References and Notes

1. R. M. Gold, *Physiol. Behav.* **2**, 211 (1967); G. D. Ellison, C. A. Sorenson, B. L. Jacobs, *J. Comp. Physiol. Psychol.* **70**, 173 (1970); S. P. Grossman, *ibid.* **75**, 23 (1971).
2. P. Teitelbaum and A. N. Epstein, *Psychol. Rev.* **69**, 74 (1962); J. F. Marshall, B. H. Turner, P. Teitelbaum, *Science* **174**, 523 (1971).
3. W. L. Rodgers, A. N. Epstein, P. Teitelbaum, *Am. J. Physiol.* **208**, 334 (1965); A. N. Epstein, in *Progress in Physiological Psychology*, E. Stellar and J. M. Sprague, Eds. (Academic Press, New York, 1971), vol. 4, pp. 263–317.
4. H. P. Zeigler and H. J. Karten, *J. Comp. Neurol.* **152**, 59 (1973).
5. T. L. Powley and R. E. Keesey, *J. Comp. Physiol. Psychol.* **70**, 25 (1970).
6. H. P. Zeigler, *Science* **182**, 1155 (1973).
7. R. Smith, *J. Comp. Neurol.* **148**, 423 (1973).
8. L. J. Pellegrino and A. J. Cushman, *A Stereotaxic Atlas of the Rat Brain* (Appleton-Century-Crofts, New York, 1967). As an approximate set of coordinates for LTr we have used anterior, −5.8; lateral, 1.0; dorsal-ventral, 9.0. However, the chances of a successful placement are markedly improved if the lesions are placed under electrophysiological control.
9. Similar deficits have been produced by peripheral trigeminal deafferentation in the rat. Lesions of the Gasserian ganglion and the Vth nerve, not involving the trigeminal motor system, were produced under electrophysiological control by using an intracranial approach to the nerve (H. P. Zeigler, A. Marwine, H. J. Karten, paper presented at Eastern Psychological Association, Philadelphia, 18 April 1974).
10. R. Reyes, S. Finger, J. Frye, *Behav. Biol.* **8**, 807 (1973).
11. S. W. Parker and S. M. Feldman, *Exp. Neurol.* **17**, 313 (1967); M. Lyon, M. Halpern, E. Mintz, *Acta Neurol. Scand.* **44**, 323 (1968); U. Ungerstedt, *Acta Physiol. Scand. Suppl.* **367**, 95 (1971).
12. The deficits seen after injections of 6-hydroxydopamine were originally attributed to a selective destruction of neurons in medial substantia nigra. However, more recent studies suggest that such injections produce severe, nonspecific neurotoxic effects distributed over a considerable area. It thus seems likely that the effects upon ingestive behaviors seen after chemical lesions of these regions are due to the almost inevitable damage to the overlying LTr [C. Sotelo *et al.*, *Brain Res.* **58**, 269 (1973); L. L. Butcher and C. K. Hodge, paper presented at Society for Neuroscience, San Diego, 1973].
13. W. Wrywicka and R. W. Doty, *Exp. Brain Res.* **1**, 152 (1969); A. Routtenberg and R. S. Kane, *Can. J. Psychol.* **20**, 343 (1966).
14. W. I. Welker, *Brain Behav. Evol.* **7**, 253 (1973).
15. C. T. Snowdon, *J. Comp. Physiol. Psychol.* **69**, 91 (1969); H. P. Zeigler, *Science* **182**, 1153 (1973).
16. A. N. Epstein, in *Handbook of Physiology*, section 6, *Alimentary Canal*, E. C. Code, Ed. (American Physiological Society, Washington, D.C., 1967), vol. 1.

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Death of American Ground Sloths

Abstract. *Organic remains, especially dung, of extinct ground sloths provide ideal material for radiocarbon dating. Rampart Cave, Arizona, revealed periodic occupation at intervals by the Shasta ground sloth from before 40,000 years ago until 11,000 years ago. Dates from other caves in the arid Southwest indicate that the Shasta ground sloth disappeared at or very soon after the time of Clovis big game hunters. Ground sloth remains in South America are slightly younger. The timing of ground sloth extinction is in accord with the model of explosive overkill.*

Among the most remarkable of the organic deposits known to survive, rivaling the frozen carcasses of mammoths and woolly rhinoceroses in the Arctic, are the dung balls, hair, and even hide of extinct ground sloths. Under conditions of low humidity and uniform temperature in certain caves the dung escapes fungal, bacterial, or insect attack and endures for at least 10,000 years. The deposits look and smell fresh, leading paleontologists of the last century into the belief that the ground sloths were not extinct. Radiocarbon dating has supported more conservative views and made possible a more critical assessment of ground sloth chronology.

