

NEOTOMA IN THE LATE PLEISTOCENE OF NEW MEXICO AND CHIHUAHUA

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ABSTRACT

Selected characters apt to be present in fossil specimens were studied in modern woodrats (*Neotoma*) in an effort to determine discriminatory features. Emphasis was on the lower first molar. Most modern specimens of the eight species studied (*N. albigula*, *N. cinerea*, *N. floridana*, *N. goldmani*, *N. lepida*, *N. mexicana*, *N. micropus*, and *N. stephensi*) can be identified correctly to species by the use of standard statistical methods and discriminant analysis. Particularly important in preliminary separation into major groups is the absence or near-absence (≤ 2 mm in height) of the lateral dentine tract of the first lower molar in one group (*N. albigula*, *N. floridana*, some *N. lepida*, and *N. micropus*) versus presence (≥ 2 mm in height) in a second group (*N. cinerea*, *N. goldmani*, most *N. lepida*, *N. mexicana*, and *N. stephensi*). Within the group possessing the developed tract, *N. goldmani* and *N. lepida* tend to have the tract lower in height than do the other members of the group.

Application of the discriminatory data to over 500 fossil specimens from 24 late Pleistocene and early Holocene sites located in New Mexico and southern Chihuahua reveals profound differences between interstadial, stadial, and early Holocene woodrat faunas. Interstadial faunas (ca. 25,000 to 33,000 B.P.) were characterized by presence of two undescribed species (apparently related to *N. cinerea* and *N. goldmani*) along with *N. albigula* and *N. micropus*. Most stadial sites were dominated by *N. cinerea*, with other species represented being *N. albigula*, *N. ?goldmani*, *N. floridana*, and *N. micropus*. Of these, *N. floridana* and possibly *N. micropus* appeared only toward the end of stadial times. Jimenez Cave, in southern Chihuahua, is not certainly stadial in age; *N. lepida* was common. Early Holocene sites had woodrat faunas similar to those of today except for the additional presence of *N. mexicana*.

INTRODUCTION

Virtually every area of the western United States and northern Mexico is inhabited by one or more species of woodrats, genus *Neotoma*. Their remains often are abundant in late Pleistocene cave faunas and their contribution to our knowledge of Pleistocene ecology by means of their preserved middens is well known. Their own skeletal remains have contributed relatively little to our knowledge of the Pleistocene, however, because identification to species often is difficult and, to the skeptical, suspect. Reasonably sure identifications would add sig-

nificantly to our knowledge of Pleistocene biogeography and, to a lesser degree, ecology. The aims of this study were to produce discriminating criteria usable with commonly preserved fossil elements for those species apt to be found in late Pleistocene of the Southwest and northern Mexico, to apply these criteria to late Pleistocene/early Holocene specimens available to me, and to interpret the finding in terms of systematics, biogeography, and paleoecology.

MATERIALS AND METHODS

Modern comparative material was assembled for species currently living in the southwestern region and for species judged to have possibly occurred in the area during the late Pleistocene. These species are *Neotoma albigula* Hartley (white-throated woodrat), *N. cinerea* (Ord) (bushy-tailed woodrat), *N. floridana* (Ord) (eastern woodrat), *N. goldmani* Merriam (Goldman's woodrat), *N. lepida* Thomas (desert woodrat), *N. mexicana* Baird (Mexican woodrat), *N. micropus* Baird (southern plains woodrat), and *N. stephensi* Goldman (Stephens' woodrat). Limitations of time and scarcity of specimens in collections (*N. goldmani*) have resulted in several samples of less than ideal size for statistical treatment.

Most effort has been directed toward the dentary with its teeth, particularly m1. This in part reflects commonness of recovery in fossil faunas and in part the potential for identification.

Measurements on both modern and fossil material were taken with an ocular micrometer to the nearest 0.1 mm except for the

greatest width of loph 2 of m1 and depth of incisor, which were taken to 0.01 mm with dial calipers. Measurements consistently taken on lower jaw elements were: 1) length of alveolar cheek-tooth row (LG-ALV); 2) mid-length of m1 (LG-M1); 3) greatest width of loph 2 of m1 (WD-M1); 4) height of antero-lateral dentine tract of m1 (TRACT); 5) distance from base of lingual fold 1 to base of fold 2 of m1 (F1-F2); 6) distance from base of lingual fold 2 to anterior face of m1 (ANT-F2); 7) development of the antero-internal reentrant fold of loph 1, m1 (FOLD); and 8) a ratio comparing depth of the m1 anterointernal reentrant fold to the width of m1 (RATIO). These measurements are indicated in Fig. 1.

LG-M1 was taken from the lingual side at a level estimated to lie between one-third and one-half the height of an unworn tooth and perpendicular to the vertical axis of the tooth (not parallel to the wear surface). Occlusal length proved to be too variable with wear and angle of wear to be as useful a measurement.

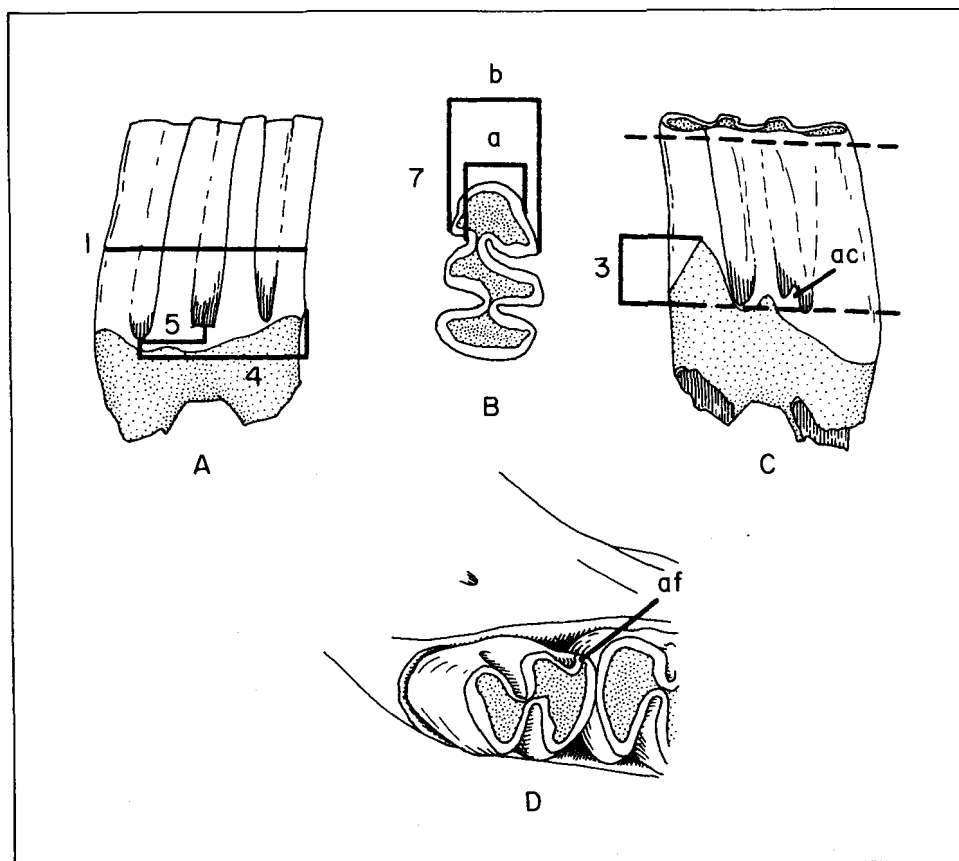


Fig. 1.—Qualitative characters and methods of taking measurements. A) Lingual view of left m1 of *Neotoma cinerea*, showing method of taking LG-M1, ANT-F2, and F1-F2. B) Occlusal view of left m1 of *Neotoma albigula*, showing measurements for calculation of RATIO (a/b). C) Labial view of left m1 of *N. cinerea*, showing method of measuring dentine tract (TRACT) and presence of accessory cusp (ac). D) Occlusal view of left m3 of *Neotoma goldmani*, showing accessory fold (af).

WD-M1 was taken with caliper blades approximately vertical. The bulge present in some teeth at the base of F2 was avoided. A series of measurements on the same specimen occasionally will vary by several hundredths millimeter; heavily worn teeth tend to give an underestimate. Very young teeth (roots broadly open) also often give smaller measurements than comparable adult teeth of the same species even when the enamel appears complete.

The anterolateral dentine tract (Fig. 1) was, to the best of my knowledge, first noted by Lundelius (1979) in *N. cinerea* and *N. mexicana*. Differing in presence and development within the genus, it is an extension of the enamel-less area ventral to the crown onto the lateral surface of loph 1 (lesser developed tracts may occur on the other lophs and on those of m2 and m3). Height was measured from a line parallel to the wear surface extended anteriorly from the base of fold 1 (Fig. 1). In most cases, a sharp demarcation between the normal enamel surface and the dentine was present and used for the upper limit. In some specimens, the transition from dentine to normal enamel is attenuate, without sharp limits; the uppermost appearance of dentine was used in these cases. With wear, the uppermost portions of the tract may be worn away and a conservative estimate of tract height

was made. Tract measurements of the high-dentine forms thus are biased slightly to the low side.

