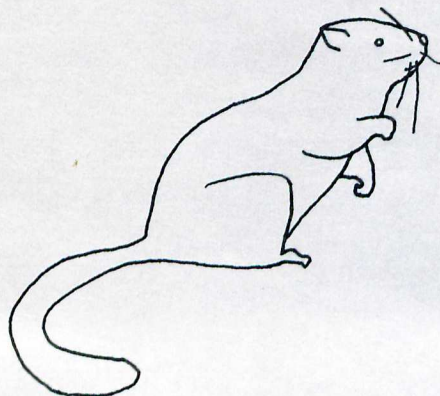
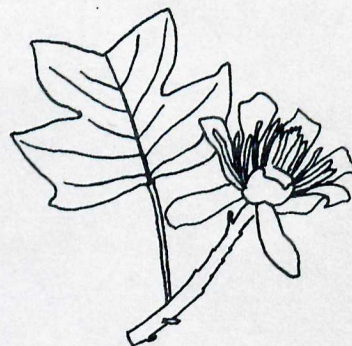


FOSSIL HISTORY OF THE RODENT GENUS SIGMODON

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EVOLUTIONARY
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ABSTRACT: Extinct and extant species of Sigmodon are referred to three species groups: the hispidus species group, including S. hispidus, S. ochrognathus, S. alleni, S. fulviventer, S. mascotensis, S. arizonae, and S. bakeri; the leucotis species group, including S. leucotis, S. alstoni, S. peruanus, S. hudspeethensis, S. curtisi, and S. libitinus (new species); and the medius species group, including S. medius and S. minor. A new subspecies of S. medius is described. The diminutive S. minor evolved from S. medius through character displacement away from large, advanced cotton rats of the leucotis species group. Increase of roots on the first lower molar, from two to four, is a feature which characterizes Sigmodon evolution, and is directly coupled with the evolution of hypsodonty and the successful transition from browsing to grazing. A chronology of North American deposits with fossil Sigmodon is provided.

* * *

INTRODUCTION

Rodents of the genus Sigmodon are common grassland mammals throughout much of the semi-arid southwestern and mesic southeastern United States. The northern limit of their distribution coincides approximately with 40 degrees north latitude, from which point they are distributed southward through Central America and northern South America (Hershkovitz, 1955; Hall and Kelson, 1959). Related genera, such as Holochilus and Neotomys, are found only in South America, where their range extends to Tierra del Fuego.

Recent evidence of the early evolution and geographic distribution of hesperomyine rodents suggests that this group evolved primarily in North America (Martin, 1974; Jacobs, 1977; Baskin, 1978). Dispersal into South America apparently began during the Chapadmalalan (roughly equivalent to the early Blancan of North America; Marshall, et al., 1977), coincident with establishment of the Panamanian land bridge (Simpson, 1969; Baskin, 1978).

Abundant fossil Sigmodon from numerous deposits ranging in time from late Pliocene to latest Pleistocene allows consideration of zoogeographic and ecological relationships among species of this genus. Representation in the fossil record of a suite of identifiable populations (= homogeneous samples; particularly when this homogeneity is statistically comparable to that of extant populations) which can be either directly or indirectly interdigitated into stratigraphic units allows the construction of a phylogeny and series of index fossils which can be of major service to our comprehension of late Pliocene and Pleistocene events.

Since the conception of this study, collection of small vertebrate materials by the washing technique introduced by Hibbard (1949)

has produced numerous samples of fossil Sigmodon, particularly from Florida, California, Texas, and Arizona, through the efforts of S.D. Webb, T. Downs and J.A. White, W.W. Dalquest, and E.H. Lindsay, respectively. Collections from the western United States include primarily members of the primitive medius species group, but from numerous quarries. I have examined some of their material, but much remains unstudied as of this time. Preliminary analyses by E.H. Lindsay (pers. commun.) indicate a potential continuum of dental evolution within the medius species group in Arizona, such that the morphologic boundaries between S. medius and S. minor are unclear. Reference of intermediate populations is now troublesome, and valid questions can be asked about the taxonomy of this complex. Given a chronocline with regard to size from the larger S. medius through the smaller S. minor, is it either practically or biologically relevant to retain these names, rather than to synonymize both under S. minor (as did Cantwell, 1969 and followed by Eshelman, 1975)? What name should morphological intermediates bear, if any? In this paper I have made an attempt to answer these questions, with full knowledge that fossils from the western United States may provide a relatively complete record of evolution within the medius species group.

The descriptions and phylogenies in this paper supercede those in Martin (1974; especially Figs. 3.6 and 3.7).

ABBREVIATIONS

UF - University of Florida, Florida State Museum
 TMM - University of Texas, Texas Memorial Museum
 UMMP - University of Michigan, Museum of Paleontology
 LACM - Los Angeles County Museum
 UAVP - University of Arizona, Vertebrate Paleontology
 MSU - Michigan State University
 MUVF - Midwestern University, Vertebrate Paleontology
 KU - University of Kansas, Museum of Natural History
 AMNH - American Museum of Natural History
 USNM - United States National Museum

SYSTEMATICS OF SIGMODON

Genus Sigmodon Say and Ord 1825

Characteristics of the genus are adequately delimited by Hershkovitz (1955). Taxonomy of the Recent North American species follows Baker (1969) and Zimmerman (1970). Much research needs to be accomplished with living South American Sigmodon, and for now I have merely lumped all Sigmodon on that continent with three roots on the first lower molar into either S. peruanus or S. alstoni, depending upon the absence (peruanus) or presence (alstoni) of grooved upper incisors.

A cross preceding a taxon indicates that it is extinct. Selected measurements may be found in Table 1. Measurement methods follow Martin (1974).

The following species accounts are based almost exclusively upon dental characteristics. For this reason the term "Identification" rather than "Diagnosis" is used to describe extant species. However, the term "Diagnosis" is retained at the species group level of classification is introduced here. Justification for this classification is found in the DISCUSSION, the details of which are presented throughout the text.

Excepting only Tables 1 and 2 and Figs. 17 and 18, lower case m indicates lower dentition and upper case M indicates upper dentition.

Table 1 - Measurements in mm of the lower dentition and mandible in extinct and extant species of *Sigmodon*. M.A. = mandibular alveolar length, L= length, W= width, N= number of specimens, \bar{x} = mean, O.R.= observed range.

Species	N	M.A.		LM ₁		LM ₂		LM ₃		MH ₁		MH ₂		MH ₃		O.R.
		\bar{x}	O.R.	\bar{x}	O.R.	\bar{x}	O.R.	\bar{x}	O.R.	\bar{x}	O.R.	\bar{x}	O.R.			
<i>Sigmodon medius</i>																
Parson	3	5.75	5.30-5.01	2	1.91-2.39	4	1.43-1.87	4	1.94	2	1.44	4	1.43-1.71	4	1.54	1.33-1.82
Roberts	25	5.70	5.30-5.13	25	1.86-2.46	26	1.35-1.81	26	1.97	26	1.44	26	1.29-1.51	26	1.54	1.44-1.82
Sandera	4	6.10	5.72-5.44	30	1.80-2.40	23	1.32-1.81	15	1.92	41	1.43	23	1.27-1.58	23	1.56	1.44-1.84
Benders	4	6.07	5.72-5.44	2	1.78-2.18	1	1.32-1.69	1	2.15	11	1.40	1	1.21-1.50	1	1.72	1.30-1.68
Smith Draw	-	-	-	-	-	-	-	-	-	1	1.37	1	1.25-1.29	1	1.51	-
Halle Xiv	1	1.98	-	1	2.10-2.22	1	1.53-1.65	1	1.92	2	1.37	1	1.51-1.57	1	1.63	-
Wendell Fox Pasture	3	6.27	6.11-6.38	3	2.16	3	1.60	3	2.02	6	1.53	6	1.51-1.57	5	1.67	1.62-1.71
<i>Sigmodon minor</i>																
Gurtis Ranch	2	5.20	4.97-5.00	2	1.88	40	1.30-1.62	6	1.84	39	1.31	40	1.21-1.44	40	1.43	1.27-1.55
Perchance	25	5.83	5.27-6.00	38	1.72-2.07	40	1.22-1.54	175	1.75	140	1.28	40	1.17-1.48	40	1.43	1.20-1.50
<i>Sigmodon surstali</i>																
Gurtis Ranch	1	7.03	-	3	2.28-2.49	3	1.87	1	2.55	3	1.62	3	1.55-1.71	3	1.89	1.85-1.92
Kennel	15	6.74	6.31-6.94	15	2.16-2.44	15	1.77	9	1.90	15	1.66	15	1.55-1.76	15	1.86	1.74-1.89
Irville IA	1	6.74	-	1	2.31	1	1.67	1	2.15	1	1.57	1	1.21-1.50	1	1.72	-
<i>Sigmodon thalidomae</i>																
Halle VIIA	23	6.22	5.72-6.74	26	2.14	25	1.53	1.43-1.68	6	1.90	26	1.57	1.42-1.66	25	1.72	1.54-1.77
<i>Sigmodon butspedensis</i>																
Hudspeth and Red Light	1	6.90	-	4	2.34	2	1.75	1.73-1.76	2	2.21	4	1.48	1.40-1.57	2	1.52	1.39-1.65
<i>Sigmodon bakeri</i>																
Ogden III	11	6.28	5.93-6.71	20	2.21	13	1.61	1.42-1.83	13	1.92	20	1.61	1.38-1.86	13	1.72	1.55-1.86
Yalison XIII	8	6.68	6.40-6.93	3	2.46	8	1.72	1.57-1.79	8	2.40	8	1.63	1.52-1.77	8	1.89	1.43-1.69
<i>Sigmodon hispidus</i>																
British IA (Recent)	18	7.27	6.82-7.65	18	2.49	18	1.82	1.62-1.95	18	2.52	18	1.73	1.62-1.86	18	2.02	1.88-2.14
Powder (Recent)	30	7.56	6.56-7.80	28	2.42	30	1.72	1.59-1.92	30	2.72	30	1.62	1.52-1.86	30	2.02	1.77-1.96
Texas (S. h. hermanniari)	8	6.68	6.31-6.93	8	2.35	8	1.72	1.57-1.79	8	2.40	8	1.63	1.52-1.77	8	1.89	1.65-1.89
<i>Sigmodon ochrometatus</i>																
Texas, Mexico Durango	5	6.70	6.28-7.09	5	2.26	4	1.67	1.57-1.82	4	2.49	5	1.64	1.57-1.69	5	1.85	1.77-1.88
<i>Sigmodon fulviventris</i>																
Mexico Durango	8	7.17	6.95-7.34	8	2.27	2	1.82	1.73-1.91	8	2.73	8	1.71	1.65-1.81	8	1.93	1.86-2.05
<i>Sigmodon alleni</i>																
Mexico Michoacan and Oaxaca	5	6.64	6.38-7.08	5	2.41	5	1.76	1.65-1.87	5	2.33	5	1.63	1.53-1.72	5	1.87	1.71-2.00
<i>Sigmodon mascochensis</i>																
Mexico Jalisco	3	7.12	6.90-7.28	3	2.22	4	1.69	1.62-1.81	4	2.57	4	1.65	1.56-1.73	4	1.81	1.72-1.93
<i>Sigmodon arizonae</i>																
Arizona, Mexico Durango	3	7.46	7.33-7.60	4	2.45	4	1.73	1.75-1.91	4	2.29	4	1.81	1.76-1.86	4	2.10	1.96-2.08
<i>Sigmodon leucotis</i>																
Mexico Durango, Hidalgo, Guerrero, Quana-jato	11	6.76	6.44-7.04	9	2.44	9	1.78	1.63-1.85	9	2.20	9	1.67	1.58-1.75	9	1.90	1.81-1.90
<i>Sigmodon panamiae</i>																
Sanctor and Fern	10	7.22	7.10-8.73	9	2.68	9	2.13	1.93-2.29	9	2.65	9	1.91	1.76-2.07	9	2.23	2.10-2.33

Hispidus Species Group

Diagnosis: This group is characterized by four well-developed roots on the first lower molar. The labial and lingual roots (here termed accessory roots) are generally less robust than either of the primary anterior and posterior roots.

Remarks: Figure 1 illustrates the nature of development of these roots in select Sigmodon species. Table 2 includes a breakdown of the development and position of these roots in various species groups. All species of the hispidus species group except S. bakeri are extant and distributed almost entirely in North and Central America.