In the Northern Hemisphere, ground sloth dung of *Nothrotheriops* (formerly *Nothrotherium*) *shastense* Sinclair is known from half a dozen caves in the arid Southwest. The least disturbed stratified deposit is found within the Grand Canyon at Rampart Cave (elevation, 525 m; 36°06′N, 113°56′W) (*1*). In the Southern Hemisphere the best known sloth dung deposit is Gruta del Milodon or Eberhardt Cave, 30 km north-northwest of Puerto Natales, Chile. More recently ground sloth dung has been found in Cuevo del Indio near San Rafael, Argentina (*2*). These are the only two South American deposits of ground sloth dung known to us.

Our purpose was to determine the time of ground sloth extinction, refine the provisional radiocarbon chronology of organic deposits in Rampart and other caves established a decade ago (*3*), and compare the results in the Northern Hemisphere with those from the Southern Hemisphere. Thirteen new radiocarbon dates are now available from Rampart Cave alone, with a total of 30 on organic remains from various ground sloth cave deposits.

We sought samples younger than the 10,000-year age reported by Martin *et al.* (*3*). In Rampart Cave, Long and Martin collected four apparently undisturbed dung balls from the surface of the deposit. Three of the softball-sized (7 to 10 cm in diameter) specimens were found about 3 m east of a trampled dung surface dated on both humic and nonhumic fractions at about 10,000 years in age (L-473A).

Rather than being younger, the new dates (A-1041, 1066, 1067, and 1068) are significantly older. Close examination of the profile point where Shutler collected L-473A (*3*) revealed that postglacial or modern wood rat (*Neotoma*) feces and food material was mixed into trampled and disaggregated dung fragments of *Nothrotheriops*. The possibility of wood rat contamination at this point is greater than in the case of the unaltered dung balls that are the source of our new dates.

In addition, we attempted to replicate I-442, 10,400 ± 275 (unpublished date by Teledyne Isotopes) by dating the remaining half of a dung ball so labeled in Remington Kellogg's (Smithsonian Institution) Rampart collection. Our result was significantly older, suggesting that the two dates were not from the same specimen.

We recollected samples from a profile in Kellogg's trench originally collected by Shutler. Except for the surface dates, our samples replicate or extend the original Lamont dates (Table 1). At the position of the profile, a buried wood rat (*Neotoma*) midden between 63 and 98 cm divides the sloth dung deposit. It is formed of stocks, seeds, and fecal pellets of rodents and artiodactyls with occasional animal bones (*Marmota, Oreamnos*). Sloth dung above 61 cm was deposited from about 12,500 to 11,000 years ago. We estimate that the main part of the deposit covers 180 m^2 with the upper sloth dung unit averaging no more than 0.5 m in thickness. The entire late-glacial dung layer represents an average annual rate of deposition of 0.1 m^{-3}, perhaps less than a week's elimination of one adult sloth (*4*). There is no suggestion of a decline in deposition rate toward the top of the deposit as might be expected if the population were coming under stress gradually.

These three units, the upper sloth (A), the pack rat (B), and the lower

sloth (C), are traceable throughout the cave where stratification is evident. We assume they are time-equivalent. A persistent blackened layer (A_2) approximately separating into halves the upper sloth zone (A_1 and A_3) may represent another depositional pause, but we have no ^{14}C verification for this.

Portions of the pack rat midden (unit B) are composed of sticks, dung, and bones. Subunits are not traceable for more than a meter. Unit B extends from between 13,000 and 16,000 ^{14}C years ago until 24,000 years ago. It contains occasional chips of sloth dung which were probably redeposited from below by wood rats. In addition, it contains the first evidence of fecal pellets of an extinct mountain goat (*Oreamnos harringtoni*); these occur downward to the floor of the cave.

Unit C contains approximately half of the sloth dung in Rampart Cave. There are occasional layers of bat guano and blackened sloth dung. Near the center rear wall of the cave, bat guano up to 10 cm in thickness overlies the white degraded limestone of the floor of the cave. Deposition of unit C began more than 40,000 years ago and ended 32,000 years ago. Evidently sloth dung in unit C accumulated more slowly than that of unit A.

