocene biogeography (Martin, 1958). Extinction of the Pleistocene megafauna is a chronological event widely used in stratigraphy, and the problem is of practical as well as theoretical importance. Particularly significant are the terminal dates of survival, the rates of gravigrade extinction, the ecology of *Nothrotherium* as deduced from its feeding habits, and the ecology of the living Pilosa, the tree sloths and anteaters.

Chronology

Radiocarbon dates of sloth dung from surface layers in Mylodon, Palli Aike, Gypsum, and Rampart Caves are remarkably concordant (table 1). They provide a terminal survival date of about 8500 B.P. for both *Mylodon* in Chile and *Nothrotherium* in the Southwest. The association of ground sloths and ceramics in the West Indies (Harrington, 1921; Aguayo, 1950) evidences survival there into late postglacial time. A similar claim for Sandia Cave, New Mexico (Hibben, 1941) has not been supported by findings elsewhere in the Southwest.

At present the stratigraphic record indicates that most, perhaps all, Pleistocene ground sloths flourished throughout the period of climatic changes, surviving four glacial and three interglacial intervals. They disappeared during the early postglacial period. West Indian sloths may have been the last survivors. On this basis it seems impossible to attribute ground sloth extinction to climatic change.

The Fossil Record

In the Pleistocene fourteen genera of ground sloths ranged from Alaska (Stock, 1942), and Northwest Territories (Stock and Richards, 1949) throughout North America, the Greater Antilles, Central and South America to Ultima Esperanza. Like the other Xenarthra, the Pilosa underwent their initial evolution in South America. They appear in North American deposits by the late Miocene or early Pliocene (Simpson, 1945). Among the native South American Tertiary mammals (liptoterns, notoungulates, old native rodents, marsupial carnivores, etc.), only the edentates invaded North America extensively.

Invasion of South America by Holarctic herbivores (perissodactyls, artiodactyls, lagomorphs, proboscideans) and their predators (modern carnivores) is generally held accountable for extinction of various native mammals (Simpson, 1950). Such an inference will not readily explain edentate extinction.

All sloths possess a peculiar dentition lacking enamel, an inturned foot structure insuring slow gait, and many primitive anatomical characteristics usually lost in advanced members of other orders. Their odd morphology has not inspired confidence in their evolutionary potential. "It would seem impossible that they could have survived and evolved in any reasonably competitive atmosphere or environment" (Gazin, 1956, p. 341). Nevertheless the fossil record reveals that ground sloths did just this. Throughout the late Cenozoic in both hemispheres they coexisted with a highly varied modern ungulate fauna.

Among the large New World herbivores the Pilosa are unique in reaching the West Indies. This feat may be explained in terms of the well-known swimming ability of tree sloths. Invasion across water barriers of both continental North America and the West Indies constitutes further evidence of their adaptability.

Ecologically, the ground sloths were euryoecic, occupying the Sonoran and Mojave Deserts (*Nothrotherium*), the temperate mesophytic forests of eastern and western North America (*Paramylodon, Megalonyx*), the subarctic taiga of Alaska and northern Canada (*Megalonyx*), the cool steppe of southern Patagonia (*Mylodon, Glossotherium*), as well as various tropical savannas and forests which are often assumed to have been their preferred habitat.

A generalized scheme for xenarthran evolution, adapted with little change from Simpson (1931), is shown in figure 8. Rates of extinction are plotted by dividing the number of genera last recorded in various geological epochs by the elapsed time for each. Unless the early fossil record of this group is found to be vastly richer than presently known (for example, 170 instead of 24 generic extinctions in the Miocene), there is only one epoch of strikingly high extinction rate, the Pleistocene. The group did not decline gradually in the Late Cenozoic or (although this is not shown in fig. 8) in the Early Pleistocene. In the Late Pleistocene it disappeared suddenly.

Paleoecology of Nothrotherium

All ground sloths were herbivores, as are living tree sloths. In view of their peculiar dentition it would seem improbable that they could have grazed extensively. Nevertheless, Eames (in Lull, 1930) found leaves, stems, and inflorescences of grasses and sedges in the dung of *Mylodon*, an assemblage quite different from that Eames encountered in dung of New Mexican *Nothrotherium*. Salmi (1955) found mainly herb pollen in *Mylodon* excrement.