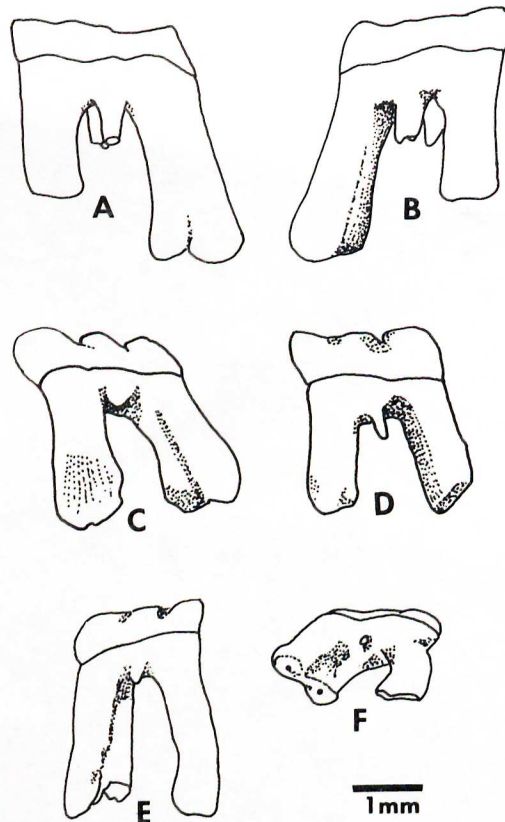


Figure 1 - Roots of the first lower molar in select species of Sigmodon. A; S. hispidus, labial view of UF 16199, L (left) m1, Reddick IA. B; S. hispidus, lingual view of UF 16199. Both accessory roots are broken, and would appear approx. one-third longer if complete. C; S. medius, ventrolabial view of UAVP 15-24/2741, Lm1, Tusker. D; S. medius, labial view of UAVP 15-24/2700, Lm1, Tusker. E; S. minor, labial view of UMMP 51310, Rm1, Borchers. F; S. minor, ventral view of UMMP 51310.

* * *

Sigmodon hispidus Say and Ord 1825
(Figures 1-7, 16, 17, 19-21)

Identification: The largest extant North American cotton rat, S. hispidus is the most advanced with respect to dental evolution. The process of lamination as described by Hershkovitz (1962) has proceeded

Table 2 - Numerical analysis of dental parameters in fossil Sigmodon. N= number of specimens, %= percent, m= medial, Sym.= symmetry, A= asymmetrical, S= symmetrical, Dev.= development, Ant. Cing.= anterior cingulum, Antcon.= anteroconid. Under development of roots: 1= weakly developed, 2= moderately developed, 3= well developed. Under anterior cingulum M₂-M₃: 0= absent, 1= moderately developed, 2= well developed.

	Number and Position of Roots				Dev. Labial Root			Dev. Lingual Root			Ant. Cing. M ₂ -M ₃		Sym. Antcon. M ₁ (%)									
	N	%4	%3	%2	N	%1	%2	%3	N	%1	%2	%3	N	%0	%1	%2	N	A	A/S	S		
<u>S. minor</u> (Borchers)	62	3	71	26	13	21	35	94	6	-	-	-	73	4	18	78						
<u>S. medius</u> (Rexroad Loc. 3)	26	4	58	38	3	19	13	100	-	-	-	-	28	-	7	93						
<u>S. medius</u> (Tusker)	31	7	67	26	11	36	14	86	14	-	-	-	18	-	-	100						
<u>S. curtisi</u> (Ingils IA)	16	13	87	-	-	-	8	-	75	25	1	100	-	14	36	36	28	11	27	27	46	
<u>S. libitinus</u> (Haile XVIA)	30	13	87	-	-	-	15	-	74	26	4	50	50	13	85	15	-	19	90	-	10	
<u>S. bakeri</u> (Coleman IIA)	9	89	11	-	-	-	9	-	11	89	9	-	78	22	20	90	10	-	20	100	-	-
<u>S. hispidus</u> (Reddick IA)	31	97	3	-	-	-	31	-	-	100	34	35	50	15	26	62	38	-				

in this species to the point of separation of the anteroconid from the paraconid and entoconid on the m1 in some specimens. The cheek teeth are highly prismatic and the reentrant folds are deep and narrow. The enamel surface at the termination of each reentrant fold is thinned relative to the enamel of the occlusal surface along the remainder of the border of each fold. The anterior cingulum on m2 and m3 tends to be reduced (Table 2). Sigmodon hispidus has the most hypsodont molars of any North American Sigmodon species (Fig. 2).

Remarks: S. hispidus probably does not represent the culmination of dental evolution within the grazing cotton rats. The dynamic processes of lamination and involution are surely continuing in this species, and the necessary masticatory platform provided by the roots is becoming sturdier.

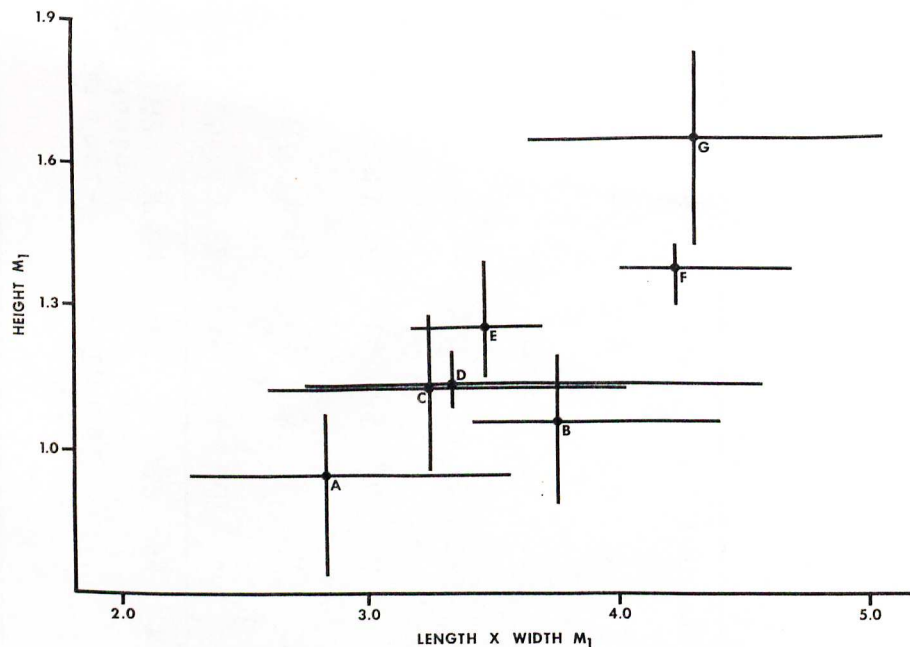


Figure 2 - Crown height of the first lower molar as a function of occlusal area in select samples of fossil and Recent Sigmodon. A, S. medius, Rexroad Loc. 3; B, S. curtisi, Inglis IA; C, S. libitinus, Haile XVIIA; D, S. bakeri, Coleman IIA; E, S. ochrognathus, extant; F, S. leucotis, extant; G, S. hispidus, Reddick IA. Horizontal and vertical lines represent the observed ranges of both measures as they pass through the grand mean.

* * *

Hypsodonty in cotton rats has been accompanied by the addition of accessory roots. For example, S. hispidus has four well-developed roots on the m1. This feature differs to some extent in the grazing arvicolines, where hypsodonty has been accomplished with a reduction in roots. However, even the combination of enlarged primary and accessory roots apparently is not sufficient to support the crown of hispidus molars, as a relatively recently evolved adaptation, root capture, is now occurring within this species.

In root capture a web (bridge) of dentin forms between roots, and the integrity of each may be lost. This phenomenon is especially obvious on the upper and lower second and third molars. The normal,

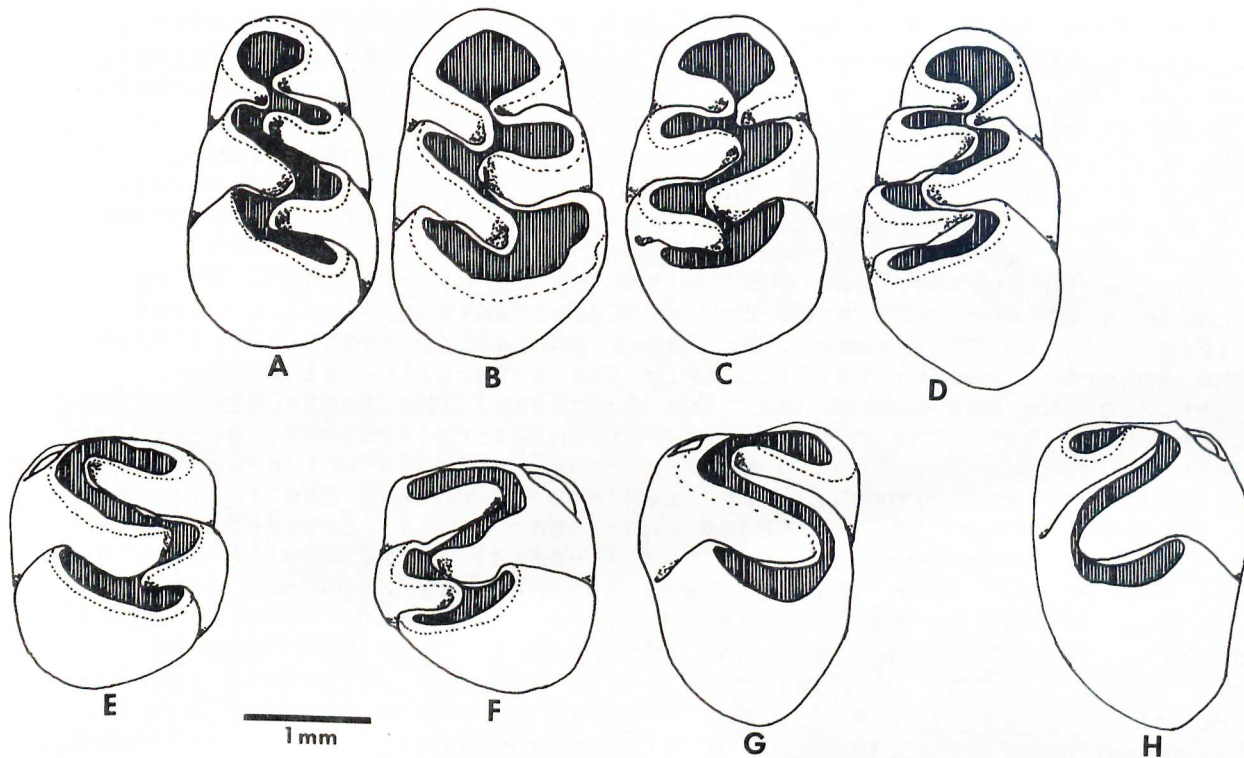


Figure 3 - Variation in the lower dentition of Sigmodon hispidus from Reddick IA, Florida. All specimens catalogued as UF 16197. A-B, Lm1; C-D, Rm1; E, Lm2; F, Rm2; G, Lm3; H, Rm3.

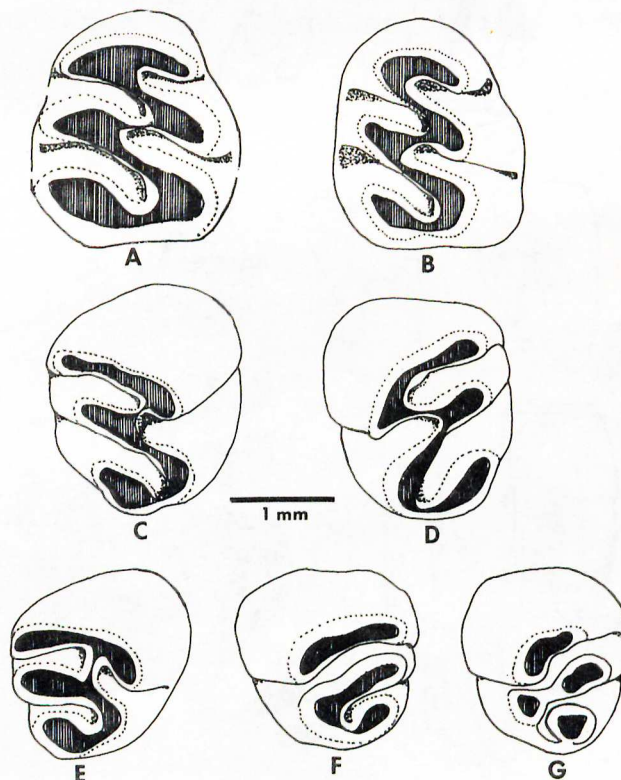


Figure 4 - Variation in the upper dentition of Sigmodon hispidus from Reddick IA, Florida. All specimens catalogued as UF 16197. A-B, RM1; C, RM2; D, LM2; E, RM3; F-G, LM3.

* * *

three-rooted pattern of M2 in S. hispidus and that of the primitive S. minor are shown in Fig. 5. In M2 there is a tendency for capture of the anterolabial root by the anterolingual root. From an anterior view, the initial roots may appear relatively prominent, with a connecting web of dentin (Fig. 6). The M3 of S. hispidus may show variations of a common three-rooted form, as is typical also of S. minor, or the posterolabial root may be captured by the lingual root.

Capture is further obvious in the m3 of S. hispidus, where three-quarters of the root area may be fused into a single, robust entity (Fig. 7). In this case, the large posterior root always captures the anterior roots; particularly the anterolingual root.

Besides the obvious supporting function, the roots are intimately involved with both the nervous and circulatory systems, providing an enrichment source for the functional odontoblasts which control dentin physiology and growth. These systems reach the dentin via canals and, in general, there is one major canal per root. However, in S. hispidus, and occasionally in other species, there may be more than one canal per root. When this is seen the primary root may demonstrate a bifurcation (Figs. 5, 6). For example, the posterior root of m1 in both the primitive S. minor and the advanced S. hispidus may be bifurcate (Fig. 1). The lingual roots of M2-M3 are bifurcate in a few specimens of S. minor (Figs. 5, 6), whereas they are usually not in other Sigmodon species. These bifurcations apparently represent developmental anomalies, not vestiges of an ancestral condition.