About 2 km upstream from Rampart are the three Muav caves, of which at least one contains a shallow, partly excavated deposit of sloth dung. Two samples collected near the mouth of the most easterly of the caves were dated at 11,140 and 11,290 years ago (see Table 1). We regard the dates as contemporary with the four from the top of Rampart Cave which average 11,070. The Rampart and Muav caves dates are also concordant with the other dates (Table 1) obtained in the last 10 years on ground sloth dung from Gypsum Cave, Nevada, and Aden Crater, New Mexico (*5*).

The new radiocarbon dates on surface sloth dung reveal no firm evidence for the survival of *Nothrotheriops* after 11,000 years ago. The last ground sloths disappeared around the time of the Clovis big mammal hunters, known from mammoth kills dated at 11,240 years ago (*6*).

Under the model of explosive overkill, Martin (*7*) proposes that few or no archeological associations will be found for *Nothrotheriops* and other extinct genera of the late Pleistocene. A brief but devastating coexistence of hunters and large animals, lasting no

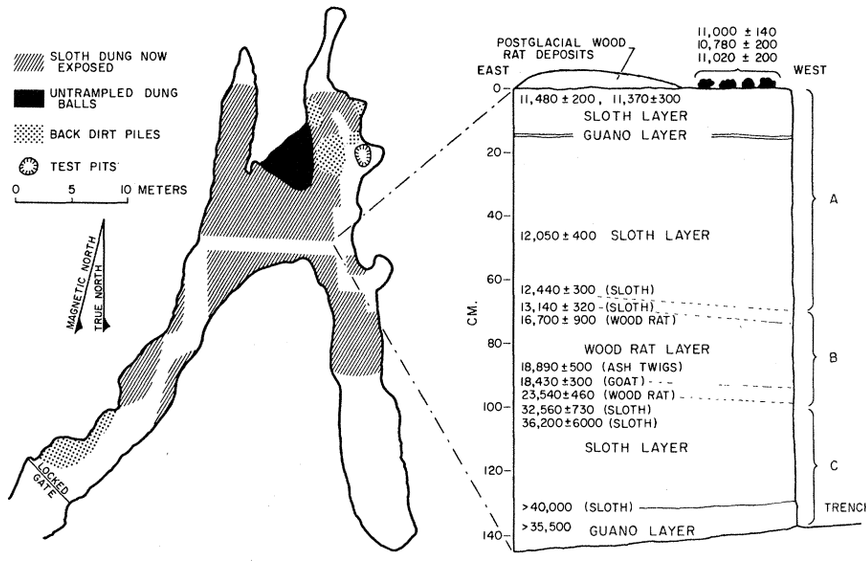

Fig. 1. Stratigraphy of the Rampart Cave sloth dung.

Table 1. Radiocarbon samples from ground sloth caves (solid carbon dates are excluded).

No.	Sample material	Location in cave	Depth (cm)*	Laboratory No.	^{14}C date (years ago)
		Rampart, Arizona			
1	Sloth dung ball	Surface		A-1066	11,000 ± 140
2		Surface		A-1067	10,780 ± 200
3		Surface		A-1068	11,020 ± 200
4		Surface		I-442	10,400 ± 275
5	Trampled sloth dung	Surface	0–5	A-1392	11,370 ± 300
6		Surface	0–5	A-1041	11,480 ± 200
7		Surface	0–5	L-473A	10,035 ± 250
8		A	46	L-473C	12,050 ± 400
9		Base of A	61	A-1070	12,440 ± 300
10	Sloth dung ball †	Unknown		A-1318	12,470 ± 170
11	Sloth dung	Top of B	67	A-1207	13,140 ± 320
12	Pack rat pellets	B	71	A-1208	16,700 ± 900
13	Twigs of ash (*Fraxinus*)	B	90	A-1356	18,890 ± 500
14	Goat dung	B	91	A-1278	18,430 ± 300
15	Pack rat pellets	Base of B	96	A-1209	23,540 ± 460
16	Sloth dung	Top of C	99	A-1210	32,560 ± 730
17		Top of C	99	A-1043	36,200 ± 6,000
18		Base of C	132	A-1042	> 40,000
19	Bat guano	Base of C	137	L-473D	> 35,500
		Muav, Arizona			
20	Sloth dung	Surface		A-1212	11,140 ± 160
21		Surface		A-1213	11,290 ± 170
		Gypsum, Nevada			
22	Sloth dung	Room 3		LJ-452	11,690 ± 250
23		Unknown		A-1202	11,360 ± 260
		Aden Crater, New Mexico			
24	Sloth dung			Y-1163B	11,080 ± 200
25	Body tissue			Y-1163A	9,840 ± 160
		Gruta del Indio, San Rafael, Argentina			
26	Sloth dung	70–80 cm, Q7		A-1351	10,740 ± 150
27		80–90 cm, Q8		A-1371	11,350 ± 180
28		1.10 cm, R8		GRW-5558	10,950 ± 60
29		70 cm, R8		A-1370	24,730 ± 860
		Cueva del Milodon, Chile			
30	Sloth dung	Unstratified		A-1390	13,560 ± 190
31	Hair and skin	Unstratified		R-4299	13,500 ± 410
32	Hide	Unstratified		A-1391	10,400 ± 330
33	Dung	Unstratified		SA-49	10,200 ± 400