Measurements involving lingual folds were taken from the most ventral point of the fold, which may not be the median point. For ANT-F2, the measurement was made to the anterior wall of the tooth above any abrupt basal constriction.

Development of the anterointernal reentrant fold was coded as shown in Fig. 2. Except for the 0.1 coding, depth may vary greatly (though fairly typical examples are shown)—closeness of the fold base to the tooth base is the criterion used. This is somewhat subjective and wear may obliterate categories 0.2 and 0.3.

RATIO was used in an attempt to quantify the depth of the anterointernal fold in relation to the width of loph 1 (Fig. 1). Corrections for wear were made. Wear categories are 1) very light (depressions on occlusal surface not yet obliterated or enamel walls not fully worn to a flat surface); 2) light (base of labial folds not erupted to level of lateral alveolar wall, or judged to have not reached that stage in the case of isolated teeth; tooth usually notably tapered toward the top); 3) moderate (fold bases erupted but wear not sufficiently close to base as to distort enamel pat-

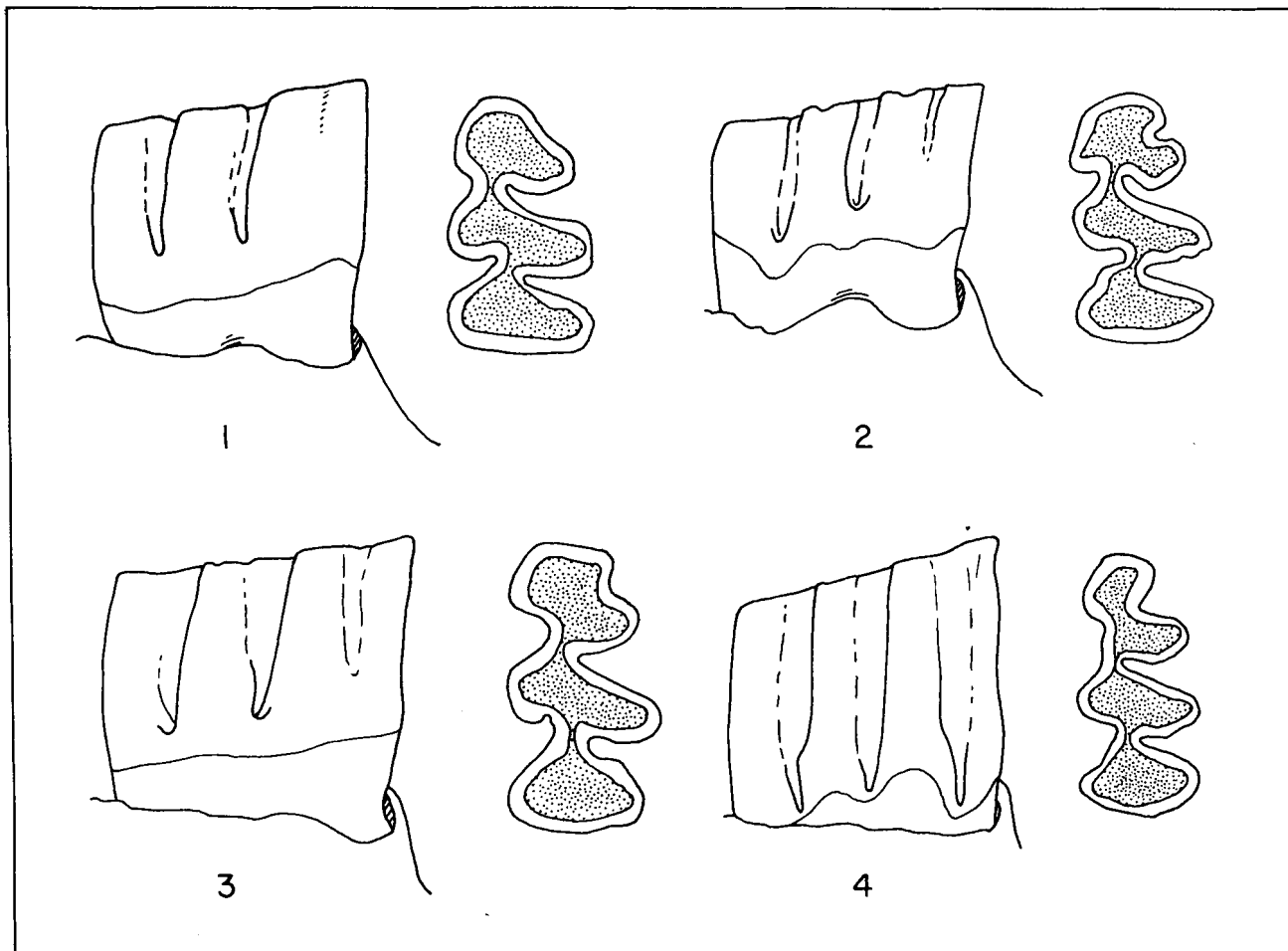


Fig. 2.—Lingual and occlusal views of m1's showing character of antero-internal grooves used for coding. 1) *Neotoma albigula*, coding 0.1. 2) *Neotoma micropus*, coding 0.2. 3) *Neotoma goldmani*, coding 0.3. 4) *Neotoma mexicana*, coding 0.4.

terns); 4) heavy (enamel patterns obviously distorted in proportions); and 5) very heavy (portions of enamel wall other than at the dentine tract missing, often fold bases isolated as islands of enamel surrounded by dentine). Very heavy wear specimens were not used in the analysis. Correctives for wear are given in Table 1 and were obtained by calculating the factors necessary to correct to the average moderate-wear category in the modern samples.

In general, more subjective weight was given to LG-M1, WD-M1, TRACT, and FOLD than to the other characters.

Additional data taken include samples of lower incisor depth (greatest distance from dorsal to ventral surface perpendicular to the tooth axis) and several qualitative characters. These included the presence of accessory cusps at the fold bases in m1 and m2 (Fig. 1), presence of an accessory fold in m3 (Fig. 1), the development of the capsule at the base of the incisor (Fig. 3), the character of the mandibular foramen (Fig. 3), and the relative depths of the external and internal reentrant folds of m3.

The quantitative data were subjected to standard statistical

Table 1.—Correction for wear for measurement RATIO. The raw measurement is multiplied by the wear corrective.

Taxon	Wear category			
	Very light	Light	Moderate	Heavy
<i>Neotoma cinerea</i> , <i>N. mexicana</i> , <i>N. goldmani</i>	1.89	1.31	1.00	0.96
<i>Neotoma lepida</i>	1.00	1.31	1.00	0.96
<i>Neotoma albigula</i> , <i>N. floridana</i> , <i>N. micropus</i>	—	1.22	1.00	0.96