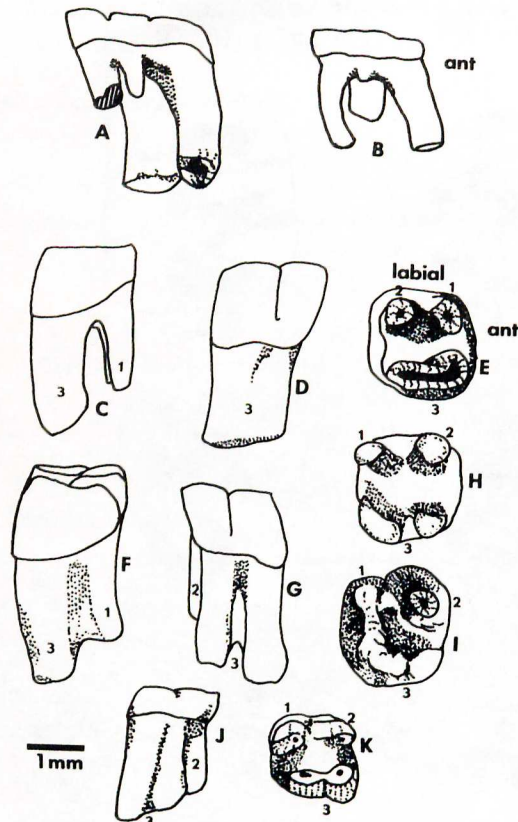


Figure 5 - Roots of the upper first and second molars in select species of Sigmodon. A; S. hispidus, labial view of UF 16197, LM1, Reddick IA. B; S. medius, labial view of UAVP 15-24/2788, LM1, Tusker. C; S. hispi-

us, anterior view of UF 16199-1 (this convention is used to facilitate comparison of illustrations, where many specimens are catalogued under a single number), RM2, Reddick IA. Note lack of webbing between roots one and three. D; S. hispidus, lingual view of UF 16199-2, LM2, Reddick IA. E; S. hispidus, ventral view of UF 16199-2. F; S. hispidus, anterior view of UF 16199-3, RM2, Reddick IA. Note webbing between roots one and three. G; S. hispidus, lingual view of UF 16199-4, RM2, Reddick IA. H; S. hispidus, ventral view of 16199-4. I; S. hispidus, ventral view of UF 16199-3. Note capture of root one by root three. J-K; S. minor, lingual and ventral views of UMMP 52306, LM2, Borchers. ant= anterior.

* * *

Temporal and geographic range of fossil material: Rancholabrean to Recent (S= Sangamonian, W= Wisconsinan).

Florida: Devil's Den (W; Martin, 1968a; Martin and Webb, 1974); Haile VIIIA (S; this report); Haile, Locs. XIB, XIIIA, C (?S; this report); Haile XIVB (Martin, 1978); Withlacoochee River, Loc. 7A (W; Webb, 1974); Ichetucknee River (W; this report); Vero (W; Weigel, 1962); Seminole Field (W; Simpson, 1929); Melbourne (W; Ray, 1958); Reddick IA (S; Gut and Ray, 1963); Reddick IIC (S; this report); Sabertooth Cave (S; Simpson, 1928); Kendrick IA (?S; this report); Maximo Moorings (W; this report); Arredondo IA (W; Webb, 1974); Arredondo. Locs. IIB, C (?S; this report). Louisiana: Kimball Creek-Little Bayou Sara (W; Martin, 1968a). Georgia: Ladds (?S; Ray, 1967). Texas: Moore Pit (?S; Slaughter, 1966); Sims Bayou (?W; Slaughter and McClure, 1965); Howard Ranch (?W; Dalquest, 1965); Clear Creek (W; Slaughter and Ritchie, 1963), Friesenhahn Cave (W; Lundelius, 1960); Longhorn Cavern (W; Semken, 1961); Ben Franklin (W; Slaughter and Hoover, 1963). New Mexico: Brown Sand Wedge (W; Slaughter, 1962). Aruba: Isla (?W; Hooijer, 1967).

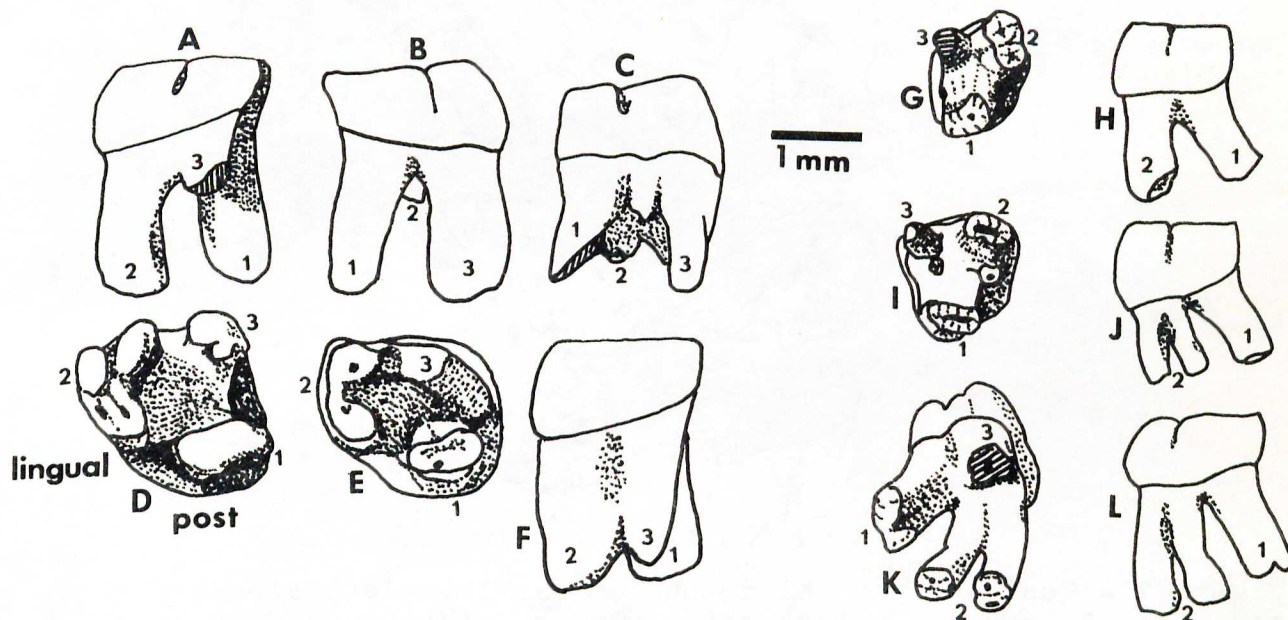


Figure 6 - Roots of the third upper molar in select species of Sigmodon. A; S. hispidus, lingual view of UF 16199-5, LM3, Reddick IA.

B; S. medius, labial view of UF 16199-5. C; S. hispidus, labial view of UF 16199-7, RM3, Reddick IA. E; S. hispidus, ventral view of UF 16199-8, RM3, Reddick IA. Note capture of root three by root two. F; S. hispidus, anterior view of UF 16199-8. G, I, K; ventral and H, J, L lingual views of left third upper molars of S. minor, Borchers, all catalogued as UMMP 51304, showing variation in development of the anterolingual root (root two). post= posterior.

* * *

Fossil material examined: Florida: Reddick IA (rodent beds), Marion County; UF 14347-14360. Reddick IIC, Marion County; UF 15204. Devil's Den, Levy County; UF 13453, 13444, 13593-13600. Kendrick IA, Marion County; UF 2658. Maximo Moorings, Pinellas County; UF 3062. Haile VIIIA, Alachua County; UF 9844, 15153, 12680-12684. Haile XIB, Alachua County; UF 13471-13592. Haile XIII A, Alachua County; UF 13096-13097. Haile XIIIC, Alachua County; UF 13049. Ichetucknee River, Gilchrist County; UF 15205. Withlacoochee River, Locality 7A; Citrus County; UF 15206. Arredondo IA, Alachua County; UF 15207. Arredondo IIB, Alachua County; UF 12589. Arredondo IIC, Alachua County; UF 12297-12303. Haile XIVB, Alachua County; uncatalogued specimens.

Sigmodon alleni Bailey 1902
(Figures 8, 21)

Identification: S. alleni is best characterized by position of the mental foramen on the mandible. This foramen cannot be seen when the mandible is viewed from the labial side, as it is located close to the base of the first lower molar and is more lingually directed than in other Sigmodon species. The dental pattern is most similar to that of S. hispidus.

Temporal and geographic range of fossil material : No fossil record.

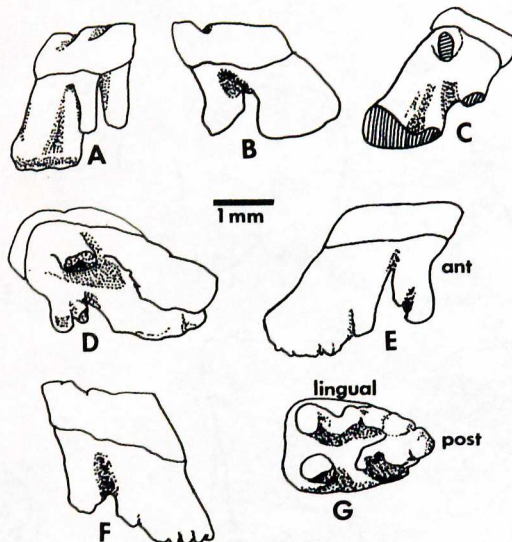


Figure 7 - Roots of the third lower molar in select species of Sigmodon. A; S. medius, anterolabial view of UAVP 15-24/3004, Rm3, Tusker. B; S. medius, lingual view of UAVP 15-24/2863, Rm3, Tusker. C; S. medius, anteroventral view of UAVP 15-24/2863. Note that the posterior root has barely "turned the corner" toward the anterolingual root. D; S. hispidus, ventrolabial view of UF 16199-9, Lm3, Reddick IA. E; S.

hispidus, lingual view of UF 16199-9, F; S. hispidus, lingual view of UF 16199-10, Rm3, Reddick IA. G; S. hispidus, ventral view of UF 16199-10. post= posterior.

* * *

Sigmodon fulviventer Allen 1889
(Figures 8, 17, 21)

Identification: In size and general dental pattern S. fulviventer approaches S. hispidus. In the few specimens I have seen the anterior cingulum on m2-m3 appears to be slightly more developed in S. fulviventer. The anteroconid of m1 in S. fulviventer is also usually smaller and more anteriorly-posteriorly compressed than it is in S. hispidus.

Temporal and geographic range of fossil material: No fossil record.

Sigmodon ochrognathus Bailey 1902
(Figures 2, 9, 17, 21)

Identification: Small S. ochrognathus can be identified easily on the basis of size, but this species demonstrates a size range which overlaps other hispidus group species. As in S. fulviventer, the anteroconid of m1 tends to be reduced and anteroposteriorly compressed.

Temporal and geographic range of fossil material: No fossil record.

Sigmodon arizonae Mearns 1890
Sigmodon mascotensis J.A. Allen 1897
(Figure 17)

Identification: I have not found any dental or mandibular features which will satisfactorily separate these species, either from each other or from S. hispidus. S. mascotensis averages larger than S. arizonae for most dental measurements (Table 1), but both species demonstrate considerable overlap with other hispidus group species.

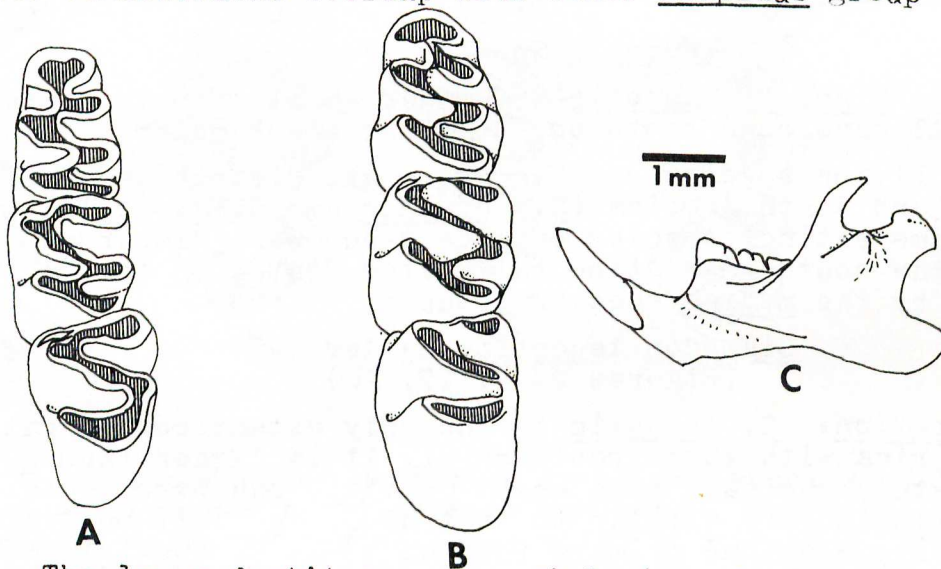


Figure 8 - The lower dentition and mandible in select species of Sigmodon. A; S. hudsouthensis, TMM 40857-3, Lm1-m3, Hudspeth fauna (Red Light local fauna). B; S. fulviventer, AMNH 20974 (female), Lm1-m3, Rosario, Mexico. C; S. alleni, labial view of mandible, MSU 12816 (male), 6 mi. W Capacuaro, Michoacan, Mexico.