Unlike *Mylodon, Nothrotherium* was a browser. Individuals at Gypsum Cave had fed on yucca (Laudermilk and Munz, 1934). Those at Rampart and Muav Caves had devoured cholla cactus, creosote, saltbush, and various herbs; *Ephedra* stems filled much of the dung balls (for complete list see table 2). Crystals of calcium oxalate, a secondary plant substance typical of Cactaceae and certain other plants, constituted over 50% of the fine-sieved fraction of dung from Gypsum Cave. In New Mexican coprolite Eames (1930) found abundant dicotyledonous twigs, especially of the mallow *Sphaeralcea*.

A capacity for browsing extensively on the desert shrubs consumed by *Nothrotherium* is not shared by existing large mammals, native or introduced. *Larrea* is shunned; *Gutierrezia* and *Chrysothamnus* poison domestic livestock; yucca fibers may cause compaction; oxalate crystals cause hemorrhage in sheep. Apparently these plants were among the normal diet of ground sloths. Thus the extinction of *Nothrotherium* must be considered ecological loss without replacement, an anomalous event that is rare but not unknown in the fossil record (e.g. mosasaurs in the Cretaceous).

Before dung studies had appeared, the gross morphology of *Nothrotherium shastense* led a foremost specialist of the group to consider it " . . . an animal living almost habitually in the dense jungles and forests or in regions having a heavy stand of timber" (Stock, 1925, p. 34). It is sobering to find that skeletal features are not completely reliable in framing deductions about habitat. On the other hand, Stock was correct in surmising that certain species of *Nothrotherium* must have inhabited mesic forests or savannas. The record of the genus in Brazilian caves obliges us to include the moist tropics within its domain. Probably it evolved from the moist tropics into the arid Southwest.

Other features of life history are not revealed by the fossil record. Clues to behavior and physiology of the extinct sloths may be found among their living relatives.