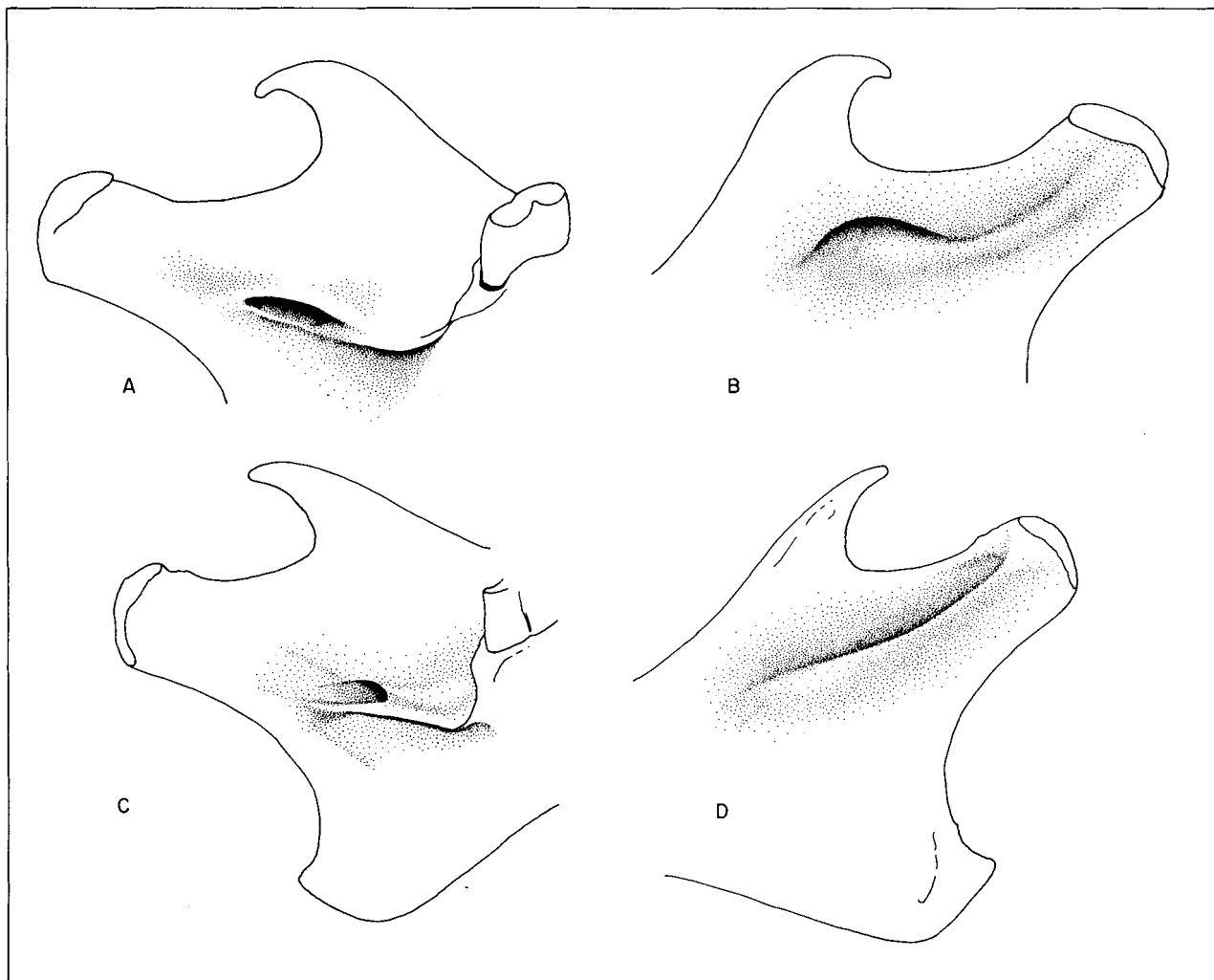


Fig. 3.—Mandibular foramen types (left) and incisor capsule types (right). A) *Neotoma albigula*, showing ventrally oriented mandibular foramen. B) *Neotoma albigula*, showing enlarged incisor capsule. C) *Neotoma goldmani*, showing more laterally directed mandibular foramen. D) *Neotoma goldmani*, showing reduced incisor capsule.

treatment, but also multivariate techniques were utilized, including discriminant analysis (BMD07M, SPSS) and clustering techniques (NT-SYS).

Although the sample statistics and scattergrams can be used for identification, a somewhat more objective method is the use of discriminant analysis. This procedure is most powerful when used between pairs of taxa, in that the weighted characters that best separate three or more taxa are not necessarily the best for separation of any single pair of taxa. In practice, unknown specimens that might belong to any of several taxa are processed with samples of the several known taxa, the results being used to segregate the unknowns to fewer probable choices. The data given in the text and in Table 2 and Figs. 5 to 7 generally should be sufficient to make a preliminary reduction to two or three probable taxa. The data given in Tables 3 and 4 may then be used to

assign discriminant scores to individual specimens and make identifications based on these scores.

Several cautions should be observed: 1) if the specimen belongs to a taxon not represented in the discriminant analysis, a spurious identification will result; 2) some specimens of one taxon overlap with members of another taxon to the point that they are indistinguishable on the basis of the characters used, again resulting in an incorrect or equivocal identification; 3) *Neotoma* has a nasty habit of occasionally having an otherwise rather stable character state shift to the mode seen in a different taxon in rare individuals; if this is a heavily weighted character, assignment may be incorrect. For this reason, measurements should be scanned for reasonableness. As an example, several unknown specimens were assigned to *N. micropus*, but WD-M1 was considerably less than minus two standard deviations from the *N. micropus* mean.

Table 2.—Basic statistics for samples of modern *Neotoma* specimens.

Taxon	Mean	SD	Observed range	N
<i>Neotoma albigula</i>				
LG-M1	3.09	0.136	2.7–3.3	36
WD-M1	1.815	0.073	1.63–1.97	72
TRACT	0.01	0.028	0.0–0.1	72
ANT-F2	2.29	0.126	2.0–2.6	36
F1-F2	0.85	0.091	0.7–1.0	36
FOLD	0.18	0.059	0.1–0.3	36
RATIO	0.671	0.062	0.55–0.83	36
<i>Neotoma cinerea</i>				
LG-M1	3.52	0.122	3.3–3.7	16
WD-M1	1.954	0.102	1.79–2.14	16
TRACT	1.14	0.242	0.8–1.6	16
ANT-F2	2.68	0.181	2.4–3.0	16
F1-F2	1.03	0.101	0.9–1.2	16
FOLD	0.32	0.098	0.1–0.4	16
RATIO	0.481	0.144	0.26–0.71	16
<i>Neotoma floridana</i>				
LG-M1	3.46	0.130	3.3–3.8	22
WD-M1	2.070	0.084	1.93–2.26	22
TRACT	0.02	0.053	0.0–0.2	22
ANT-F2	2.57	0.109	2.4–2.8	22
F1-F2	0.98	0.102	0.9–1.2	22
FOLD	0.27	0.089	0.1–0.4	22
RATIO	0.479	0.076	0.32–0.59	22
<i>Neotoma goldmani</i>				
LG-M1	2.78	0.128	2.6–3.0	8
WD-M1	1.639	0.071	1.54–1.79	8
TRACT	0.35	0.120	0.2–0.5	8
ANT-F2	1.93	0.158	1.7–2.1	8
F1-F2	0.80	0.053	0.7–0.9	8
FOLD	0.20	0.093	0.1–0.3	8
RATIO	0.645	0.083	0.56–0.75	8
<i>Neotoma lepida</i>				
LG-M1	3.04	0.137	2.8–3.3	28
WD-M1	1.708	0.081	1.54–1.83	28
TRACT	0.28	0.188	0.0–0.7	28
ANT-F2	2.30	0.129	2.1–2.5	28
F1-F2	0.84	0.057	0.7–0.9	28
FOLD	0.25	0.079	0.1–0.3	28
RATIO	0.569	0.087	0.42–0.70	28
<i>Neotoma mexicana</i>				
LG-M1	3.17	0.145	2.9–3.5	42
WD-M1	1.723	0.063	1.61–1.85	42
TRACT	1.32	0.345	0.7–2.2	42
ANT-F2	2.39	0.144	2.1–2.7	42
F1-F2	0.87	0.077	0.7–1.1	42
FOLD	0.39	0.034	0.2–0.4	42
RATIO	0.546	0.081	0.39–0.77	42
<i>Neotoma micropus</i>				
LG-M1	3.17	0.106	2.9–3.4	26
WD-M1	1.998	0.090	1.84–2.21	26
TRACT	0.004	0.020	0.0–0.1	26
ANT-F2	2.29	0.141	2.0–2.6	26
F1-F2	0.94	0.110	0.6–1.1	26

Table 2.—Continued.

Taxon	Mean	SD	Observed range	N
FOLD	0.069	0.014	0.1–0.3	26
RATIO	0.609	0.072	0.47–0.77	26
<i>Neotoma stephensi</i>				
LG-M1	2.79	0.178	2.5–3.1	12
WD-M1	1.713	0.087	1.62–1.93	12
TRACT	1.17	0.328	0.6–1.7	12
ANT-F2	2.14	0.144	1.9–2.4	12
F1-F2	0.84	0.051	0.8–0.9	12
FOLD	0.29	0.051	0.2–0.4	12
RATIO	0.564	0.110	0.43–0.77	12

Some idea of the trustworthiness of discriminant analysis for identifying members of two taxa can be gained by using discriminant criteria to assign identifications to individual members of the modern samples. Results are given in Tables 3 and 4. The assignment error of non-sample specimens is expected to be greater, particularly when the discriminant analysis has available as "knowns" only samples of small size.

Final identifications of the fossil material were by an amalgamation of all multivariate and statistical techniques as tempered by characteristics of the specimens and samples themselves (wear, preservation, identifications of other *Neotoma* in the site, etc.).

Table 3.—Pair-wise unstandardized canonical discriminant function coefficients for computing discriminant scores of non-dentine tract *Neotoma m1*'s apt to be confused. To determine score for an unidentified individual, each measurement is multiplied by the respective coefficient and these are summed and added to the constant. The specimen is assigned to species according to its position along the discriminant function (greater or less than the division point). Some measurements are not of value for some species and are omitted. Taxa are identified by initial of species name.