* * *

Remarks: S. mascotensis and S. arizonae clearly represent recently evolved cryptic species, separable through computer analysis of a wide range of anatomical and karyological features (Zimmerman, 1970). Most of these features are not useful for the identification of fossil materials. Perhaps in the future we will be able to recognize a suite of subtle dental characteristics which will allow identification of all members of the hispidus species group, but until that time the best that can be done with late Pleistocene remains from the southwestern United States is to tentatively refer the material to species based upon the modern distribution of the group, size range, and overall gestalt.

Temporal and geographic range of fossil material: No fossil record.

+Sigmodon bakeri Martin 1974
(Figures 2, 10-12, 16, 17, 19-21)

Diagnosis: The first lower molar of S. bakeri possesses four well-developed roots, indicating alliance with the hispidus species group. S. bakeri differs from all extant members of this group by lacking an anterior cingulum on m²-m³. The anteroconid of m¹ is asymmetrical, extending labially and posteriorly. S. bakeri is smaller than any living species of Sigmodon.

Remarks: S. bakeri represents the only recognized extinct member of the hispidus species group. However, it is a rather distinct species without any apparent bearing on the evolution of this group. Sigmodon bakeri was replaced in Florida by S. hispidus during Rancholabrean time.

Temporal and geographic range of fossil material: Latest Irvingtonian through early Rancholabrean of Florida (I= Illinoian): Coleman IIA (?I; Martin, 1974); Haile VIIA (S; Martin, 1974); Williston IIIA (S; Martin, 1974); Bradenton 51st St. (S; Martin, 1974).

Fossil material examined: All specimens reported by Martin (1974).

Leucotis Species Group

Diagnosis: Sigmodon leucotis and other species in this group demonstrate three well-developed roots on the first lower molar.

Remarks: Living species of this group are distributed in Mexico (S. leucotis) and South America (S. peruanus and S. alstoni). During Pleistocene time extinct species of this group were dispersed throughout most of the southern continental United States in the range formerly occupied by the medius species group.

Sigmodon leucotis Bailey 1902
(Figures 2, 9, 17, 21)

Identification: S. leucotis is the only extant cotton rat north of South America with three roots on m¹. It is larger than S. libitinus; approximately the same size as S. curtisi. The worn dental pattern of S. leucotis is very similar to that of S. curtisi. However, there is occasionally a second primary fold on m³ in S. curtisi which is a very primitive feature that I have not seen in S. leucotis. The second primary fold on m² is usually reduced to absent in S. leucotis, whereas it tends to be well-developed in S. curtisi (most obvious on unworn teeth).

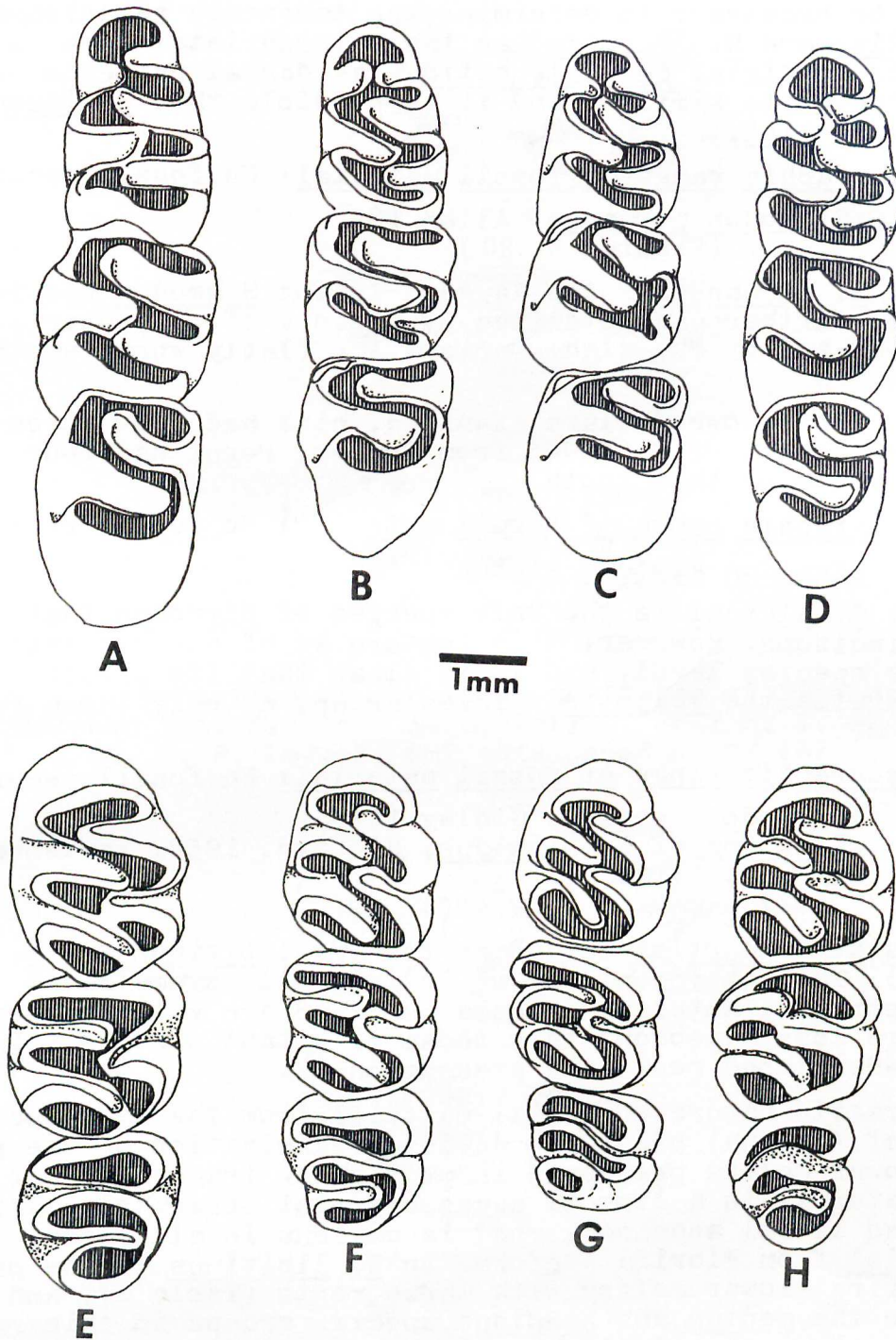


Figure 9 - Left lower and upper dentition in select species of Sigmodon. These specimens were chosen to illustrate variation, particularly of the m_2 , that can be expected due to wear. A, E; S. peruanus, USNM 279605 (sex unknown), Guayaquil, Ecuador. B, F; S. alleni, MSU 12816 (no data); C, G; S. ochrognathus, AMNH 136423 (male), Brewster Co., Texas. D, H; S. leucotis, MSU 1462 (female), Rancho Las Margaritas, 28 mi. S, 17 mi. W Vicente Guerrero, Durango, Mexico.

* * *

Remarks: Earlier (Martin, 1974) I indicated that cranial material would probably be necessary to determine the taxonomic relationship between S. curtisi and S. leucotis, as the interparietal bone is either absent or vestigial in S. leucotis. The dental patterns of these species are quite similar, and it is possible that S. leucotis evolved from S. curtisi.

Temporal and geographic range of fossil material: No fossil record.

Sigmodon peruanus Allen 1897
(Figures 9, 20)

Identification: S. peruanus is the largest living Sigmodon species (Table 1). It is further characterized by absence of the anterior cingulum on m2-m3 and by the highly prismatic, flatly worn reentrant fold borders.

Remarks: Of ten first lower molars examined, nine had only three roots and one specimen, USNM 303005 from Tumbes, Peru, had four well-developed roots on this tooth.

Temporal and geographic range of fossil material: No fossil record.

Sigmodon alstoni Thomas 1880

Identification: S. alstoni is the only species of Sigmodon that has grooved upper incisors. However, this feature is of dubious taxonomic value above the species level, and it is clear that its closest relationship is with the leucotis species group, as only three roots are present on m1.

Temporal and geographic range of fossil material: No fossil record.

+Sigmodon curtisi Gidley 1922
=Sigmodon cf S. hispidus, Hibbard, 1952. Vertebrata,
Art. 2: 1-14.
(Figures 2, 16, 19, 20)

Emended diagnosis: S. curtisi is larger than S. libitinus and S. bakeri (Table 1). The anteroconid of m1 is generally symmetrical or slightly asymmetrical. Anterior cingula on m2-m3 are well-developed. Lower molars are less hypsodont than those of extant species (Fig. 4). Three well-developed roots are present on m1.

Remarks: The fragile nature of dental material from the type locality (Curtis Ranch of Arizona) precludes detailed examination of the roots of the first lower molars preserved in mandibular fragments, but in none of this material is a lingual accessory root observable, while a well-developed labial accessory root is obvious in all cases.

S. curtisi from Florida conforms to S. libitinus in the preponderance of first lower molars with three roots (Table 2), and is intermediate to the medius and hispidus species groups in this regard.

Temporal and geographic range of fossil material: Late Blancan through early Irvingtonian (L= late, B= Blancan, Irv= Irvingtonian): Arizona: Curtis Ranch (LB; Gidley, 1922); Kansas: Kentuck (?E Irv; Hibbard, 1952; Martin, 1975); Florida: Inglis IA (?E Irv; Webb, 1974); California (cf): Vallecito Creek (?E Irv; Downs and White, 1968).

Fossil material examined: Arizona: Curtis Ranch, Cochise Co.; USNM 10510, 10511, 16605-16607. Florida: Inglis IA, Citrus Co.; UF 15155, 22016-22032. Kansas: Kentuck, McPherson Co.; KU 7361. California:

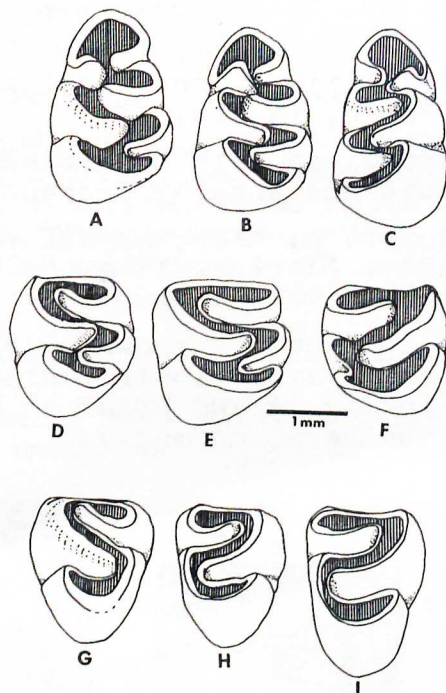


Figure 10 - Variation in the lower dentition of Sigmodon bakeri from Coleman IIA, Florida. A, B, Lm1; C, Rm1; H, I, Rm3 catalogued as UF 16202. D, E, Lm2; F, Rm2 catalogued as UF 16201.

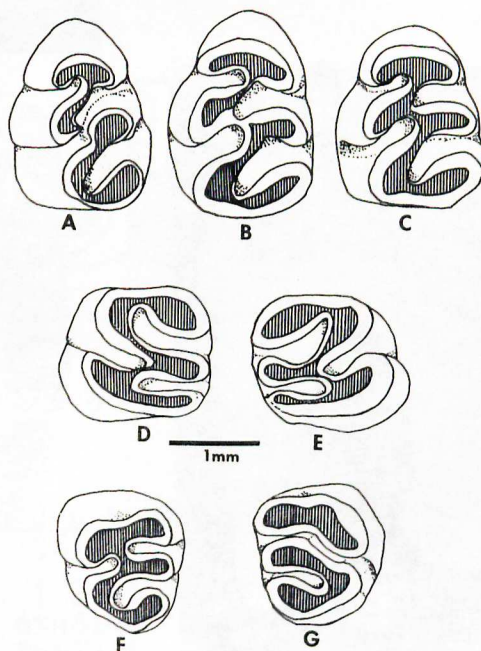


Figure 11 - Variation in the upper dentition of Sigmodon bakeri from Coleman IIA, Florida. All specimens catalogued as UF 16201. A-C LM1; D, RM2; E, LM2; F, LM3; G, RM3.

* * *

Vallecito Creek Fauna, 274 to 463 meters from top of sequence, San Diego Co.; LACM 1615/4389, 1114/3394, 1297/6941, 1114/3395, 1461/4445, 1615/4396, 1615/4398.

+Sigmodon libitinus new species
(Figures 2, 13, 19, 20)

Holotype: UF 21972, left mandible with moderately worn m1, m2, and m3. First incisor, condyloid and angular processes missing.