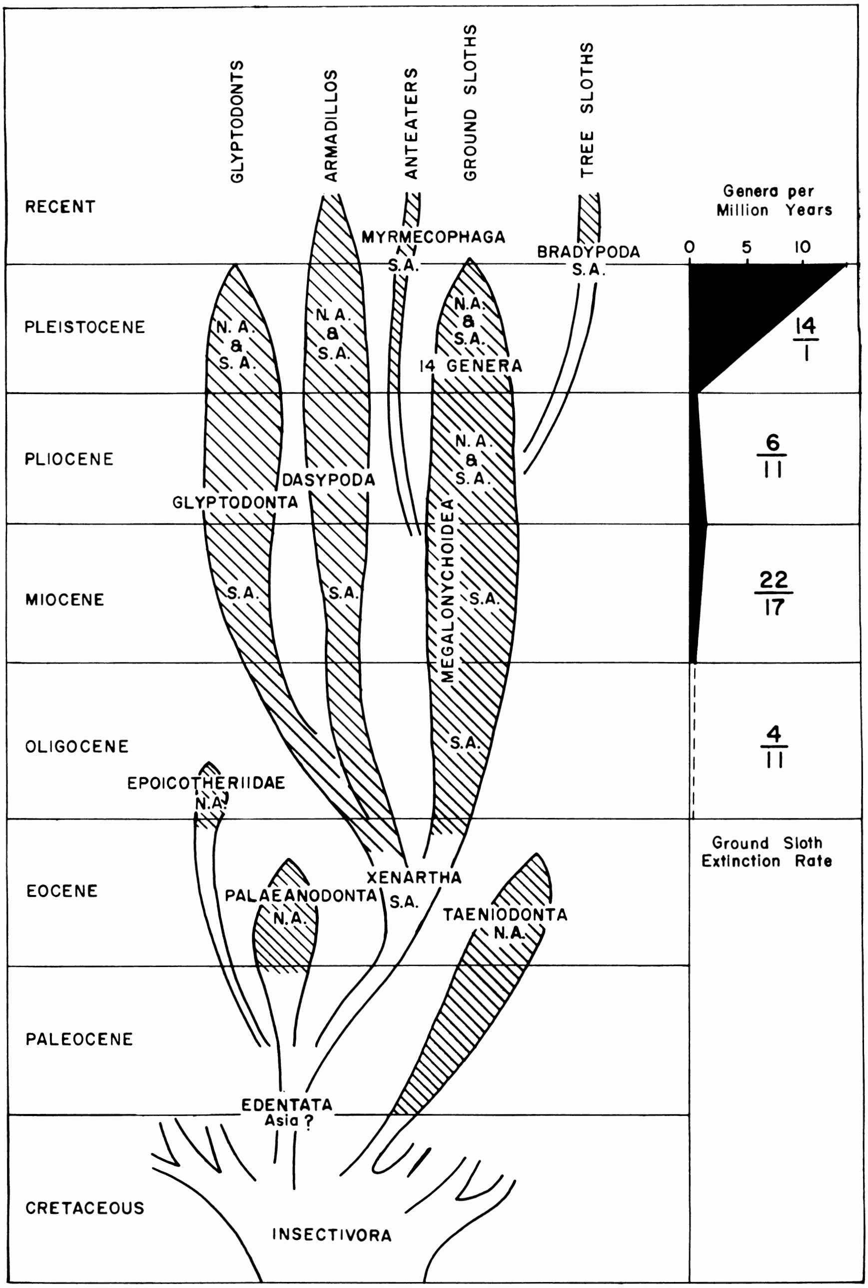

Fig. 8. Phylogeny of the Xenarthra. Ground sloth (Megalonychoidea) extinction rates shown for various periods of the Tertiary (adapted from Simpson, 1931 and 1945).

TABLE 2

Diet of the Ground Sloth, *Nothrotherium shastense*

Location and source:	*Aden Crater, New Mexico*	*Gypsum Cave, Nevada*	*Rampart Cave, Arizona*	
	Eames, 1930	Laudermilk and Munz, 1934	Laudermilk and Munz, 1938	Present study
1. Polypodiaceae	d			d
2. _Adiantum capillus-veneris_			a	
3. *_Pinus_				d
4. *_Juniperus utahensis_		a		c (gen.)
5. _Ephedra nevadensis_		a	a	c (gen.)
6. _Typha_		d		
7. Gramineae		a		c
8. _Aristida_			a	
9. _Phragmites communis_			a	
10. Cyperaceae				d
11. _Yucca brevifolia_		a,b (genus)		
12. _Y. baccata_		a		
13. _Y. mohavensis_		a	a (Mauv)	
14. _Nolina_			a	
15. *_Agave utahensis_		a		
16. _Populus_			a	
17. *_Juglans_				d
18. *_Betula_				d
19. *_Quercus_				d
20. Chenopodiaceae	a			d
21. _Atriplex_	a	a	a	
22. Nyctaginaceae				b
23. Cruciferae	a			
24. *_Ribes_				b
25. _Prunus_			a	
26. _Cassia_			a	
27. _Larrea tridentata_		a,b	a	b
28. Malvaceae		b		b
29. _Sphaeralcea_	a	a	a	
30. _Sida_	?			
31. _Petalonyx_		a		
32. _Opuntia_			a	
33. Onagraceae		b		b
34. _Oenothera_		a		
35. _Fraxinus_			a	
36. Polemoniaceae				b
37. _Physalis_			a	
38. *Caprifoliaceae				b
39. Compositae	a	a,b		b,c
40. _Gutierrezia_	a			
41. _Chrysothamnus_		a		
42. *_Artemisia_				c
Major portion of diet:	dicotyledonous angiosperms	_Yucca, Agave_	_Ephedra_	
Upper Sonoran elements (*)	0%	24%	0%	42%

a=plant parts identified in dung

b=zoögamous pollen

c=anemogamous pollen, abundant

d=anemogamous pollen or spores, not abundant

Living Pilosa

Flower and Lydekker (1891) pointed out that the extinct ground sloths were morphologically intermediate to the two surviving families of Pilosa. They combined the head and dentition of the tree sloths (Bradypodidae) with the vertebral structure, limbs, and gait of the giant anteater (*Myrmecophaga*). Although it will climb under duress (Krieg, 1939), *Myrmecophaga* is more terrestrial than other anteaters. It is about two-thirds the total length of *Nothrotherium*, and weighs up to 43 kg. Presumably those characteristics shared by both anteaters and tree sloths are highly likely to have typified *Nothrotherium* and other ground sloths.