Variable	Coefficients for species pairs			
	A/F	A/L	A/M	F/M
LG-M1	—	—	—	5.483
WD-M1	8.892	-7.236	-11.757	—
TRACT	—	6.146	—	9.495
ANT-F2	—	2.134	6.830	7.058
F1-F2	—	—	-4.515	-8.473
FOLD	—	—	5.189	—
RATIO	-9.851	-5.748	11.771	-2.622
Constant	-11.044	10.674	1.941	-25.741
Division point	-0.514	0.182	-0.267	0.156
Species above point	<i>N.f.</i>	<i>N.l.</i>	<i>N.a.</i>	<i>N.f.</i>
Modern sample discriminated	100%	91%	100%	96%

Table 4.—Pair-wise discriminant function coefficients for dentine tract *Neotoma*. See caption of Table 3 for explanation.

Variable	Coefficients for species pairs					
	C/M	C/S	G/L	G/S	L/S	M/S
LG-M1	-2.270	6.431	—	—	-3.120	5.685
WD-M1	13.109	3.642	—	7.779	3.408	-4.880
TRACT	—	—	—	3.908	3.913	—
ANT-F2	5.825	—	7.378	—	—	—
F1-F2	—	—	—	—	—	-4.038
FOLD	-16.030	-4.952	—	—	—	15.803
RATIO	—	—	—	—	—	—
Constant	-24.390	-25.844	-16.333	-16.375	1.296	-11.519
Division point	1.148	-0.387	-0.761	-0.377	0.853	-0.998
Species above point	<i>N.c.</i>	<i>N.c.</i>	<i>N.l.</i>	<i>N.s.</i>	<i>N.s.</i>	<i>N.m.</i>
Modern sample discriminated	100%	100%	89%	100%	100%	94%

More than 500 specimens of *Neotoma* from the late Pleistocene and early Holocene of Chihuahua and New Mexico were available for study. These specimens are preserved in the Resource Collections, Laboratory for Environmental Biology, University of Texas at El Paso (UTEP). Sites and site data are given in Table 5; site localities are shown in Fig. 4.

RESULTS AND DISCUSSION

The basic statistics of the modern species samples are given in Table 2 and in part displayed in Figs. 5 to 7.

Specimens of *Neotoma* can be divided into two major groups on the basis of the development of the lateral dentine tract on m1. Most specimens of *N. albigula*, *N. floridana*, and *N. micropus* basically lack the tract, though a few individuals have the tract developed to a height of ca. 0.1 mm (0.2 mm in *N. floridana*). The remaining species have a tract height of ≥ 0.2 mm except for some *N. lepida* (ca. 36% of the modern sample).

Qualitative characters of the dentary differing between the two groups include generally greater development of the incisor capsule and a somewhat more ventrally oriented mandibular foramen in the non-dentine tract group (Fig. 3). Neither character is entirely clearcut in all cases, and *N. lepida* is more similar to the non-dentine tract species.

Within the group possessing a dentine tract, there is a dichotomy between those that possess a relatively low tract (*N. goldmani* and *N. lepida*) and those with a high tract (*N. cinerea*, *N. mexicana*, and *N. stephensi*) (Fig. 7).

Table 6 shows the identifications of the *Neotoma* found in each site treated.

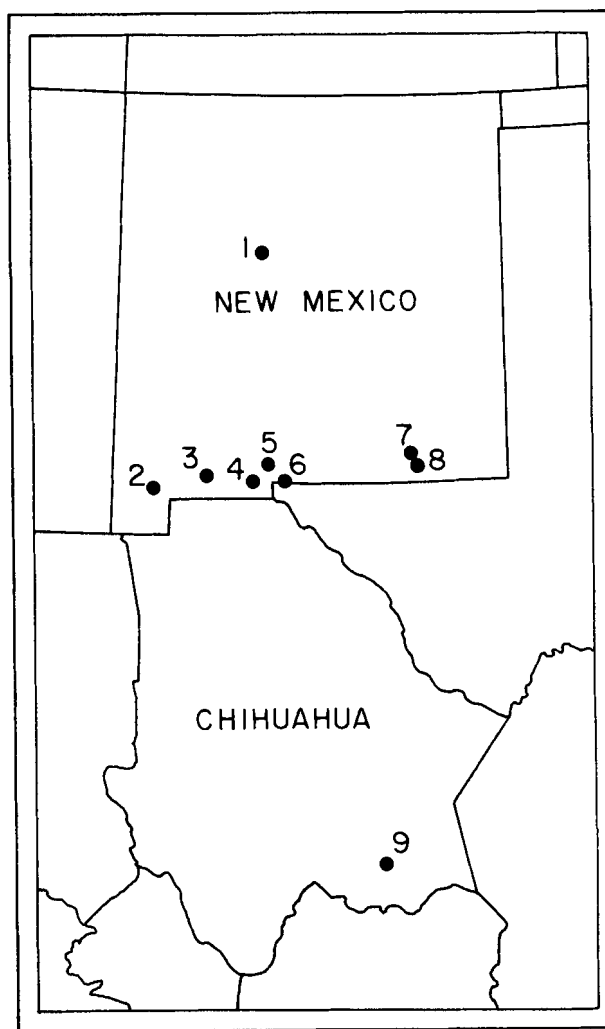


Fig. 4.—Sketch of New Mexico and Chihuahua, showing late Pleistocene sites. 1) Isleta Caves; 2) Howell's Ridge Cave; 3) Baldy Peak Cave; 4) Khulo Site; 5) Conkling's Cavern and Shelter Cave; 6) Anthony Cave; 7) Dry Cave; 8) Dark Canyon Cave; 9) Jimenez Cave.

Table 5.—Sites from which fossil *Neotoma* were examined. Those marked with an asterisk are in the Dry Cave system.

UTEP no.	Name	Age (BP)	Reference
1, 17	*Lost Valley	29,290 ± 1,060	Harris, 1977
4	*Bison Chamber	<14,470, >10,730	Harris, 1977
5	*Sabertooth Camel Maze	25,160 ± 1,730	Harris, 1977
6	*Harris' Pocket	14,470 ± 250	Harris, 1977
21	Khulo Site	<10,000	Harris, 1977
22	*Animal Fair	15,030 ± 210	Harris, 1977
23	*Stalag 17	11,880 ± 250	Harris, 1977
24	*Entrance Chamber	<11,880	Harris, 1980
25	*Camel Room	Est. >12,000	Harris, 1977
26, 27	*Rm Vanishing Floor	33,590 ± 1,500	Harris, 1977
28	*Rick's Cenote	Est. 11,000	Unpublished
29	Anthony Cave	stadial	Harris, 1977
30	Shelter Cave	stadial, Holocene	Harris, 1977
32	Howell's Ridge Cave	stadial, Holocene	Harris, 1977; Van Devender and Wiseman, 1977
41	Isleta Cave No. 1	stadial, Holocene	Harris and Findley, 1964
46	Isleta Cave No. 2	stadial, Holocene	Harris and Findley, 1964
54	*TT II	10,730 ± 150	Harris, 1977
75	Dark Canyon Cave	stadial	Harris, 1977
90	Conkling Cavern	stadial	Harris, 1977
91	Jimenez Cave	?stadial and ?Holocene	Unpublished
94	Baldy Peak Cave	stadial and ?Holocene	Unpublished
122	*Pit N & W Animal Fair	?early stadial	Harris, 1977

Table 6.—Taxa identified from each site.

UTEP Loc.	Taxon							A	B
	<i>Neotoma albigula</i>	<i>Neotoma cinerea</i>	<i>Neotoma floridana</i>	<i>Neotoma goldmani</i>	<i>Neotoma lepida</i>	<i>Neotoma mexicana</i>	<i>Neotoma micropus</i>		
Interstadial									
1	X						X	X	X
5	X								
17	X							X	X
26								X	X
27	X								X
Stadial									
4							?		
6	X	X					cf.		
22	X	X		?					
23		X	X						
25		X							
28			cf.						
29	X	X		?					
30		X							
32	X	X							
41	X	X					?		
46	X	X					?		
54		cf.	cf.				X		
75	X	X							
90	X	X							
91	X	?	cf.		X		X		
94		X				X			
122		X							
Holocene									
21	X						X	?	
24	X						X	X	