Type locality: Pit XVI, quarry A, near the defunct town of Haile (Haile XVIIA), Alachua County, Florida. NE $\frac{1}{4}$, NE $\frac{1}{4}$ Sec. 25, T9S, R17E; elevation approx. 25 meters above sea level.

Distribution and age: S. libitinus is known only from the type locality, of Irvingtonian (?Yarmouthian) age. Biostratigraphic data indicate deposition subsequent to Inglis IA and prior to Coleman IIA time in Florida (S.D. Webb, 1974 and Pers. commun.).

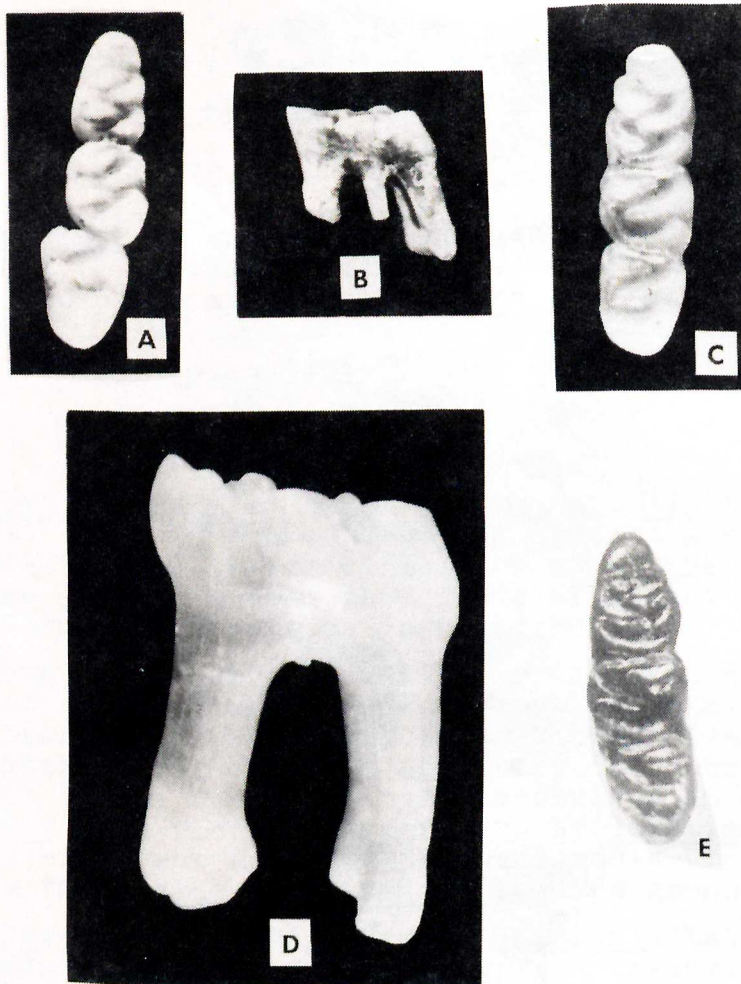


Figure 12 - The lower dentition of select species of Sigmodon. A, S. medius, uncatalogued specimen from the Beck Ranch Fauna, Texas; x7.5. B, S. bakeri, labial view of UF 16202(RAM 1), Lm1, Coleman IIA; x11. C, S. libitinus, UF 21975, Rm1-m3, Haile XVIIA; x7.5. D, S. medius, labial view of uncatalogued Lm1 from Beck Ranch, Texas. E, S. bakeri, UF 11703, Lm1-m3, Coleman IIA; x7.5.

* * *

Paratypes : UF 21973-22007; 22 right and 14 left mandibles, UF 22008-22015; five right and three left maxillae.

Etymology: libitinus; from the Latin Libitina, goddess of corpses.

Diagnosis and comparisons: Measurements of the lower dentition (Table 1) indicate that S. libitinus is a small cotton rat, approximately the size of S. bakeri. The first lower molar has three roots, occasionally four (Table 2). Of those specimens that have four roots, the labial root is generally well-developed, but the lingual root is not. The anteroconid of m1 extends posterolabially in 90% of the specimens (Table 2). In this feature S. libitinus is similar to S. bakeri. The anterior cingulum of m2-m3 is absent from 85% of the specimens, a feature also more typical of S. bakeri than of S. curtisi. However, those specimens from Haile XVIIA which are not similar in crown morphology to S. bakeri can be duplicated by specimens of S. curtisi from Inglis IA.

These data provide a composite of a small cotton rat that has an occlusal pattern most similar to S. bakeri. The m1 is buttressed by roots in a fashion typical of the larger S. curtisi. This association of features allows two hypotheses regarding phylogenetic relationships: 1) S. libitinus was derived from S. curtisi and is ancestral to S. bakeri and 2) S. libitinus was derived from S. curtisi, but resemblance to S. bakeri is the result of parallel evolution.

In either case, S. libitinus represents an evolutionary grade temporally distinct from either S. curtisi or S. bakeri, and therefore is of biostratigraphic significance.

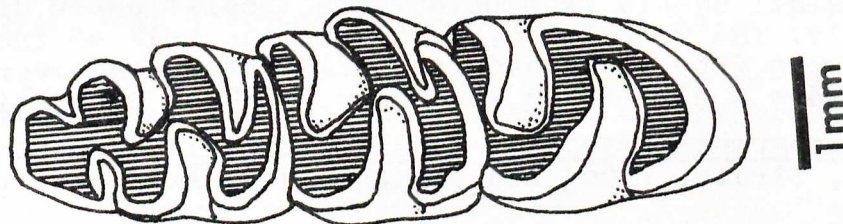


Figure 13 - Lower dentition of Sigmodon libitinus. Holotype Lm1-m3, UF 21972.

* * *

+Sigmodon hudsouthensis Strain 1966
(Figures 8, 16, 19, 20)

Unfortunately, I lost the holotype m1 (TMM 40240-1) before it could be properly studied. However, I had measured it, and these data are included in Table 1. Considering that my species groups are defined upon the number of roots on the first lower molar, and that the paratypes collected from the type locality of S. hudsouthensis are inadequate for determination of root number and development, the diagnosis reported here, insofar as roots are concerned, is based upon material collected by William Akersten from the Red Light Bolson (Akersten, 1970). According to Akersten (1970, p. 86):

"The Red Light local fauna correlates very well with the

Hudspeth local fauna...from the Hueco Bolson just upriver from the Red Light Bolson. The stratigraphic successions are very similar and faunal differences are the result of accidents of collection and different taxonomic interpretations."

Akersten contends that "There can be little doubt that these two faunas were contemporaneous." He further identifies Sigmodon hudspethensis from the Red Light locality.

I have studied the available material from both localities in detail and can find no quantitative or qualitative differences between Strain's paratypes and Akersten's material that does not fall into the realm of individual variation. With the exception of comments on root development, the emended diagnosis is based upon Strain's paratypes.

Since both Akersten (1970) and I agree that the fossil Sigmodon from the Red Light and Hudspeth faunas are conspecific, it does not seem prudent to either 1) designate a neotype from inadequate paratypes or 2) name a new species based upon Akersten's collections. It is my opinion that further collections from the Hueco Bolson will confirm the diagnosis and that adding another name will merely add confusion.

Emended diagnosis: The worn dental pattern of S. hudspethensis resembles that of S. medius. Reentrant angles are obtuse and tend to be shallow. The dentition differs from the medius species group in possessing a well developed labial root on the first lower molar (obvious in TMM 4057-10 from the Red Light locality. The m1 of TMM 4057-10 also has a fourth, peg-like lingual root). The teeth are large, about the size of those of small S. hispidus, but are less hypsodont than those of S. hispidus.

Remarks: The small sample from both Texan localities is difficult to assess properly. The worn teeth, making up the bulk of the sample, appear to be worn from a brachyodont configuration. However, a few unworn teeth show a similarity to unworn teeth of S. curtisi.

Temporal and geographic range of fossil material: Hudspeth Fauna (Hueco Bolson, Strain, 1966; Red Light Bolson, Akersten, 1970; ?late Blancan).

Fossil material examined: Hudspeth local fauna, Hueco Bolson, Hudspeth Co.: TMM 40240-1, 40240-2; Red Light local fauna, Red Light Bolson, Hudspeth Co.: TMM 40857-10, 40857-11.

+Medius Species Group

Diagnosis: Members of this group, S. medius and S. minor, are the most primitive of known Sigmodon species. They are small cotton rats with little development of labial and lingual roots on the first lower molar. The capsular process for the reception of the incisor is poorly developed in these species; a primitive trait for cricetid rodents in general.

+Sigmodon medius Gidley 1922

=Sigmodon intermedius Hibbard 1938. Trans. Kansas Acad. Sci., 40: 239-265.

=Sigmodon minor (in part), Cantwell, 1975. Jour. Mammalogy, 50(2): 375-378.

=Sigmodon minor, Eshelman, 1975. C.W. Hibbard Memor. Vol. 4, Univ. Michigan, Ann Arbor: 1-60.

(Figures 1, 2, 5, 7, 12, 16, 18, 19, 20)

Emended diagnosis: S. medius has only two well developed roots on the first lower molar. When accessory roots are present, the labial root is always better developed than is the lingual root. However, both are usually tiny pegs and may be located medially rather than on the peripheral margins of m1 (Figs. 1, 12). Reentrant folds on all teeth are relatively shallow. Relative to all other Sigmodon species, the dentition is brachydont (Fig. 2). S. medius averages larger than S. minor and is distinctly smaller than S. hudsouthensis.

Remarks: Hibbard (1972) emphasized the taxonomic utility of dental root morphology, particularly within the genus Sigmodon. Large samples of medius group species now allow quantitative examination of the variation expressed by these roots. Although study of the roots of all molars is instructive, only the first lower molar appears now to have extensive taxonomic utility.

Four roots are present in two of 54 specimens of S. medius from Loc. 3 of the Rexroad fauna. The two accessory roots are located medially and are very minute. These accessory roots may have aided in supporting the m1, but the variation expressed in position and size of these roots (Table 2) indicates that the genetic fields governing root development were not fixed at this level of evolution. Coupled with the brachydont nature of the dentition, it is conceivable that S. medius, and probably S. minor as well, represents a grade in transition between a granivorous and browsing mode of existence to one of pastoral grazing.

The Rexroad Sigmodon was first described by Hibbard (1938) as S. intermedius, distinct from S. medius primarily on the basis of size. Statistical comparisons made between members of the medius species group by Martin (1970) suggested synonymy of S. intermedius under S. medius. This taxonomic arrangement was later followed by Hibbard (1972).

Distinct populations of Sigmodon medius are recognizable from deposits in the Meade Basin of Kansas. Their descriptions, including referred specimens from other states, are as follows:

+Sigmodon medius medius

Holotype: USNM 10519; the holotype of S. medius described by Gidley (1922).

Type locality: Post Ranch, Cochise County, Arizona.

Distribution and age: During much of Blancan time, S. m. medius was probably continuously distributed from southern California through Arizona and Texas and north through central Kansas. Samples from Texas (Blanco, Beck Ranch) now classified as indeterminate subspecies of S. medius will probably be shown to belong to this subspecies.

Referred specimens: Arizona: Benson Ranch, Cochise County; USNM 10520-10523. Tusker, Loc. 15-24, Graham Co.; UAVP 899, 905, 914, 914, 922, 925, 927-936, 938-941, 945, 949, 966-970, 972-1003, 1007, 1020, 1023-1025, 1030, 1036-1042, 1054, 1056, 1057, 1059-1069, 1075, 1077-1079, 1081, 1087, 1089, 1090, 1094, 1100, 1104, 1105, 1111, 1114, 1118, 2494-2510, 2513, 2514, 2519, 2700-3053. Kansas: Rexroad, Loc. 3, Meade Co.; UMMP 29162, 29669, 31085, 31086, 41193, 44589, 56249, KU 3887. Sanders, Locs. 1, 2, 4, Meade Co.; UMMP 32003-32005, 31997, 56247, 56248, 50263, 50264. California: Layer Cake fauna, 2057 meters from top of sequence, San Diego Co.; LACM 1711/7005. Arroyo Seco fauna, 1494 to 1631 meters from top of sequence, San Diego Co.; LACM 6554/13754, 6552, 6550, 6552/12505.

Table 3 - Statistical comparison of Sigmodon samples from the Wendell Fox Pasture (WFP) and Rexroad Loc. 3 (R3) deposits. N= number of specimens, \bar{x} = mean, s^2 = variance, t= Student's t value, p= probability value, *= statistically significant difference at 0.10 level, MA= mandibular alveolar length.

	WFP			R3			t	p
	N	\bar{x}	s^2	N	\bar{x}	s^2		
MA length	3	6.27	.007	8	6.17	.028	.01	.900
Length m1	5	2.16	.002	39	1.98	.015	*3.09	.010
Length m2	5	1.60	.002	23	1.56	.009	.90	.4>p>.3
Length m3	2	2.02	.040	15	1.93	.016	.90	.4>p>.3
Width m1	6	1.53	.001	41	1.43	.004	*10.46	.001
Width m2	5	1.67	.003	23	1.56	.005	*3.19	.010
Width m3	2	1.59	.003	15	1.48	.006	*1.89	.1>p>.05

Diagnosis: This subspecies averages smaller than S. m. hibbardi in length of m1 and width of m1, m2, and m3 (Table 3). This quantitative distinction is described in further detail under S. m. hibbardi.