Living Pilosa have certain traits unusual among mammals, such as a relatively low body temperature, a low basal metabolism, and limited thermal regulation. Tree sloths and the arboreal anteater (*Cyclopes*) are remarkable in their tendency toward poikiliothermism. The extreme hypoactivity, also typical of tree sloths and *Cyclopes*, is not characteristic of *Myrmecophaga*. Nevertheless the giant anteater is not inclined to escape enemies by flight (Krieg, 1944).

Despite its tropical habitat, the three-toed sloth (*Bradypus*) is quite vulnerable to hyperthermy and will succumb in captivity if no shade is provided (Britton, 1941). Under direct sun at 35°-40°C the rectal temperature of an individual observed by Britton (1941) rose to 40°C and the animal expired after about two hours. The two-toed sloth (*Choloepus*) ranges up to 8000 feet where it withstands the penetrating damp cold of the montane fog forests (Britton, 1941). In Chiriqui Province, where water freezes in the dry season, Enders (1940) reported two-toed sloths between 6000 and 7000 feet. "Adult sloths inhabiting these areas were found to differ from those taken at sea level, chiefly in the length and quality of the hair . . . very much like dressed beaver, both in texture and quality" (Enders, p. 5). It would seem that assumptions about sloths being climatically restricted to the warm tropics must be abandoned.

Living Pilosa are relatively independent of water. Britton (1941, p. 202) comments: " . . . sloths would not need to eliminate heat rapidly by sweating under normal conditions in their tropical forest environment." He found that captive sloths will take water regularly, lapping with the tongue like a dog. This is not a necessity in nature; Krieg (1939) claimed they never drink and that sufficient water is absorbed from their forage to provide a water balance. The feces are relatively dry, an observation that may help explain the unleached nature of Rampart Cave dung. Beebe (1926) mentions the large bladder of *Bradypus* and claimed he never saw one drink: " . . . it is probable that it obtains sufficient moisture in the tissues of the leaves."

Less is known regarding water consumption in *Myrmecophaga*, an animal inhabiting tropical savannas and presumably exposed to greater thermal stress than the tree sloths. Honigmann (1935) was unable to confirm Schomburgk's claim that this animal sweats profusely. Krieg (1944) reported that in the Matto Grosso the giant anteater licks dew from plants and may occasionally drink.

Large diurnal grassland herbivores such as horses and artiodactyls generally require a water supply independent of their food source. On the other hand, many of the more successful of the desert herbivores are dependent only on metabolic water and evade thermal stress by nocturnalism, burrowing habits, and other behavioral adaptations. It seems quite likely that some of these adaptive features were shared by *Nothrotherium*, which could have derived most of its water from cactus, yucca, and other succulents, and perhaps sought refuge in caves or rock shelters in the day. The nature of dung in Rampart Cave indicates no leaching by urine.

Gregariousness is highly developed in most large cursorial herbivores inhabiting savannas, grassland, or tundra. In evading predators and protecting young such behavior has an adaptive advantage. On the basis of its morphology and fossil record it appears that *Nothrotherium* was solitary. In captivity tree sloths are decidedly antisocial (Beebe, 1926; Britton, 1941; Enders, 1935). According to Cabrera and Yepes (1940) the anteaters tend to be solitary except in the mating season or when the females are carrying their single young.

Although tree sloths can scarcely be considered gregarious, they do have certain remarkable social behavior. In a park at Santos, Krieg (1939) observed that four three-toed sloths used a common dung midden, climbing down from their trees to defecate in turn. He was unable to explain this behavior, which resembles that of the vicuna and guanaco. If *Nothrotherium* voided in similar fashion, it is likely that the dung deposits in Rampart Cave grew as isolated midden mounds. In such event the stratigraphic sequence in one part of the cave would not be comparable to that elsewhere.