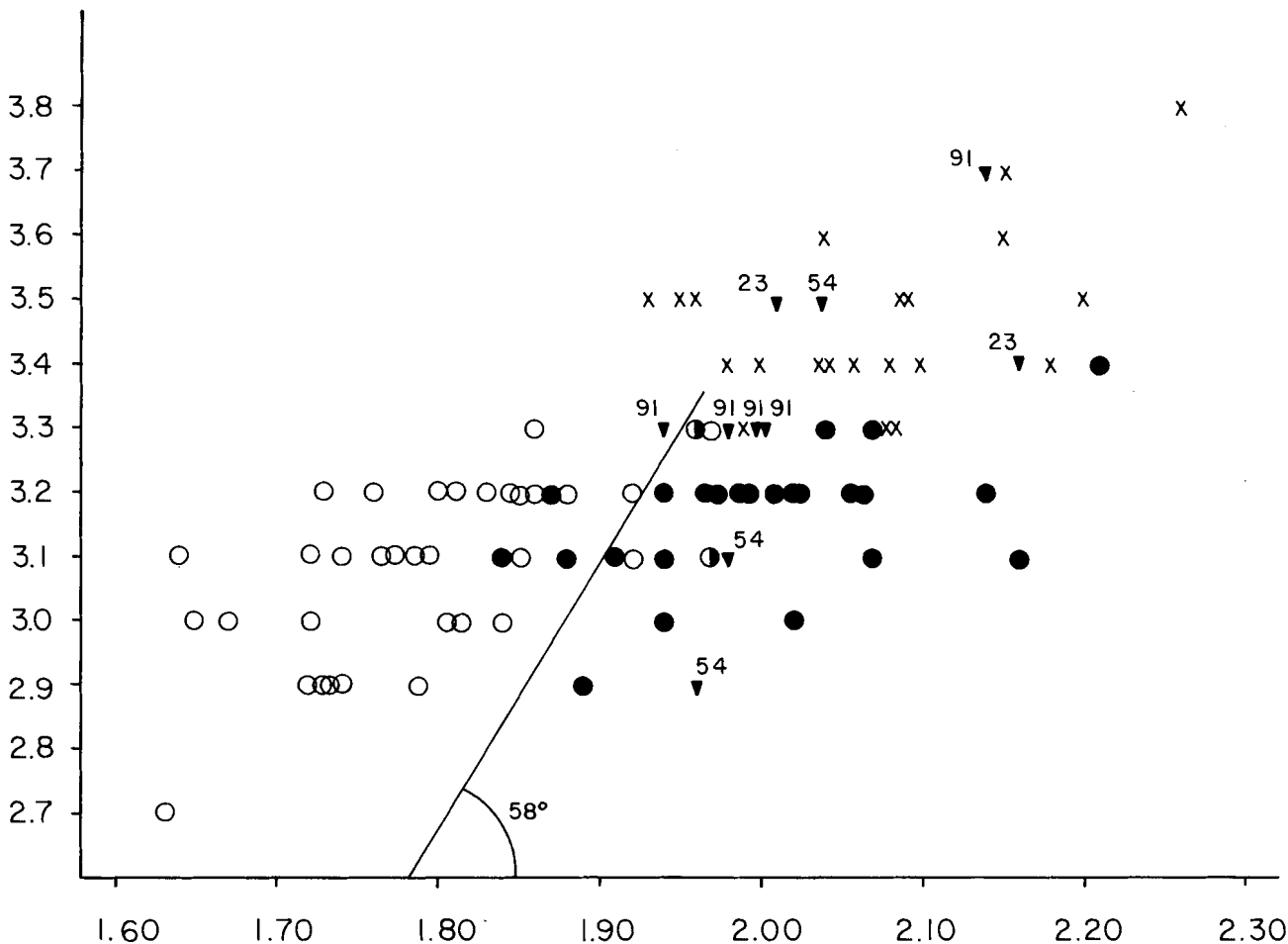


Fig. 5.—Scattergram of LG-M1 (ordinate) against WD-M1 (abscissa). Circles, modern *Neotoma albigula*; dots, modern *Neotoma micropus*; X, modern *Neotoma floridana*; triangles, selected fossil specimens from sites shown by numbers. Line shows best separation between *N. albigula* and *N. micropus*.

SPECIES ACCOUNTS

Neotoma albigula

The white-throated woodrat now occurs at or near all sites. It apparently was as ubiquitous in the past, occurring in interstadial, stadial, and early Holocene sites.

This rat is easily separable from other *Neotoma* except for *N. micropus* and some individuals of *N. lepida* on the basis of m1. Dalquest et al. (1969) and Lundelius (1979) have discussed separation criteria between *N. albigula* and *N. micropus*. Dalquest et al. found no overlap in width of loph 2 of m1, *N. albigula* having a width of <1.94 mm and *N. micropus* a width of >1.94 mm. Lundelius, in a sample of 32 *N. albigula* and 30 *N. micropus*, found 9.4%

of the former with breadths >1.94 mm and 16.7% of the latter with widths <1.94 mm. In the present study, a sample of 72 *N. albigula* showed three (4.2%) exceeding 1.94 mm, and five of 26 (19.2%) *N. micropus* with measurements of <1.94 mm. A bivariate scattergram of LG-M1 and WD-M1 (Fig. 5) does a somewhat better job of separation, but some misidentifications on the basis of these measurements are inevitable.

Confusion between *N. albigula* and *N. lepida* results from the inability to separate those *N. lepida* with dentine tracts <0.2 mm from *N. albigula*.

There is some variability within the species (Fig. 8), with some tendency for smaller size in the stadial sites and with the length of m1 from Jimenez Cave (UTEP 91) and the Khulo Site (UTEP 21) being

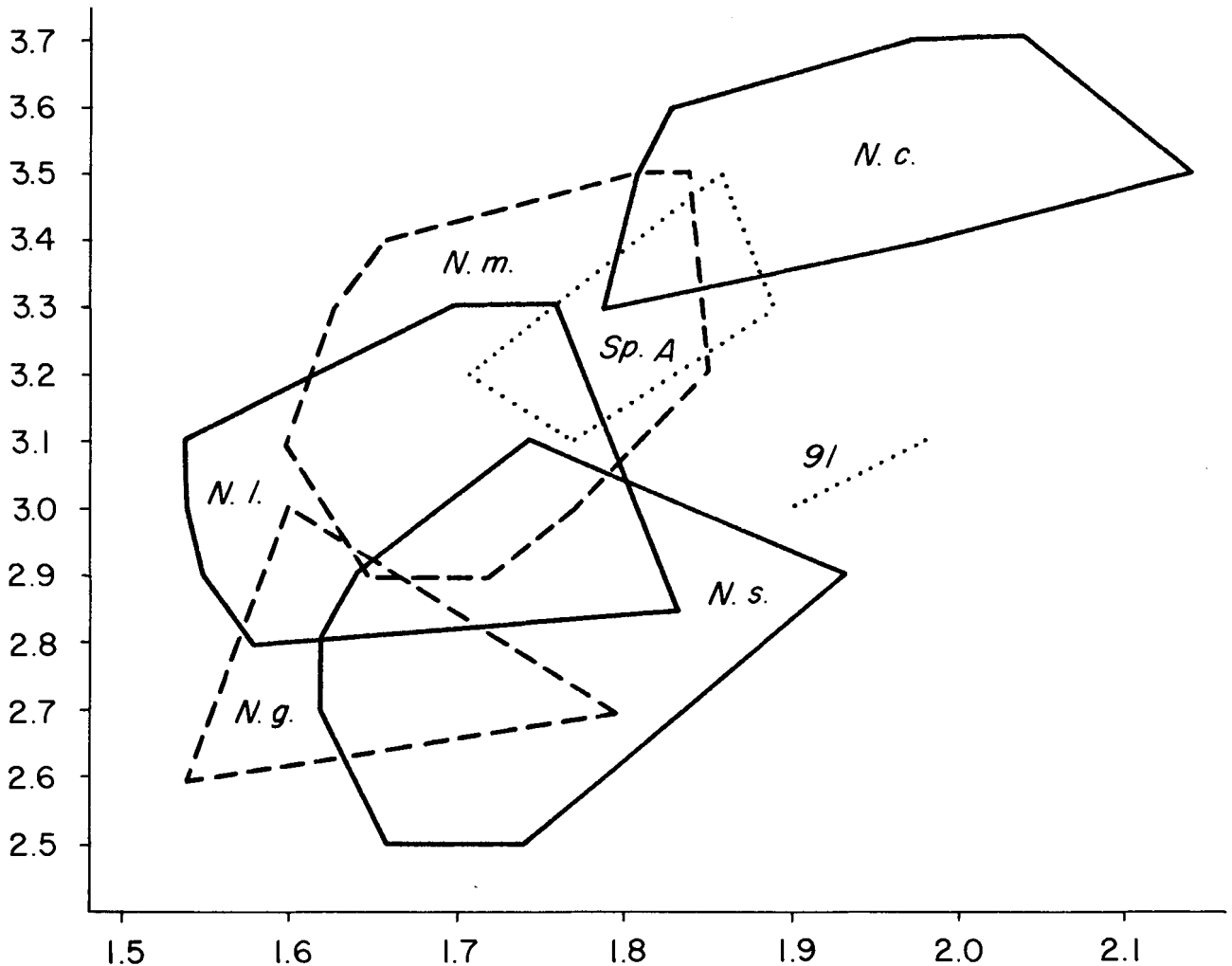


Fig. 6.—Dispersal of plotted points of LG-M1 (ordinate) against WD-M1 (abscissa) for modern specimens of five high dentine tract species, fossil specimens of extinct Species A, and two fossil specimens from UTEP 91 (species identified by initials). Polygraphs were constructed by connecting marginal points.

somewhat large. Jimenez Cave lies within the current range of *N. albigula durangae*, which Anderson (1972) notes as being somewhat intermediate between *N. a. albigula* and *N. micropus*; this may be showing up here. No such explanation is available for the Khulo Site sample, nor do width measurements indicate much chance of *N. micropus* biasing the sample by wrongful inclusion.