+Sigmodon medius hibbardi new subspecies

Holotype: UMMP 35093, right mandible with first incisor and m1-m3.

Type locality: Wendell Fox Pasture, Meade County, Kansas.

Distribution and age: S. m. hibbardi is recognized only from the type locality. The exact age of this locality is not known, but it probably represents a period of deposition during Blancan time.

Paratypes: UMMP 57050-57054.

Diagnosis and comparisons: Measurements of the sample of S. medius from the Wendell Fox Pasture were graphed by Martin (1970), but at that time no taxonomic reference was attempted. The mean values of four of the seven measurements (Table 3) from the Wendell Fox Pasture Sigmodon are significantly different from those of S. m. medius of the Rexroad fauna ($p < .10$). S. m. hibbardi represents a large subspecies of S. medius which apparently does not differ in any qualitative manner from S. m. medius.

Etymology: This subspecies is named in honor of the late Claude W. Hibbard of the University of Michigan for his manifold contributions to the field of Pliocene and Pleistocene paleontology.

Remarks: I do not appreciate making taxonomic distinctions based solely on size, nor do I usually accept statistical significance at anything greater than the .05 level. However, for reasons which will be expressed shortly, I suspect that in Sigmodon (and perhaps in all r-selected small mammals) we are dealing with a group capable of rapid speciation that may not be reflected by gross morphological changes in hard parts. This certainly seems to be the case with the hispidus species group, which I have considered earlier (see especially S. arizonae and S. mascotensis).

+Sigmodon medius subspecies indeterminate

S. medius has been recovered from the localities listed below, but small samples preclude satisfactory statistical treatment at this time. Fossil specimens examined are noted with each locality account:

Texas: Blanco, Crosby Co. (B; W.W. Dalquest, pers. commun.); MUVP 7146. Beck Ranch, Crosby Co. (B; W.W. Dalquest, pers. commun.); uncatalogued sample. Florida: Haile XVA, Alachua Co. (?LB; Robertson, 1976); UF 12334, 12336, 12338, 12342. Nebraska: Sand Draw, Brown Co. (EB; Hibbard, 1972); UMMP 57056. Kansas: Benders, Meade Co. (EB; C.W. Hibbard, pers. commun.; Martin, 1970); UMMP 45820. White Rock, Republic Co. (B; Eshelman, 1975*). California: Transition zone between Arroyo Seco and Vallecito Creek faunas, 914 to 991 meters from top of sequence (B; Downs and White, 1968); LACM 1588/4442, 1451/4447.

+Sigmodon minor Gidley 1922

= Sigmodon hilli Hibbard 1941. Bulletin Kansas Geological Survey, No. 38: 197-220.

= Sigmodon minor (in part), Cantwell, 1969. Journal Mammalogy, 50(2): 375-378.

(Figures 1, 5, 6, 14-16, 18-20)

Emended diagnosis: S. minor is the smallest known Sigmodon. The dentition of S. minor is most similar to that of S. medius. Unworn and slightly worn teeth of S. minor demonstrate relatively deep and narrow reentrant folds as compared to S. medius, but separation of isolated, well-worn teeth of these species is difficult.

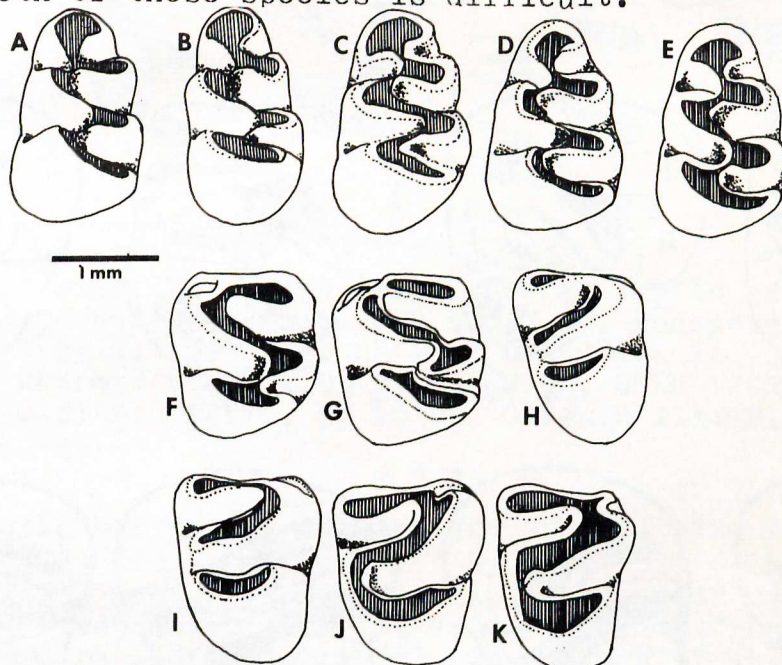


Figure 14 - Variation in the lower dentition of Sigmodon minor from Borchers, Kansas. A-E; UMMP 51309 Lm1. F, G; UMMP 51311, Lm2, H-K; UMMP 51515, Rm3.

*Eshelman's data (Eshelman, 1975, Table 7) suggests that the White Rock Sigmodon is assignable to S. m. medius. However, since some of his published measurements are at variance with mine, an indeterminate status appears to be most reasonable now.

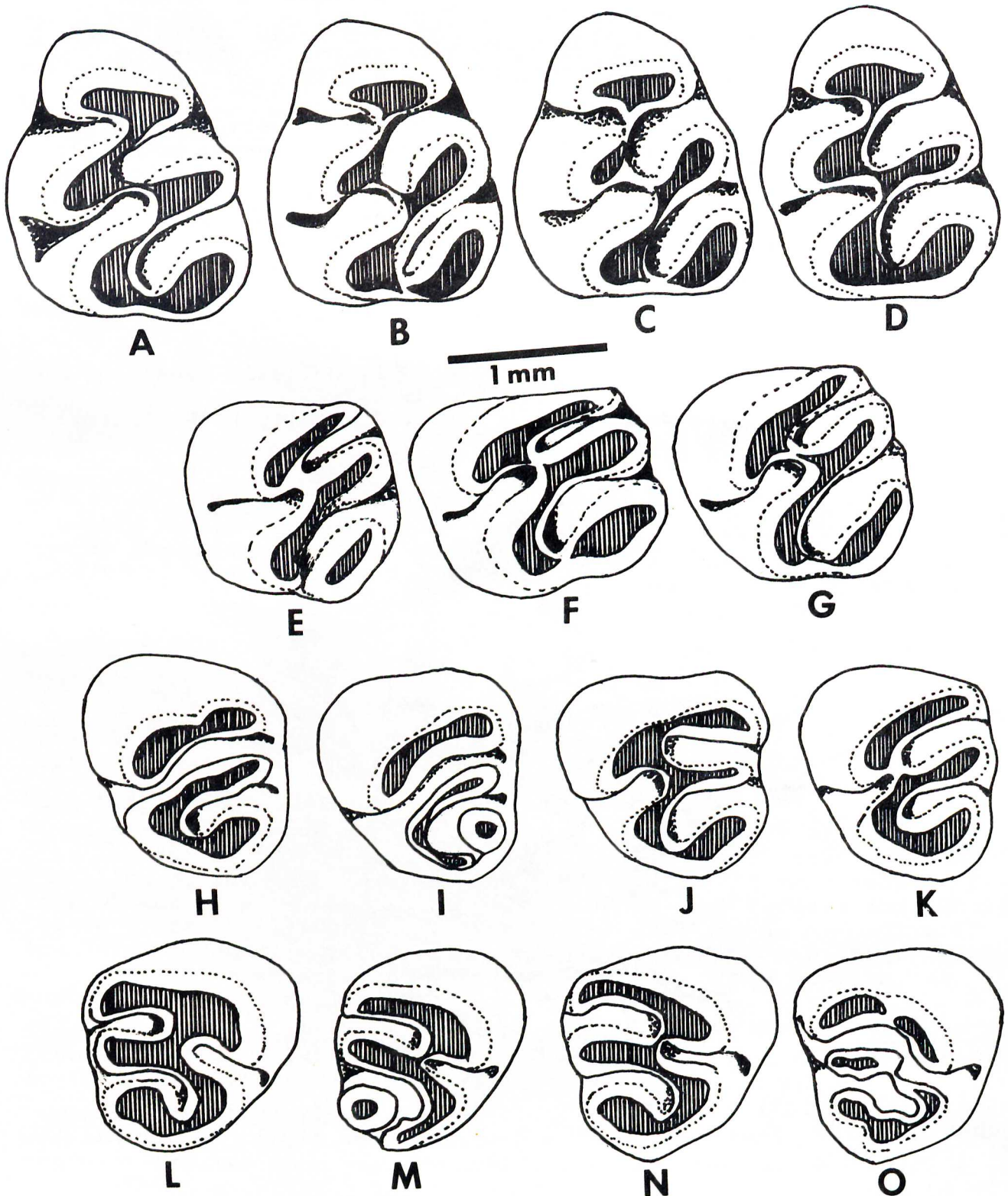


Figure 15 - Variation in the upper dentition of *Sigmodon minor* from Borchers, Kansas. A-D; UMP 51308, LM1. E-G; UMP 51306, LM2. H-K; UMP 51304, LM3. L-O; UMP 51303, RM3.

* * *

Remarks: The primary distinction between S. hilli and S. minor, as originally defined by Hibbard (1941) was based upon size. S. hilli was considered to be larger than S. minor. Cantwell (1969), Martin (1970, 1974), and Eshelman (1975) independently demonstrated that this dichotomy does not exist. Further corroboration is provided here in Table 1 and Figs. 17 and 18. Recent preliminary studies by Hibbard (1972) suggested that the number of roots on the first lower molar of the Borchers Sigmodon differed from the number on the m1 of the Rexroad, Sanders, and Sand Draw Sigmodon. This sort of a distinction was not noted by Eshelman (1975), and Table 2 further demonstrates the close conformity of the Borchers and Rexroad Sigmodon in this regard. My sample of first lower molars from the Borchers local fauna (N= 27) includes five with four roots. A random selection of 27 S. medius from Rexroad, Loc. 3, includes two specimens with four roots on this tooth. This difference is not statistically significant (χ^2 with Yates Continuity Correction = 0.657; one degree of freedom).

Temporal and geographic range of fossil material: Late Blancan to early Irvingtonian: Kansas; Borchers (LB; Hibbard, 1941). Arizona; Curtis Ranch (EIr; Gidley, 1922).

Fossil material examined: Kansas: Borchers, Meade Co.; UMMP 35766, 56244, 56355, 51302-51309, 51311-51314, KU 5431. Arizona: Curtis Ranch, Cochise Co.; USNM 10512-10518, 16608-16611.

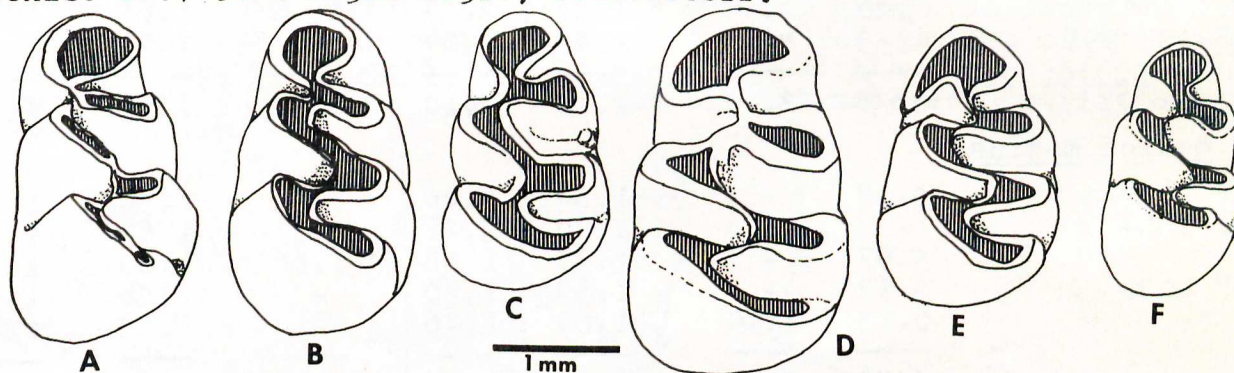


Figure 16 - Comparison of the first lower molar in select species of Sigmodon. A; S. hudspehthensis, TMM 40857-11, Hudspeth fauna (Hudspeth local fauna). B; S. hispidus, UF 16197, Reddick IA. C; S. medius, UMMP 44589, Rexroad Loc. 3. D; S. peruanus, USNM 120236 (male), Puna Is., Ecuador. E; S. bakeri, UF 16202, Coleman IIA. F; S. minor, UMMP 51309, Borchers.

* * *

Remarks: Within the medius species group three size classes of samples* may be found: 1) small, represented by S. minor, 2) medium, represented by S. medius medius, and 3) large, represented by S. m. hibbardi and an undescribed taxon from the Vallecito-Fish Creek sequence of California (Downs and White, 1968). Chronology of the large form is problematical. Within the Vallecito-Fish Creek sequence a large member of the medius species group may be found in the transition zone between the Arroyo Seco and Vallecito Creek faunas (Table 4), above deposits containing S. medius and below those containing (cf) S. curtisi. In size and dental morphology this taxon resembles S. m. hibbardi from the Wendell Fox Pasture locality of Kansas. If both samples could be

*Recognized as taxa; there are finer subdivisions which I consider as geographical subspecies, but have not named. See Martin (1970) and discussion on p.27.