* All depths listed are from same vertical profile. Values are midpoints of 3-cm depth ranges.
† Originally thought to be same specimen as I-442, but date does not verify this (see text).

more than a decade in any one region, would be largely invisible to paleontologists. A test of extinction by overkill is in the radiocarbon chronology. The apparently synchronous loss of the Shasta ground sloth with the arrival of big game hunters in Arizona and the slightly younger age of ground sloth remains in South America are in accord with the model (*7*).

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References and Notes

1. The mouth of Rampart Cave can be seen from the Colorado River just inside the Grand Wash Cliffs at the extreme lower end of the Grand Canyon, Mohave County, Arizona. It opens near the base of the Muav limestone about 200 m above river level. The scientific significance of Rampart Cave was recognized in 1936. Surface collections and two test pits yielded abundant bones of *Nothrotheriops*, mainly of young animals [R. W. Wilson, *Carnegie Inst. Washington Publ. No. 530* (1942), p. 171]. There was no evidence of prehistoric human occupation [G. C. Baldwin, *Masterkey* **20**, 94 (1946)]. Our map (Fig. 1) is based on study of the well-preserved face cut in the sloth dung in 1942 by Remington Kellogg of the U.S. National Museum.
2. J. Emperaire and E. Laming, *J. Soc. Am.* **42**, 173 (1954); H. A. Lagiglia, *ibid.* **57**, 161 (1968).
3. P. S. Martin, B. E. Sabels, D. Shutler, Jr., *Am. J. Sci.* **259**, 102 (1961).
4. Occupation was probably confined to the late winter or spring, as suggested by high counts of *Sphaeralcea* and *Ephedra* pollen in the dung (*3*).
5. A younger date on sloth hide from Aden Crater (Y-1163A) is from the same animal dated by Y-1163B. It is considered possibly contaminated by organic preservatives [E. L. Simons and H. L. Alexander, *Am. Antiq.* **29**, 390 (1964)]. Younger dates on sloth dung from Gypsum Cave (C-221, 10,455 ± 340; C-222, 8,527 ± 260) were based on the now superseded solid carbon technique of 25 years ago. Unless they can be replicated, we believe they do not constitute adequate evidence of the postglacial survival of *Nothrotheriops*. The youngest date on sloth dung from Gypsum Cave that we would accept is that of A-1202. The alleged association of sloths and prehistoric people at Gypsum Cave [M. R. Harrington, *Southwest Museum Paper No. 8* (1933)] may be questioned on the basis of 2400 and 2900 year dates on wooden artifacts found beneath sloth dung [R. F. Heizer and R. Berger, *Contr. Univ. Calif. Archaeolog. Res. Facility No. 7* (1970), p. 13]. Wood rat intrusion appears likely.
6. C. V. Haynes, in *Pleistocene and Recent Environments of the Central Great Plains*, O. Dort, Jr., and J. K. Jones, Jr., Eds. (Univ. Press of Kansas, Lawrence, 1970), p. 77.
7. P. S. Martin, *Science* **179**, 969 (1973).
8. Supported by NSF grant GA-16600 to A.L. and NSF grant GB-27406 to P.S.M. and the State of Arizona. R. Brumbaugh, A. Gottesfeld, J. E. King, D. LaRocca, E. Robbins, B. Robbins, and T. Van Devender aided at Rampart Cave; H. Lagiglia, A. Russell, and J. Russell helped collect samples in South America; S. R. Woodmansee identified and quantified the plant fragments in the dung from the sloth caves. D. Evans and other personnel of the U.S. Park Service, Boulder City, Nevada, authorized our research effort, provided access to photographs, collections, and records in their care, and authorized our visits to the caves. This is contribution 68, Department of Geosciences, University of Arizona.