Today, *N. albigula* occurs in a variety of habitats from desert to pinyon-juniper woodlands and ponderosa pine forests, though seldom found in pure grassland. In various parts of its range it may be associated with all of the species considered here, though only marginally with some.

Neotoma cinerea

The bushy-tailed woodrat occurs in every stadal fauna for which there is at least a moderate-sized sample, and often makes up the majority of the recovered specimens.

There is remarkably little variation from site to site and from Pleistocene populations to modern populations, no significant differences being found among the three characters looked at closely (LG-M1, WD-M1, TRACT). The two specimens (queried) from Jimenez Cave, however, are exceptionally short, though of normal width and dentine tract height (Fig. 6); these suggest intraspecific variation at this far southern extension of the geographic range,

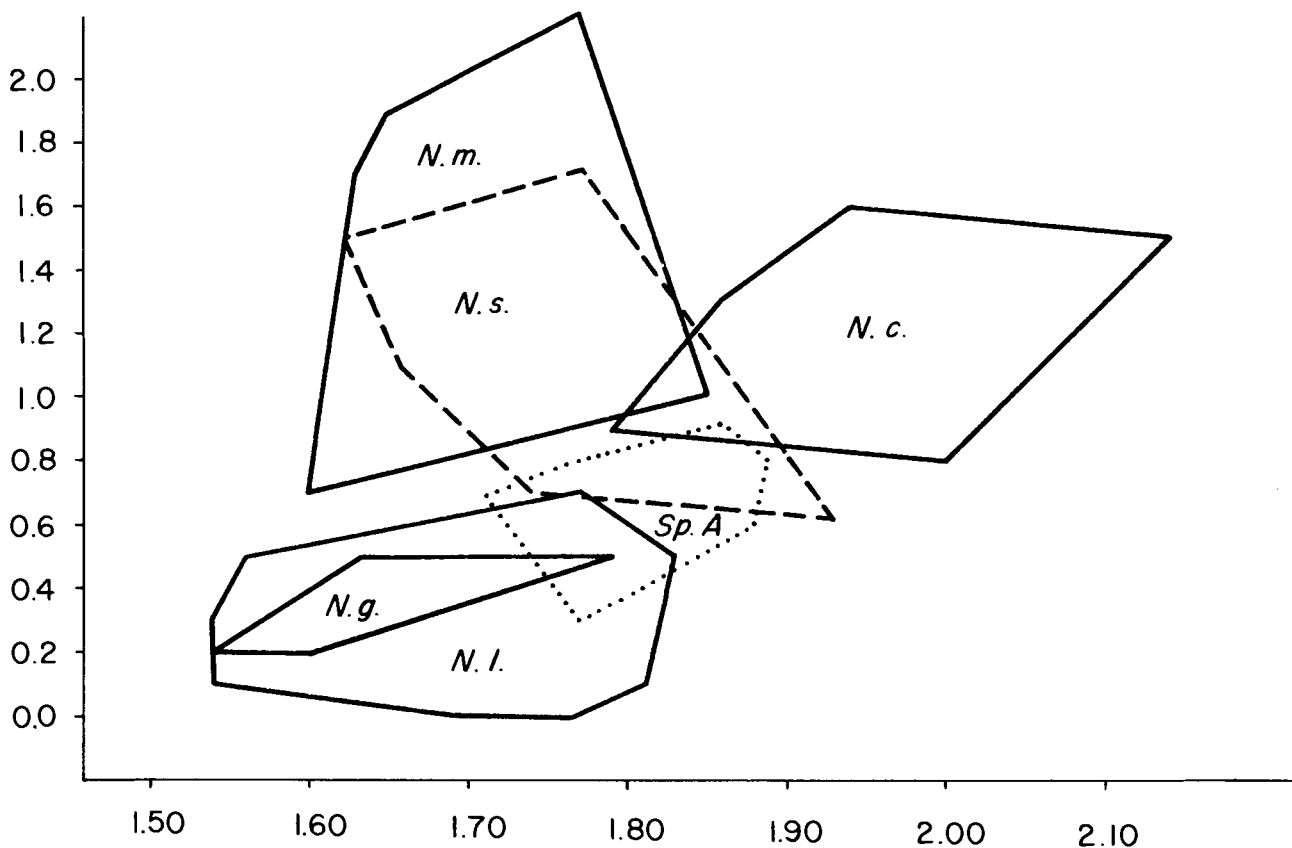


Fig. 7.—Dispersal of plotted points of TRACT (ordinate) against WD-M1 (abscissa). Specimens as in Fig. 6, without the two fossil specimens from UTEP 91.

but may represent an unknown taxon. Table 7 gives the basic statistics for three measurements from the three largest samples.

Lundelius (1979) identified *N. cinerea* from Pratt Cave (located in the Texas portion of the Guadalupe Mountains just south of the New Mexico border; age is considered Holocene by Lundelius, but some material may be Pleistocene) and from Dark Canyon Cave (Texas Memorial Museum specimens). He suggested that these specimens represented populations with larger m1's than those of modern *N. cinerea* from New Mexico; that they were of a size more like modern specimens from Wyoming. However, there is no significant difference between the present small sample of Recent *Neotoma* from New Mexico ($n = 9$) and the UTEP sample from Dark Canyon Cave ($n = 9$ adults). The Dark Canyon sample of Lundelius averaged 0.41 mm larger than his small sample ($n = 4$) of modern New Mexican specimens, whereas the difference in the present study

is 0.1 mm (the Lundelius measurement, however, was occlusal length of m1 rather than mid-length).

Neotoma cinerea apparently was absent from the

Table 7.—LG-M1, WD-M1, and TRACT statistics for *Neotoma cinerea* from UTEP 22, 29, and 75.

Locality	Mean	SD	Observed range	N
UTEP 22				
LG-M1	3.54	0.214	3.2–4.1	29
WD-M1	1.962	0.115	1.78–2.21	29
TRACT	1.10	0.219	0.7–1.6	29
UTEP 29				
LG-M1	3.49	0.151	3.2–3.7	11
WD-M1	1.986	0.071	1.88–2.12	11
TRACT	1.16	0.401	0.4–1.9	11
UTEP 75				
LG-M1	3.56	0.167	3.3–3.8	9
WD-M1	1.970	0.105	1.85–2.14	9
TRACT	1.04	0.255	0.6–1.4	9

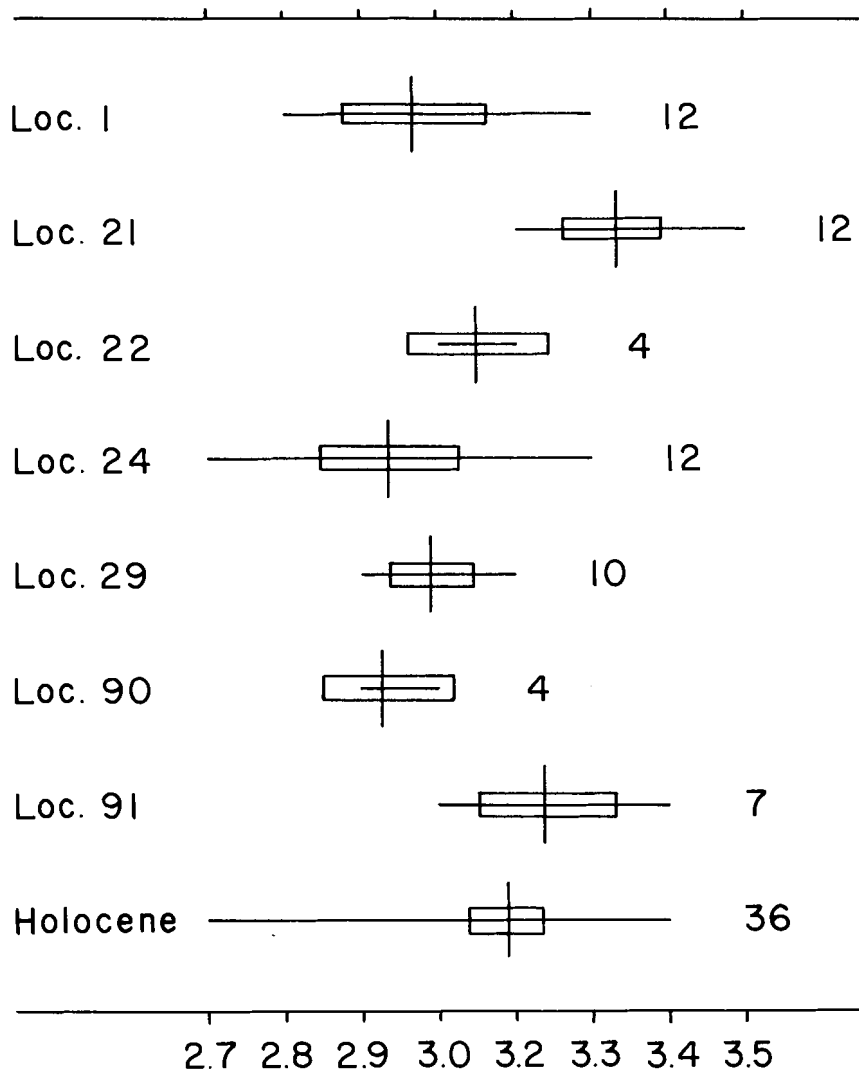


Fig. 8.—m1 lengths of fossil and modern *Neotoma albigula*. Vertical lines, sample means; horizontal lines, observed range; box, 95% confidence interval of the mean; numbers to right of figures, sample size.