* * *

Table 4 - Measurements in mm of the lower dentition and mandible of Sigmodon samples from the Vallecito-Fish Creek beds of California. LCF= Layer Cake Fauna, ASF= Arroyo Seco Fauna, VCF-ASF= transition zone between Arroyo Seco Fauna and Vallecito Creek Fauna. MA= mandibular alveolar length, l= length, w= width, \bar{x} = mean. Elevation in meters (m) from top of sequence is provided for each specimen.

	MA	lm1	lm2	lm3	wm1	wm2	wm3
cf <u>S. curtisi</u>							
VCF 274 m	-	-	1.84	-	-	2.02	-
VCF 335	7.64	-	1.94	2.66	1.98	2.29	2.05
VCF 442	-	-	1.85	-	-	1.99	2.05
VCF 463	7.64	2.79	2.06	2.58	1.85	2.00	1.97
"	6.99	2.47	2.00	2.82	2.07	2.24	2.04
"	-	2.41	1.96	2.47	2.00	2.27	1.83
"	-	-	1.82	-	1.75	1.86	-
	\bar{x}	\bar{x}	\bar{x}	\bar{x}	\bar{x}	\bar{x}	\bar{x}
	7.42	2.56	1.92	2.63	1.93	2.10	1.97
cf <u>S. medius</u>							
VCF-ASF 975 m	6.10	2.14	1.73	2.25	1.47	1.70	1.60
"	-	-	1.60	2.08	-	1.50	1.48
"	6.20	2.24	1.77	2.04	1.48	1.65	1.63
VCF-ASF 991	6.53	-	1.69	2.04	-	1.73	1.62
	\bar{x}	\bar{x}	\bar{x}	\bar{x}	\bar{x}	\bar{x}	\bar{x}
	6.28	2.19	1.70	2.10	1.48	1.65	1.58
<u>S. medius medius</u>							
ASF 1494 m	5.68	-	1.54	2.06	1.45	1.50	1.36
ASF 1554	-	-	1.70	2.21	-	1.64	1.59
"	5.97	-	1.67	1.96	1.66	1.60	1.51
ASF 1631	5.92	-	1.59	1.80	-	1.56	1.39
"	6.15	2.14	1.62	1.76	-	1.55	1.49
	\bar{x}	\bar{x}	\bar{x}	\bar{x}	\bar{x}	\bar{x}	\bar{x}
	5.93	2.14	1.62	1.96	1.56	1.57	1.47
<u>S. medius medius</u>							
LCF 2057 m	5.79	2.03	1.72	1.89	1.44	1.51	1.45
"	-	-	1.51	2.02	-	1.44	1.47
	\bar{x}	\bar{x}	\bar{x}	\bar{x}	\bar{x}	\bar{x}	\bar{x}
	5.79	2.03	1.62	1.96	1.44	1.48	1.46

definitely shown to belong to a single taxon, the evidence would suggest placement of the Wendell Fox Pasture locality in Blancan time, somewhat above Rexroad Loc. 3. However, Hibbard (pers. commun.) tentatively considered Wendell Fox Pasture to represent a period of deposition prior to Rexroad Loc. 3. Coupled with the preliminary conclusions of Downs and White (1968) that the Arroyo Seco-Vallecito Creek Transition zone Sigmodon (species B of Downs and White, 1968) is a taxon distinct from S. medius and S. curtisi, it becomes conceivable that the similarities in form between the Wendell Fox Pasture population and that from the Vallecito-Fish Creek deposits represent parallelism.

An evolutionary trend toward small size is apparent within the medius species group. The latest deposits in which a member of the medius species group may be found (Borchers of Kansas and Curtis Ranch of Arizona) contain the smallest individuals of this group. During Curtis Ranch time these small cotton rats were sympatric with a member

of the leucotis species group, S. curtisi. Cantwell (1969) synonymized S. medius under S. minor, concluding that only one widespread temporal and geographic species was represented. This suggestion is certainly within reason and deserving of careful evaluation.

As demonstrated by Cantwell (1969) and verified by independent measurements I made of the same sample, the range of size evidenced by teeth of Sigmodon from the Tusker locality of Arizona includes many specimens from Curtis Ranch (and Borchers). Further, I agree with Cantwell that the morphology of the teeth from these localities demonstrates striking similarities. New material from Arizona will, I suspect, provide more samples intermediate to Tusker and Curtis Ranch. Nevertheless, biological reality is probably stilted by the synonymy of S. medius under S. minor.

It is axiomatic that the only valid species definition is one that incorporates reproductive isolation. Because this phenomenon can never be directly demonstrated in extinct populations distributed allochronically, we must attempt to invoke this dictum indirectly by considering the morphologic variation of closely allied living species, together with evidence provided by the fossil record. Measurements taken from the teeth of living Sigmodon species are portrayed in ratio diagram form in Fig. 17. In addition, a large sample of fossil S. hispidus from the Rancholabrean Reddick IA deposit of Florida is compared to extant S. hispidus from Florida. Fig. 17 demonstrates that conformity exists within the hispidus species group. Variance from the hispidus species group response is seen only for members of the leucotis species group, S. leucotis and S. peruanus. Within the hispidus group, only S. hispidus demonstrates any notable intraspecific variation with regard to size.

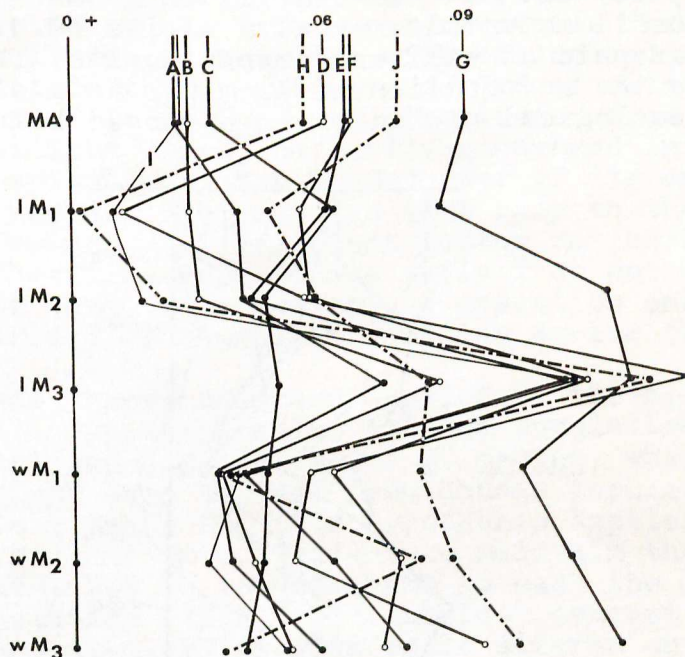


Figure 17 - Composite ratio diagram of measurements of the lower dentition and mandible in extant species of Sigmodon. A, S. alleni; B, S. hispidus berlandieri; C, S. leucotis; D, S. fulviventris minimus; E, S. hispidus (extant, Florida); F, S. hispidus (fossil, Reddick IA); G, S. peruanus; H, S. mascotensis; I, S. ochrognathus; J, S. arizonae. MA= mandibular alveolar length, l= length, w= width. Standard is S. bakeri from Coleman IIA.

* * *

When these data are compared to similar data for members of the medius species group (Martin, 1970, 1974; Fig. 18), it is clear that the size differences noted between the Benson and Curtis Ranch Sigmodon do not fall within the boundaries of a single species of Sigmodon as demonstrated by living species. Further corroboration is gained by a consideration of the distinction between S. m. medius and S. m. hibbardi. Differences in size between these subspecies are actually slightly greater than the differences between extant populations of S. hispidus from Florida (compare Figs. 17 and 18).

I conclude that the small Sigmodon from the Borchers local fauna of Kansas and the Curtis Ranch local fauna of Arizona represents a distinct species, S. minor, that would have been reproductively isolated from its early progenitor, the Rexroad and Benson S. medius. Intermediate populations exist, but probably should carry no formal taxonomic names except S. medius or S. minor, depending upon best fit. In the above conclusion I may be wrong, as the medius-minor lineage can be regarded as a linear, time-transgressing rosencreis, perhaps unworthy on that basis alone of taxonomic partitioning. But I take the position that I do, at least in part, in order to solidify methodology. Species categorization should only be affixed to a thanatopopulation when the full spectrum of features from extant relatives has been first considered. A knowledge of statistical variation and its meaning is fundamental in this process (see Krohn, 1979). Evidence from living Sigmodon suggests that the evolution of the genus is characterized by the rapid formation of species groups, and that the denotation of these sibs may differ somewhat in size and size patterns (re. Figs. 17, 18) but not necessarily in gross morphology. Statistical analyses of fossil materials reveal a series of discrete size classes, including geographic as well as temporal units. The whole of the evidence mandates the recognition of S. minor as a distinct species. An evolutionary-ecological mechanism is proposed below.

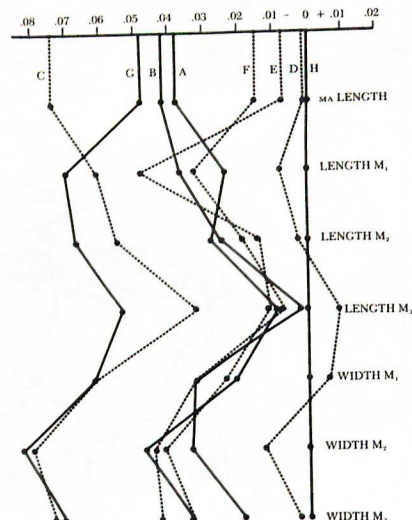


Figure 18 - Composite ratio diagram of measurements of the lower dentition and mandible of the medius species group from Kansas and Arizona (from Martin, 1974). A= S. medius medius, Benson. B= S. medius medius, Tusker. C= S. minor, Curtis Ranch. D= S. medius hibbardi, Wendell Fox Pasture. E= S. medius medius, Rexroad Loc. 3. F= S. medius medius, Sanders. G= S. minor, Borchers. H= S. bakeri, Coleman IIA.

* * *

When two closely related mammalian species are sympatric, they will usually be found to differ substantially in size. This sympatric morphometric response is termed character displacement, and has been reported in many species (McNab, 1971; Martin, 1967, 1968b). In some species character displacement also occurs between males and females (Jolicoeur, 1963). This mechanism allows for maximization of natural resources and minimization of competition. I interpret the small size of the Borchers and Curtis Ranch S. minor to be a response to the invasion of Sigmodon habitats by the larger, more advanced S. huds-pethensis and its relative, S. curtisi. The absence of S. curtisi from the Borchers local fauna is not particularly troublesome, as S. curtisi-like species are recorded from late Blancan and early Irvingtonian deposits ranging from California to Florida (including the Kentuck local fauna of Kansas; see Hibbard, 1952 and Martin, 1975), and it is reasonable to assume that the medius species group, distributed geographically in a similar fashion, responded phenotypically in a fairly uniform manner throughout most of its range. An exception to this pattern, which bolsters the concept of evolution of S. minor through character displacement, is seen in the Arroyo Seco-Vallecito Creek transition zone S. medius (as noted previously, this is a population characterized by its relatively large size). This population was directly replaced during Vallecito Creek time by a member of the leucotis species group similar to S. curtisi. Coexistence was not possible, and the large size of individuals within the S. medius population presumably contributed to its demise.

Speciation events within the genus Sigmodon generally support the notion that speciation occurs as a relatively brief, explosive event (see Eldredge and Gould, 1972). In fact, the vast majority of small mammal speciation events that I can recognize from the Pliocene and Pleistocene fossil record coincide with ecological or geological shifts of some magnitude that break up a period of relatively prolonged stasis. Populations of S. medius were distributed from coast to coast for more than two million years, basically unchanged in size and dental anatomy. Within a period less than one-quarter of its ancestor's lifespan, S. minor was derived, existed (but only on the High Plains), and went extinct. New and more efficient cotton rat herbivores were introduced during that time period, and while I do not wish to digress now to discuss other taxa, this pattern of evolution and replacement occurs also in a variety of mammalian families during the same contracted interval.

Line and grade theory has been applied to the medius species group (Martin, 1970). Hypothetically, Arizona populations of S. minor were derived from Arizona populations of S. medius, whereas Kansas populations of S. minor were derived from Kansas populations of S. medius. The hereditary basis for this hypothesis implies that lateral gene flow (between states) is sufficient to maintain the integrity of each temporal species, but is insufficient to mask the integrity of each geographic population (this "multispecies" concept has recently been reviewed by Van Valen, 1976). The ratio diagram on which this hypothesis is based is reproduced here (Fig. 18).