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Neonatal Tolerance Induced by Antibody against Antigen-Specific Receptor

Abstract. *Specific immunologic unresponsiveness is induced by injecting adult or neonatal mice with antibody against antigen-specific receptor (antireceptor antibody). Suppression in mice treated as adults lasts several weeks, and cells from these suppressed mice respond normally in culture. In contrast, unresponsiveness induced in neonatal mice is long-lasting; cells from these mice do not respond in culture and do not affect the response of normal cells. Evidently, antireceptor antibody reversibly blocks antigen receptors in adult animals, but induces unresponsiveness in neonatal mice by depleting the clone of receptor-bearing cells.*

Classically, immunological tolerance is produced by giving antigen to neonatal animals. For antigens that persist, tolerance is long-lasting. Cells from tolerant animals are specifically unresponsive to these antigens when immunized in vitro or after transfer to irradiated syngeneic recipients (*1*). Furthermore, cells from tolerant animals usually do not affect the response of normal cells to the antigen in question (*2*). One hypothesis suggested by these findings, taken together, is that the clones of cells responsive to the antigen producing tolerance have been depleted (*3*).

Adults may be made specifically unresponsive in several ways (*4*), one of which is to give antibody directed against the cell membrane receptor for an antigenic determinant.

The receptor for an antigen and the antibody that the cell produces to that antigen have identical antigen-combining regions. These antigen-binding sites are themselves potentially antigenic; antibody directed against them may be termed antireceptor antibody (ARA) (*5, 6*).

We report here that suppression in adults by ARA is not due to depletion of the receptor-bearing clone. Rather, ARA blocks the interaction between receptors and antigen, and this blockade probably lasts about as long as the passively administered antibody persists. On the other hand, ARA given to neonates produces long-term specific unresponsiveness, and cells from such animals remain unresponsive in vitro and in irradiated hosts. These cells do not suppress the response of normal cells in vitro or in vivo. These results are most readily explained by assuming that ARA depletes the clone of receptor-bearing cells in the neonate. Furthermore, we suggest that this mechanism may be involved in the induction of classic neonatal tolerance produced by antigen.

In our model, ARA is directed against the receptor for the hapten phosphorylcholine. BALB/c mice respond to phosphorylcholine with an immunoglobulin M (IgM) antibody of restricted heterogeneity. The antigen-combining region of this antibody is very similar or identical to the combining region of the phosphorylcholine-binding immunoglobulin A (IgA) protein produced by the BALB/c myeloma TEPC-15 (*7, 8*). The antigen-combining site of this myeloma protein itself serves as an antigen, and elicits antibody to TEPC-15 when injected into A/He mice. This antibody to TEPC-15 (i) neutralizes the specific antibody activity of antibody to phosphorylcholine and of TEPC-15 myeloma protein; (ii) specifically suppresses the response of BALB/c mice and spleen cells to phosphorylcholine; and, therefore, (iii) may be characterized as an ARA (*5, 7*).

The antigens used to immunize against phosphorylcholine were the heat-killed vaccine of R36A strain pneumococcus, or phosphorylcholine diazonium coupled to the protein carriers: keyhole limpit hemocyanin, *Salmonella typhi* flagella, or bacteriophage fd coat protein; all of these antigens induce high responses of antibody of the same idiotype to phosphorylcholine and are referred to as PC (*9*). The different PC's were used to ensure that suppression of response to PC did not depend on the form in which the hapten was presented (*8*). Other antigens used as controls were the trinitrophenyl hapten coupled to a carrier (TNP), sheep erythrocytes (SRBC), and horse erythrocytes (HRBC). Responses to antigens were measured by enumerating cells producing specific antibody by using the plaque-forming cell (PFC) technique of Jerne and Nordin (*9*) as modified for use with glass microscope slides (*10*). Responses to PC were measured by using SRBC coupled to *p*-phenylphosphorylcholine (*11*) or coated with the C-polysaccharide extract obtained from R36A vaccine (*12*). Responses to