interstadial deposits of Dry Cave (but see comments below, in the "Species A, undescribed" account) and from deposits that are surely Holocene, but as noted above, was virtually ubiquitous during stadial times with little morphological variation. Likely there was an essentially continuous population throughout the region. Holocene occurrence is possible at several sites, including the Isleta Caves, Howell's Ridge Cave (UTEP 32, possibly representing *N. mexicana*), and Pratt Cave, but its absence and replacement by *N. mexicana* at the presumably uncontaminated Entrance Chamber deposit (UTEP 24) at Dry Cave and the Khulo Site (UTEP 21) suggest otherwise.

Some earlier workers have interpreted presence of *N. cinerea* at low elevations south of their present range as indicative of the forests where they are found now at their point of nearest occurrence in the Sangre de Cristo Mountains of northern New Mexico (for example, Murray, 1957). This, however, ignores their occurrence under far different conditions and at lower elevations in northwestern New Mexico (extending into pinyon-juniper woodland and occasionally lower) and their widespread habitation of sagebrush and the like farther north (Cary, 1917). Likely *N. cinerea* inhabited all vegetational zones from timberline down to, and in-

cluding, steppe-woodland (terminology after Harris, in press), an open woodland with well developed growth of grasses, herbs, and shrubs. Pure grassland, however, probably was not inhabited. Within these vegetational types, they likely were limited as today (Armstrong, 1972) to areas of cliffs, jumbled rocks, and caves.

Neotoma floridana

The most convincing evidence of the eastern woodrat in the southwestern Pleistocene is the central portion of a skull (UTEP 23-79) from the Stalag 17 site in Dry Cave. Qualitative features, including the presence of a well-forked palatine spine, fit *N. floridana* rather than *N. micropus*. Dalquest et al. (1969) suggest that the two species are separable on the basis of breadth of the maxillary molar rows (*N. micropus*, 8.0 to 8.7 mm; *N. floridana*, 8.7 to 9.2 mm). The method of taking molar row breadth is not described. In the present study, measurement was done by applying caliper blades to the outer sides of the tooththrows at the alveolar line (measurements to the most lateral tooth surfaces are much larger). In 26 *N. micropus*, breadth measurements ranged from 7.67 to 8.64 mm; in 26 *N. floridana*, 8.06 to 9.48 mm, with 10 of the specimens <8.7 mm. Molar row breadth in 23-79 is 8.85 mm, well beyond any *N. micropus* measured by myself, Dalquest et al. (1969), or Lundelius (1979). Two dentaries with m1's from the same site are identified as *N. floridana* by discriminant analysis (see also Fig. 5). Both m1's have the deep anterointernal fold that occurs with fair frequency in *N. floridana* but is rare in *N. micropus*.

Two specimens from the early Holocene Khulo Site (UTEP 21) could be *N. floridana*, but are assigned here to *N. ?micropus*. If *N. floridana*, they would be at the small end of their size range. A similar situation occurs in the Holocene Entrance Chamber deposits (UTEP 24) of Dry Cave, but here *N. micropus* also seems present and the possible *N. floridana* again would have to be at the lower limits of its size distribution. Other equivocal specimens come from UTEP 46; they are identified here as *N. ?micropus*.

A much better candidate for *N. floridana* is specimen 28-1, an m1 from Rick's Cenote (UTEP 28) within Dry Cave. Identified by discriminant analysis as this species, its length (3.5 mm) is beyond any in the modern sample of *N. micropus* (longest, 3.4 mm). This site should be very late Pleistocene, as is another site in Dry Cave, UTEP 54 (approx-

Table 8.—Basic statistics for combined sample of *Neotoma ?goldmani* from UTEP 22 and 29.

Measurement	Mean	SE	Observed range	N
LG-M1	2.86	0.052	2.8-2.9	8
WD-M1	1.698	0.055	1.60-1.77	8
TRACT	0.23	0.116	0.0-0.4	8
ANT-F2	2.04	0.074	1.9-2.1	8
F1-F2	0.79	0.064	0.7-0.9	8
FOLD	0.18	0.071	0.1-0.3	8
RATIO	0.673	0.059	0.57-0.76	8

mately 10,730 radiocarbon years, but with extinct fauna). Two of the three available specimens seem to be *N. micropus*, but the third clearly falls into the *N. floridana* area (Fig. 5). Four m1 specimens from Jimenez Cave (UTEP 91) in Mexico are identified as *N. floridana* by discriminant analysis, and another as *N. micropus*. Four of the specimens, including the latter, fall into the intermediate length-width area, but the fifth specimen is unequivocally within the *N. floridana* area (Fig. 5).

Thus, in summary, *N. floridana* seems defensibly identified from near the Pleistocene-Holocene boundary in UTEP 23, and the evidence is rather strongly suggestive of presence in two other Dry Cave sites of latest Pleistocene age. Evidence also suggests presence at the undated Jimenez Cave, in southern Chihuahua, Mexico. Occurrence at two other sites (UTEP 21 and 46), both sites with early Holocene materials, is possible but judged unlikely.

Neotoma ?goldmani

Five m1's from the Animal Fair site (UTEP 22) of Dry Cave and three from Anthony Cave (UTEP 29) are closer in most measurements (Table 8) to *N. goldmani* than to *N. lepida*. Width and dentine height are slightly more similar to *N. lepida* than to *N. goldmani*, nearly reaching a significant difference from *N. goldmani* on dentine height in the combined sample (n = 8). In all other traits, however, *N. lepida* is more dissimilar (significantly so for M1-LG, $P \leq 0.001$; ANT-F2, $P \leq 0.001$; F1-F2, $P = 0.033$; GROOVE, $P = 0.028$; and RATIO, $P = 0.003$). In addition, one of two m3's associated with the m1's has an accessory fold and the other a suggestion of such. Six of eight modern *N. goldmani* possess this fold and it was probably developed on a seventh (the foldlet becomes unclear and then disappears with moderate to heavy wear). In 30 *N. lepida* from east of California, only one definitely

has such a fold. Of 15 specimens of *N. lepida* from California and Baja California, however, six show folds (this population, however, is much larger in size than interior *N. lepida*).

Today, *N. goldmani* occurs in eastern Mexico almost north to the Big Bend of Texas. A continuous distribution northward through the mountain ranges of Trans-Pecos Texas and into southeastern New Mexico would not be startling, and this rare rat may well occur today north of its recognized range. It probably is an inhabitant today of rocky areas in arid mountains.

Neotoma lepida

The m1 of this animal seems to differ from that of *N. albigula* primarily in the possession in about two-thirds of the individuals of a dentine tract ≥ 0.2 mm in height; length averages significantly less, but with much overlap. Six of 72 m1's of *N. albigula* had a dentine tract height of 0.1 mm; none had a higher tract. Thus possession of a tract ≥ 0.2 mm rules out *N. albigula* beyond reasonable doubt. Basic statistics for UTEP 91 are given in Table 9. A comparison of dentine tract heights between the UTEP 91 sample and that of modern *N. lepida* shows a significantly lower tract in modern *N. lepida* ($P = 0.017$); this probably is biased, however, because fossil *N. lepida* m1's with a dentine tract that is < 0.2 mm cannot be separated from those of *N. albigula* except when the teeth are notably smaller, and thus most such low-height tract teeth would not appear in the sample. The UTEP 91 population also differs significantly from modern *N. lepida* in slightly shorter length of m1 ($P = 0.023$) and the measurement ANT-F2 ($P \leq 0.001$), and in larger RATIO measurement ($P = 0.001$). These differences are interpreted as geographic/chronologic variation, Jimenez Cave being far from any modern population of *N. lepida*. A modern sample identified as *N. lepida* from California and Baja California shows far more difference in m1 length, for example (mean = 3.25, $n = 13$).

Neotoma mexicana

Demonstrable *N. mexicana* are surprisingly rare in the sites considered, and those that do occur do so in generally unexpected circumstances. Unless a few individuals are mixed in with the large number of *N. cinerea* identified from stadial sites (and this is a possibility), *N. mexicana* is absent from all stadial sites with the exception of Baldy Peak Cave (UTEP 94). This site had little fill, and post-Pleistocene remains would be inseparable from older fos-

Table 9.—Basic statistics for *Neotoma lepida* from UTEP 91.