In tree sloths the passage of food through the digestive tract is extremely slow. Britton (1941, p. 32) reported the stomach contents may exceed 25% of the body weight. Food remains in the stomach 70 to 90 hours and requires a week to traverse the alimentary canal (Britton, 1941; Enders, 1940). The anteater *Tamandua* stores fecal material before defecation; a peculiar fecal sheath may prevent absorption of decomposition products (Enders, 1935, p. 494). Possibly the hardened mucus varnish enclosing *Nothrotherium* dung (Laudermilk and Munz, 1934) had a similar function. Both the dry nature of sloth feces, commented on by Krieg, and the mucus sheath reduce the chance of leaching and chemical alteration between strata after deposition.

One aspect of sloth ecology neglected by most authors is the raison d'être of its success. Buffon felt that "one more defect and they could not have existed." This anthropomorphism was quashed by Beebe (1926) who suggested that a sloth in Paris would survive longer than Buffon in a tropical forest hanging by his limbs. Subsequent authors have also taken a more positive view in appraising the sloth's morphology. Ecologically speaking, the main point is the vast trophic opportunity available to any herbivore able to harvest energy from the photosynthetic surface of a forest. Except through secondary sources as fruits, seeds, saplings, or bark, this energy is untapped in any systematic way by other New World vertebrate herbivores.

It is quite probable that *Nothrotherium* enjoyed a similar adaptive advantage, browsing on desert vegetation such as cresote bush, yucca, and cactus that many of its mammalian competitors rejected.

In brief, the ecology of living gravigrades reveals no clues to explain extinction of the ground sloths.

Trace Elements and Extinction

Salmi (1955) has proposed that trace element deficiency, induced by drought in Late-glacial time, triggered the demise of *Mylodon* and other sloths. He found the amount of certain elements (copper, selenium, cobalt, silver) to be lower in the feces of *Mylodon* than in that of certain animals investigated in Finland (laboratory rhesus monkeys, native *Alces* and *Lepus*). In dung from South American caves, he detected about one-tenth the copper found in feces of the Finnish animals. Monkeys fed bread, carrots, and potatoes with an ash content of about 5% voided feces with an ash content of about 20%. The proportions of most trace elements increased in about the same ratio as did the ash content. Depletion of trace elements during digestion was slight. To Salmi the pronounced low values for certain elements in sloth feces seemed to indicate their scarcity in the food ingested by these animals. On this basis he concluded that the diet of *Mylodon* was critically deficient in cobalt, copper, and possibly other elements.

Salmi's experimental methods and conclusion raise interesting questions: (1) Are trace element diseases important in limiting populations of animals? (2) Are native as opposed to introduced species affected? (3) Are feces adequate indicators of dietary deficiency?

With regard to the first, deficiency diseases in domestic ruminants are well known (Orr, 1929; Russell, 1944; Stiles, 1946; Underwood, 1956). Ruminants require cobalt to enable bacteria of the rumen to synthesize vitamin B12, which contains this element. Most cases of copper and cobalt deficiency occur in Africa, Australia, and New Zealand where stock raising was developed with the introduction of fastgrowing European breeds. These have higher mineral requirements than the native herbivores. Attempts to induce copper-cobalt deficiency diseases in animals other than ruminants have failed. Rats and rabbits reared and maintained on a deficient diet for several generations gave no indication of abnormality (Tompsett, 1940; Underwood, 1956).

Regarding the second question, our literature search unearthed no examples of copper-cobalt deficiency disease limiting native herbivores in their natural habitat. Such examples must appear before any such hypotheses can be advanced.

It is known that animals living under deficient soil conditions seek food of high mineral content and, if necessary, are able to supply themselves with minerals directly from the ground (Orr, 1929). If sheep afflicted with copper-cobalt deficiency are removed to a plowed field in an area where the deficiency does not occur, they will recover themselves, even though they are fed grass cut and transported from their old pasture (McNaught and Paul, 1939). On poor pastures with low mineral content the forage selected by animals is richer in minerals than that left uneaten (Orr, 1929).

In their native environment and on an open range it would appear extremely unlikely that large herbivores would fail to fill their mineral requirements under any geoclimatic circumstances.