DISCUSSION

From their first appearance in late Pliocene deposits of the central and western United States, cotton rats rapidly spread throughout most of the continental United States in what may have been the equivalent to today's southeastern and southwestern oldfield and

LAND MAMMAL AGES	MAGNETIC STRATIGR. YEARS B.P. (x 10 ⁶)	California	Arizona	New Mexico	Nebraska	Kansas	Texas	Louisiana	Georgia	Florida	SIGMODON Sp.
RANCHOLABREAN				Brown Sand Wedge			Friesenhahn Cave	Kimball Creek		Devil's Den	hispidus
							Moore Pit		Ladds	Reddick IA	
										Williston IIIA	
IRVINGTONIAN	0.69									Coleman IIA	bakeri
										Haile XVIIA	libitinus
		Vallecito Creek (274-463 m)					?Kentuck				cf
	1.86		Curtis Ranch							Inglis IA	curtisi
BLANCAN						Borchers		?Hudspeth			minor
	2.43										hudspethensis
						White Rock				Haile XVA	
		Arroyo Seco (1494-1631 m)			Sand Draw	Sanders	?Blanco				
	3.32		Post Ranch			Rexroad (Loc. 3)					
	GILBERT	Layer Cake (2057 m)									medius

Figure 19 - Correlation of some deposits in North American containing fossil *Sigmodon*. Many deposits of Sangamonian and Wisconsinian age have been omitted. This chronological framework is partly based on the work of Hibbard (1972), Lindsay, Johnson, and Opdyke (1975), and Opdyke, Lindsay, Johnson, and Downs (1977).

* * *

prairie plant communities. Conditions suitable for their opportunistic (r-selected) lifestyle existed as far north as Nebraska and as far west as the now arid deserts of southern California. Although we cannot be certain of their evolutionary and geographic origin, we can speculate on the levels of adaptation to a pastoral, grazing mode of energy capture in the earliest appearing cotton rats. Comparisons between members of the medius and leucotis species groups will serve to illuminate the extremes of adaptation in the genus.

The diminutive S. medius and S. minor appear to have had several disadvantages relative to their more highly advanced relatives. First, if we assume that the size of S. minor was approximately the same as that of a large peromyscine such as Peromyscus gossypinus (about 25g; original data), then we find that the theoretical weight-specific metabolic rate of this small cotton rat was distinctly elevated over that of an average S. curtisi at about 100g. Utilizing the equation M_b/W (weight-specific basal metabolic rate in cc $O_2/g-hr$) = $3.4W^{-0.25}$ for mammals, where W = weight, we find that the theoretical M_b/W of S. minor was approximately one and one-half times that of S. curtisi. This increase in M_b/W also correlates with a decrease in home range size (McNab, 1971). Applying McNab's formula for home range (R), $R = 0.05M_b/W$ for "croppers" we see that the theoretical home range of S. minor was reduced by a factor of 2.8 times from that of S. curtisi. The tiny S. minor was probably forced to expend more energy in less area than were larger cotton rats of the leucotis (and hispidus) species group. Additionally, the level of hypsodonty evidenced by the medius species group was far below that of S. curtisi (Fig. 2).

While small size is often a good (theoretical) strategy, this particular strategy, at least in cotton rats (and horses) has not panned out. Further speculation here is probably unwarranted, for it is not clear that 1) the environmental conditions that would favor large size, such as colder winters, were present during the push for large size or that 2) heightened aggression or superior fecundity are genetically coupled with large size in Sigmodon. Runway-making rodents such as Sigmodon and Microtus are antisocial, aggressive beasts in general. Further, while weight-specific metabolism points to a clear energetic advantage of large size, it must also be noted that small cotton rats should require less energy on an absolute scale for survival. Yet this latter advantage may be offset by increased activity and increased surface area to volume ratio. In any case, the fossil record is clear. The small cotton rats; S. medius, S. minor, S. libitinus, and S. bakeri are extinct.

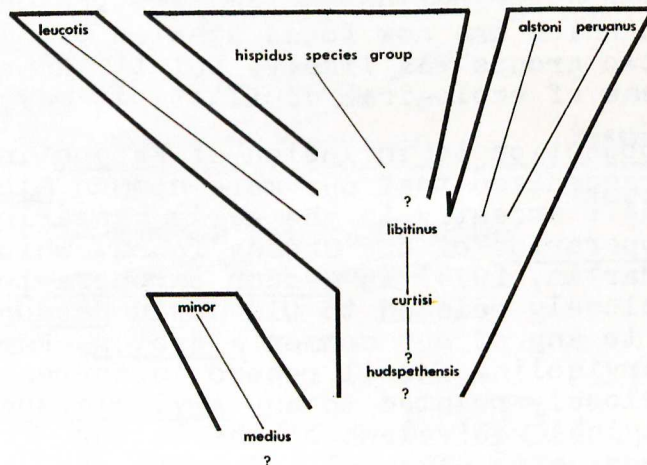


Figure 20 - Possible phylogeny for the rodent genus Sigmodon.

Dominance of pastoral communities by the leucotis species group begins approximately during the Blancan and culminates during the Irvingtonian (Fig. 19). Large cotton rats of the leucotis species group replace the medius species group throughout its geographic range. This replacement is securely documented in the Vallecito-Fish Creek beds of southern California, where (cf) S. medius of the Arroyo Seco-Vallecito Creek transition zone is replaced by (cf) S. curtisi during Vallecito Creek time. Large and with moderately hypsodont dentitions, members of the leucotis species group possess a stout labial root on the first lower molar.

It seems likely to me that S. leucotis populations in the Mexican highlands represent relics of the middle Pleistocene radiation of the leucotis species group. Sigmodon leucotis is found in a variety of unusual habitats, including bare volcanic talus. Species of the hispidus group are usually trapped in the more conventional oldfield and prairie ecosystems that surround leucotis habitats (Baker, 1969). Since extinct members of the leucotis species group have been recovered from numerous deposits across North America, it is highly probable that these cotton rats once dominated austral pastoral habitats, much as does the hispidus group today. The pastoral arvicolines show similar, and perhaps ecologically related chronological replacements. Species recognized as Allophaiomys, Pitymys, or Neodon are not recognized in North America until Irvingtonian time (Martin, 1974, 1975), but they become fairly widespread through the North American high plains during this time. Evolution or immigration of the Microtus complex (including such species as M. pennsylvanicus, M. xanthognathus, M. chrottorhinus, M. richardsoni, M. oregoni and other species with at least five closed triangles and a symmetrical anterior loop on m1) begins during the latest Irvingtonian and ends during the RanchoLabrean. With the exception only of Pitymys ochrogaster (taxonomy after Martin, 1974), all extant arvicolines with dental patterns similar to those arvicolines found in middle Pleistocene deposits (that is; m1 with three to five triangles; in five triangle forms, triangles three and five are confluent; or m1 as in *Neodon, with elongate and asymmetrical anterior loop) are either sylvan and fossorial (e.g., P. pinetorum) or are found in a variety of Mexican and Central American habitats (e.g., P. oaxacensis, P. guatemalensis, P. quasiater, M. (?Neodon) umbrosus), often at high elevation.

Although the grazing arvicolines are primarily Holarctic, temperate-adapted species, their modern presence in Mexico and Central America proves that their distribution in the past included all of the geographic areas within which are now found species of Sigmodon. Some contact between these two groups was likely, but it is not possible now to pinpoint any areas of ecological conflict. It may be, as I have

* I would have little objection to inclusion of Neodon in Microtus as long as it would be recognized that our more common Microtus species probably do not find their ancestry in the early appearing arvicolines such as "Microtus" paroperarius of the Cudahy fauna; which I have classified elsewhere (Martin, 1974) as Neodon paroperarius to make the point that it is more closely related to Old World Neodon species such as N. irene than it is to any of our common Microtus. Further, if my interpretation of the arvicoline fossil record is correct, Microtus richardsoni cannot be closely related to any Arvicola species, and is rather simply the ecological equivalent of the latter. M. richardsoni characteristically demonstrates seven closed triangles on m1; all Arvicola species have but three; the primitive condition for the entire group.

suggested earlier (Martin, 1974), that the mid-Pleistocene North American radiation of Pitymys-like arvicolines contracted for the sylvan-fossorial habitats, in which case competition would have been minimal. Today we see that the hispidus complex of cotton rats is the austroriparian ecological equivalent of the temperate-boreal Microtus complex, which suggests that there certainly should be competitive interaction in areas of sympatry. However, I am unaware of studies designed to test a hypothesis of this sort.

Morphological features probably cannot explain the explosive radiation of hispidus group species during Rancholabrean time into the habitats where we find them today. Extant members of this group do not average any larger than S. leucotis, and the largest extant species of the genus is the leucotis group species S. peruanus found in South America. S. hispidus and its closest relatives generally possess the most hypsodont teeth and all possess four roots on M_1 , but I do not think that these features are sufficient to account for the demise of S. curtisi and S. libitinus throughout their geographic ranges. It is likely that behavioral traits (including heightened aggression) and limited habitat preference may have been as significant as any morphological parameters. Nevertheless, I have chosen the correlation of M_1 features with ecological success upon which to base my division of extinct and extant cotton rats into three phylogenetic units (Fig. 20). Each unit, or species group, represents a level (grade) of adaptation to a grazing mode of foraging behavior. The conditions of hypsodonty and dental root morphology thus transcend their usage as simple taxonomic tools. They reflect the relative success of any species in balancing its energy budget in a grassland community.

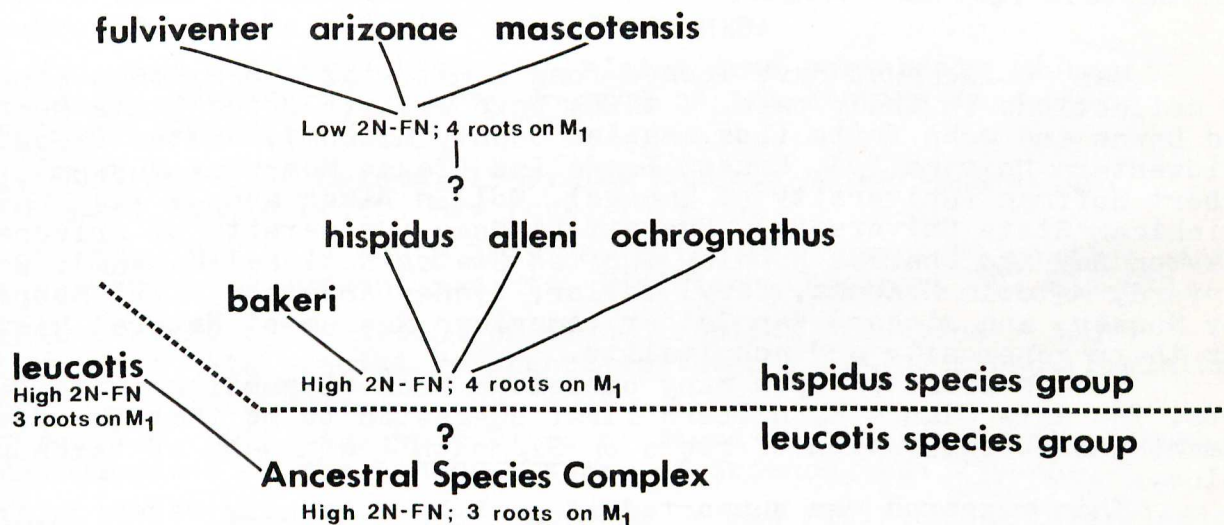


Figure 21 - Possible phylogeny of the hispidus species group. Presumed relationships of extant species follow Zimmerman (1970).

* * *

Conclusions derived from various anatomical, physiological, and ecological studies of living species generally support this theory of relationships. Both Baker (1969) and Dalby and Lillevik (1969) agree that Sigmodon leucotis is not closely related to S. hispidus. Baker (1969, p. 218) independently concluded that "The reduction or absence of the lingual root on the first lower molar is possibly the most distinctive character and sets this species apart..." from other species in the genus. However, in a detailed morphological-karyological study of Sigmodon, Zimmerman (1970) concluded that S. leucotis was more closely related to S. hispidus than it was to S. fulviventer, S. mascotensis, and S. arizonae. The latter three possess a low diploid and low fundamental number of chromosomes, whereas both S. hispidus and S. leucotis possess a high diploid and high fundamental number. The high numbers are considered by karyologists to be primitive. It appears likely that S. hispidus and S. leucotis share a common primitive feature in their karyology, but I doubt that this represents a close phylogenetic relationship. The fossil record seems to indicate otherwise. Tentatively accepting the suggested relationship among extant Sigmodon described by Zimmerman (1970), my views of this pattern, together with data from the fossil record, are depicted in Figs. 20 and 21. Sigmodon leucotis, rather than standing as a member of the hispidus species group, is the informal name bearer of the group which radiated so successfully through the continental United States during the middle Pleistocene, only to be banished to refugia in Mexico and South America during late Pleistocene time. The hispidus species group includes all extant species in Mexico and the United States except S. leucotis: S. hispidus, S. ochrognathus, S. alleni, S. fulviventer, S. mascotensis, S. arizonae, and the extinct S. bakeri. Perhaps subdividing the hispidus species group could be useful, but Elder (1977 and pers. commun.) has recently suggested that S. fulviventer may not be particularly closely related to S. mascotensis and S. arizonae, and I doubt the wisdom of creating any formal taxonomy within these obviously very closely related and recently evolved species.

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