Measurement	Mean	SD	Observed range	N
LG-M1	2.95	0.112	2.8–3.2	23
WD-M1	1.733	0.061	1.61–1.82	23
TRACT	0.39	0.122	0.1–0.5	23
ANT-F2	2.07	0.118	1.9–2.3	23
F1-F2	0.83	0.076	0.7–0.9	23
FOLD	0.25	0.095	0.1–0.4	23
RATIO	0.665	0.117	0.48–0.90	23

sils. This is the only site where both *N. cinerea* and *N. mexicana* are solidly identified.

Other sites with *N. mexicana* are Holocene. The largest sample is from UTEP 21, the Khulo Site ($n = 7$), and it seems comparable to modern New Mexican *N. mexicana*. From the Entrance Chamber of Dry Cave (UTEP 24), however, two of the three specimens are notably small for *N. mexicana*, but resemble no other known taxon.

Neotoma micropus

This large woodrat occurs from interstadial time to the present, though not found in large numbers. It may have been absent during full stadial conditions. Difficulties in discrimination from *N. albigula* and *N. floridana* have been described in those accounts.

Species A, undescribed

An interstadial population of relatively large woodrats with moderate development of the dentine tract is represented by 12 m1's as well as by additional material. The specimens clearly are separable from all other interstadial populations (Figs. 6 and 7). They do show a relationship in morphological characters to *N. mexicana* and *N. cinerea*. They differ significantly from these species as a population (Table 10), though some individual specimens of *N. cinerea* and *N. mexicana* cannot be discriminated. Although intermediate in several characters between those two species, the height of the dentine tract averages conspicuously lower than in either. A qualitative character, the presence of small accessory cusps at the base of fold 2 of m2 on three specimens, suggests closer relationship to *N. cinerea* than to *N. mexicana*.

Species B, undescribed

A woodrat from the interstadial deposits of Dry Cave (UTEP 1, 17, 26, 27) currently is being described.

Table 10.—Comparison of UTEP 1 "cinerea-type" specimens (=Species A) ($n = 10$) with modern *N. cinerea* ($n = 16$) and *N. mexicana* ($n = 42$). A = mean UTEP 1 (1 SD). B = mean *N. cinerea* (1 SD). C = t between UTEP 1 and *N. cinerea*. D = mean *N. mexicana* (1 SD). E = t between UTEP 1 and *N. mexicana*.
*, significant at $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

Character	A	B	C	D	E
LG-M1	3.29 (0.110)	3.52 (0.122)	4.81***	3.17 (0.145)	2.37*
WD-M1	1.814 (0.056)	1.954 (0.102)	3.95***	1.723 (0.063)	4.23***
TRACT	0.65 (0.158)	1.14 (0.242)	5.71***	1.32 (0.345)	5.97***
ANT-F2	2.50 (0.149)	2.68 (0.181)	2.56**	2.39 (0.144)	2.24*
F1-F2	0.92 (0.9)	1.03 (0.101)	2.82**	0.87 (0.077)	1.65
FOLD	0.40 (0.0)	0.32 (0.098)	2.60*	0.39 (0.034)	0.66
RATIO	0.487 (0.082)	0.481 (0.144)	0.11	0.546 (0.081)	2.07*

This taxon is significantly different from *N. lepida* ($P \leq 0.001$) in all but GROOVE and RATIO, and from *N. goldmani* in TRACT ($P \leq 0.001$), ANT-F2 ($P = 0.042$), and RATIO ($P = 0.003$). The most meaningful difference from *N. goldmani* probably is in the dentine tract height, which averages almost 0.2 mm higher in Species B (0.54 mm versus 0.35 mm). Three of four m3's have accessory folds preserved.

Species B presumably is most closely related to *N. goldmani* among all extant *Neotoma*. It is more than twice as common in the interstadial deposits than the next most common species, *N. albigula*.

GENERAL DISCUSSION

Interstadial, stadial, and early Holocene *Neotoma* faunas all differ radically from the modern condition, emphasizing the uniqueness of modern climate and biology.

The recognized interstadial faunas from the region are all from Dry Cave, in southeastern New Mexico. These faunas indicate conditions with greater effective moisture than today, though probably less than during stadial times (or differently distributed), an absence of cold winter temperatures, and rather warm summer temperatures (Harris, 1977; Van Devender et al., 1976; Harris and Crews, 1983).

The interstadial woodrat faunas include the mod-

ern forms *N. albigula* and *N. micropus*. These two species occur today in grassland and desert situations, usually with brush, cacti, or rocky areas available. They show local differences in habitat preference, but occur in close physical proximity. *N. micropus* becomes rare to the west now, apparently not reaching west as far as the New Mexico-Arizona border.

The other two species in the interstadial faunas appear to represent undescribed, extinct species. One, the Species A of this study, seems to be allied with *N. mexicana* or *N. cinerea*, more probably the latter. A reasonable scenario would be isolation in the southeastern New Mexican moderate to high elevations following an earlier stadial expansion of *N. cinerea*. This would allow a period of differentiation during isolation, perhaps even from early Wisconsin stadial conditions. Late Pleistocene re-expansion of *N. cinerea* could then cause extinction by competition or genetic swamping.

The other species (Species B) seems to have its affinity with the *N. goldmani-lepida* group. The rarity of *N. goldmani* in collections and the large geographic variation seen in modern nominal *N. lepida* make assessment of exact relationships difficult. Species B might well be ancestral to *N. goldmani* or both *N. goldmani* and *N. lepida*, or of course be a distinct taxon becoming extinct without leaving an issue.

By mid-stadial times, the woodrat fauna had changed considerably. An *N. goldmani*-like form occurs at Dry Cave, a possible descendant of Species B (the occurrence of the *goldmani*-type woodrat at Anthony Cave, north of El Paso on the Texas-New Mexico border, is undated, but apparently full-stadial, at least in part). *N. albigula* remains are widespread, but *N. cinerea* of modern character now is the most commonly represented species in the cave faunas. As the complete faunas make clear (Harris, in press), some of the sites considered here were below the coniferous forest zone, lying in sagebrush-grasslands or steppe-woodlands. Notably cooler summers, cold winters (but probably not to the extremes of today), and more effective moisture allowed invasion of a vast area by the bushy-tailed woodrat, even possibly to southern Chihuahua.

Changing conditions near the end of the Pleistocene allowed invasion by *N. floridana* into the Dry Cave area, probably in the context of better grassland habitat. *Neotoma cinerea* still is present, however, as are other species of mammals now extirpated from the lower elevations of southern New Mexico (Harris, 1977). Jimenez Cave, in southern

Chihuahua, may show presence of *N. floridana*, but the age is not definitely known to be late stadial.

Neotoma micropus may have been present during full stadial times (UTEP 6, cf.; UTEP 4, ?), but is not reasonably surely present until latest Pleistocene (UTEP 54). It also occurred at Jimenez Cave. As with *N. floridana*, it may denote increasing summer temperatures and possibly increased emphasis on summer precipitation.

At the close of the Pleistocene, a major change occurs—*N. cinerea* abruptly disappears, replaced by *N. mexicana* (this assumes presence of *N. cinerea* at Pratt Cave is Pleistocene in age). With the exception of *N. mexicana*, the *Neotoma* fauna is modern. Midden evidence indicates the early Holocene maintained woodland in the lowlands of the Southwest until at least 8,000 B.P. (Van Devender and

Spaulding, 1979). It seems evident that *N. mexicana* could replace *N. cinerea* under those conditions, either by out-competing it or by moving in as *N. cinerea* succumbed to other factors. *N. mexicana* appears equipped to survive under such conditions, hanging on even today in a few jumbled-rock areas far below its more common elevational and vegetational range (Findley et al., 1975).

Of the original list of species considered, only *N. stephensi*, now occurring from western New Mexico across central and northern Arizona, has not been identified. With the present study as a base, it can be hoped that examination of *Neotoma* from other sites in the western United States and Mexico can clarify the geographic and chronologic distribution of late Pleistocene *Neotoma*.

ACKNOWLEDGMENTS

I wish to thank T. Yates and W. Barber of the Museum of Southwestern Biology, The University of New Mexico; D. Hoffmeister of the Illinois Natural History Museum, The University of Illinois at Urbana-Champaign; and R. Fisher of the Fish and Wildlife Service Museum Section, National Museum of Natural History, for the loan of modern comparative material. Other

comparative material was collected under permits from the New Mexico Department of Game and Fish. Many of the fossil specimens reported on here were collected under a grant from the National Geographic Society with the permission of the Bureau of Land Management. H. Messing allowed study of *Neotoma* from the Jimenez Cave fauna, currently under study by him.

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