Concerning question three, Salmi found that only very small amounts of trace elements were absorbed by laboratory monkeys in the process of digestion. This led him to conclude that absence of an element in the feces can be interpreted as absence of the same element in the food. However, Underwood (1956) has shown that under conditions of deficiency selective concentration of minerals can occur. Animals and man may absorb up to 90% of certain trace elements in their diets. Even in high quality diets man absorbs 73 to 97% of the cobalt ingested, eliminating about 14% in the feces and an average of 67% in the urine. If *Nothrotherium* depended upon cobalt, it probably absorbed most of that available and eliminated only a few percent, which would be undetectable with instruments of 1 ppm sensitivity limit. More sensitive techniques (neutron activation) must be applied to this problem. But there is no evidence that sloths ever depended upon cobalt or copper to a greater extent than other non-ruminants, which are quite independent of these two elements.

It appears that neither the stratigraphic record at Rampart Cave nor our knowledge of deficiency diseases indicate copper-cobalt shortage as a possible cause of sloth extinction.

The Durable Mystery

Taking stock of the fossil and ecological record we note the following: (1) *Nothrotherium shastense* browsed on a variety of xeric and semixeric Southwestern shrubs; its South American relatives lived in a tropical environment. (2) The chronology of extinction indicates that most ground sloths survived the glacial period into early postglacial time. (3) The Pliocene radiation of Pilosa northward into North America, their diversified browsing habits in both forest, savanna, and desert, and their wide range through a variety of climatic zones do not suggest overspecialization, senescence, or vulnerability to environmental stress.

The interesting suggestion of Salmi that copper and cobalt deficiency will account for the extinction phenomenon is unsupported by trace element analysis of *Nothrotherium* dung in Rampart Cave.

We conclude that, despite their apparent clumsy build and bizarre morphology, the Pilosa were occupying a very important ecological role—one to which most other mammalian herbivores were less perfectly adapted. We are unable to identify a superior large browsing mammal that might have replaced *Nothrotherium* in postglacial time. Its niche as a desert herbivore remains unfilled today. On all biological evidence this sloth should have survived into historic times.

In the Late Pleistocene the archaeological record shows that man and sloth were contemporaneous, a circumstance inconclusive in itself. Nevertheless, extinction might become understandable if Early Man were identified as the main cause. We find no other.

REFERENCES

Aguayo, C. G., 1950, Observaciones sobre mamiferos cubanos extinguidos: Historia nat. soc. Felipe Poey Bol. [Havana], v. 1, p. 121-134.

Auer, V., 1954, Suomalainen tutkimus Tulimaassa ja Patagoniassa: Finnish research in Tierra del Fuego and Patagonia: Terra, v. 1, p. 1-21.

Beebe, W., 1926, The three-toed sloth: Zoologica, v. 7, p. 1-67.

Britton, S. W., 1941, Form and function in the sloth: Quart. Rev. Biology, v. 16, p. 13-34, 190-207.

Cabrera, A., and Yepes, J., 1940, Mamiferos Sud-Americanos: Buenos Aires, Historia Natural Ediar, Compania Argentina de Editores, 370 p.

Eames, A. J., 1930, Report on ground sloth coprolite from Dona Ana County, New Mexico: Am. Jour. Sci., 5th ser., v. 120, p. 353-356.

Enders, R. K., 1935, Mammalian life histories from Barro Colorado Island, Panama: Harvard Coll. Mus. Comp. Zoology Bull., v. 78, p. 385-502.

———— 1940, Observations on sloths in captivity at higher altitudes in the tropics and in Pennsylvania: Jour. Mammology, v. 21, p. 5-7.

Flower, W. H., and Lydekker, R., 1891, An introduction to the study of mammals living and extinct: London, Adam and Charles Black.

Gazin, C. L., 1956, Exploration for the remains of giant ground sloths in Panama: Smithsonian Inst. Ann. Rept., Pub. 4272, p. 341-354.

Harrington, M. R., 1921, Cuba before Columbus: New York, Indian Notes and Monographs, Museum of the American Indian, Heye Foundation.

———— 1933, Gypsum Cave, Nevada: Southwest Mus. Papers, v. 8, p. 1-197.

Hibben, F. C., 1941, Evidences of early occupation in Sandia Cave, New Mexico: Smithsonian Misc. Colln., v. 99, p. 1-44.

Honigmann, H., 1935, Beobachtungen am Grossen Ameisenbären: Zeitschr. Saugetierkunde, v. 10, p. 78-104.

Kearney, T. H., and Peebles, R. H., 1951, Arizona flora: Berkeley, University of California Press.

Krauskopf, K. B., 1955, Sedimentary deposits of rare metals: Econ. Geology, 50th Anniv. Vol., p. 1-463.

Krieg, H., 1939, Begegnungen mit Ameisenbären und Faultieren in freien Wildbahn: Zeitschr. Tierpsychologie, v. 2, p. 282-292.

———— 1944, Ameisenbären: Naturwissenschaften, v. 32, p. 40-43, p. 283-290.

Laudermilk, J. D., and Munz, P. A., 1934, Plants in the dung of *Nothrotherium* from Gypsum Cave, Nevada: Carnegie Inst. Washington. Pub. 453, p. 29-37.

———— 1938, Plants in the dung of *Nothrotherium* from Rampart and Muav Caves, Arizona: Carnegie Inst. Washington. Pub. 487, p. 271-281.

Little, E. L., 1950, Southwestern trees: U. S. Dept. Agriculture Handbook 9, 109 p.

Lull, R. S., 1930, The ground sloth, *Nothrotherium*: Am. Jour. Sci., 5th ser., v. 20, p. 344-352.

Martin, P. S., 1958, Pleistocene ecology and biogeography of North America: in Zoogeography, Am. Assoc. Adv. Sci. Pub. 51, p. 375-420.

McNaught, K. J., and Paul, G. W., 1939, Seasonal variations in cobalt content of North Island: New Zealand Jour. Sci. and Technology, sec. B, v. 21, p. 95-101.

Mercer, H. C., 1897, The findings of the remains of the fossil sloth at Big Bone Cave, Tennessee, in 1896: Am. Philos. Soc. Proc., v. 36, p. 36-70.

Nichol, A. A., 1952, The natural vegetation of Arizona: Arizona Univ. Tech. Bull. 127, p. 186-230.

Orr, J. B., 1929, Minerals in pastures and their relation to animal nutrition: London, H. K. Lewis and Co., Ltd.

Rusconi, C., 1949, La supuesta existencia de milodontes en la Patagonia austral (*Milodon listai*) : Mus. Historia Nat. de Mendoza Rev., v. 3, p. 252-264.

Russel, F. C., 1944, Minerals in pasture deficiencies and excess in relation to animal health: Aberdeen, Scotland, Imperial Bureau of Animal Nutrition, Tech. Comm. no. 15.

Salmi, M., 1955, Additional information on the findings in the *Mylodon* Cave at Ultima Esperanza: Acta Geographica, v. 14, p. 314-333.

Simpson, G. G., 1931, *Metacheiromys* and the Edentata: Am. Mus. Nat. History, Bull. 59, p. 295-381.

———— 1945, The principles of classification and a classification of mammals: Am. Mus. Nat. History, Bull. 85, p. 1-350.

———— 1950, History of the fauna of Latin America: Am. Scientist, v. 38, p. 361-389.

Snedecor, G. W., 1956, Statistical Methods: Ames, Iowa, Iowa State College Press.

Sokoloff, V. P., and Carter, G. F., 1952, Time and trace metals in archaeological sites: Science, v. 116, p. 1-5.

Stiles, W., 1946, Trace elements in plants and animals: Cambridge, England, Cambridge University Press.

Stock, C., 1925, Cenozoic gravigrade edentates of Western North America: Carnegie Inst. Washington. Pub. 331, 206 p.

——— 1942, A ground sloth in Alaska: Science, v. 95, p. 552-553.

Stock, C. and Richards, H. G., 1949, A *Megalonyx* tooth from the Northwest Territories, Canada: Science, v. 110, p. 709-710.

Tompsett, S. L., 1940, Factors influencing the absorption of iron and copper from the alimentary tract: Biochem. Jour., v. 34, p. 961-969.

Underwood, E. J., 1956, Trace elements in human and animal nutrition: New York, Academic Press.

Webb, D. A., and Fearon, W. R., 1937, Studies on the ultimate composition of biological material: Royal Dublin Soc. Sci. Proc. 21, p. 487-539.

Wilson, R. W., 1942, Preliminary study of the fauna of Rampart Cave, Arizona: Carnegie Inst. Washington. Pub. 530, p. 169-185.