



Variation in the lower dentition of a late Blancan (Late Pliocene) Cotton rat (*Sigmodon curtisi*)

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ABSTRACT

Two late Blancan (late Pliocene) localities from the west coast of Florida, Inglis 1A and Inglis 1C, produced a large number of specimens of the extinct cotton rat *Sigmodon curtisi*. The teeth recovered represent a wide range of wear stages. These large samples provide a rare opportunity to examine variation within the species. No correspondence was found between the wear stage and the number of roots on the lower first molar (m1). Qualitative changes, however, were pronounced. The anterocoid is the last feature on the occlusal surface of the m1 to obtain the mature wear pattern. Subsequently, the lower second and third molars develop an enamel pit from the constriction of the second buccal reentrant angle by the anterior cingulum. With further wear, the lingual reentrant angles become constricted in all lower molars, and eventually are completely worn away.

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INTRODUCTION

Identifying fossil specimens taxonomically relies almost exclusively on morphology. This identification can be especially difficult at the species level, where there may be only slight differences distinguishing unique forms. Therefore, intraspecific variation should be documented in order to understand the limits within and between fossil species. Additionally, understanding life-history changes can facilitate the formation of possible evolutionary scenarios and yield insights into the population dynamics of extinct taxa. Unfortunately, such documentation of intraspecific variation has

not, or cannot, be done with most extinct species. In many fossil mammals, the diagnostic characters are confined to the dentition; among fossil cotton rats (*Sigmodon*) species-level diagnoses have been further restricted to characters from the lower molars. This paper focuses on the ontogenetic variation in occlusal and root morphology of the lower dentition of two samples of the late Pliocene (Blancan) *Sigmodon curtisi*. Ontogeny as used here extends beyond embryonic development and includes all changes during the life of an individual (*sensu* Hale and Margham 1991). Although other definitions of ontogeny do not include the time

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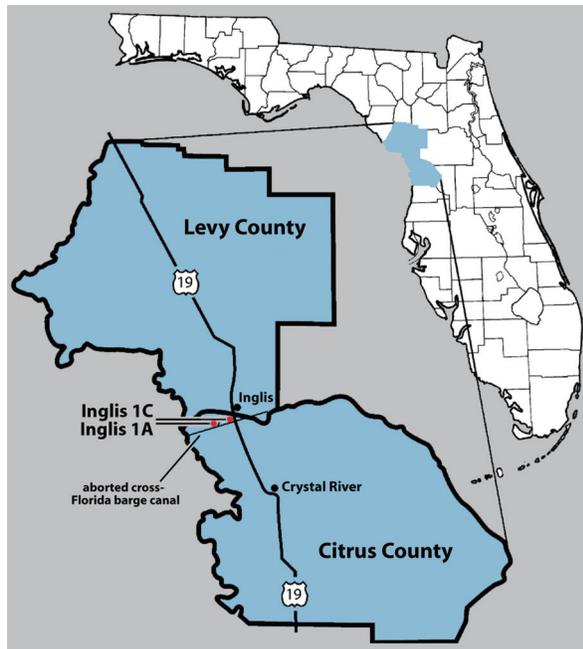


FIGURE 1. Location of Inglis 1A and Inglis 1C.

beyond sexual maturity, it is not known when the extinct *S. curtisi* became mature.

Sigmodon curtisi is an early species of cotton rat that occurs in late Pliocene and early Pleistocene localities in Arizona (Harrison 1978; Johnson et al. 1975; Lindsay and Tessman 1974); Colorado (Hager 1975); Florida (Morgan and Hulbert 1995; Ruez 2001); Kansas (Izett and Honey 1995; Martin et al. 2003; Peláez-Campomanes and Martin 2005); and Sonora, Mexico (Lindsay 1984). However, *S. curtisi* is abundant only at two of the Florida localities, Inglis 1A and Inglis 1C. The most similar species morphologically are the modern *Sigmodon leucotis*, and the extinct *S. hudsphethensis* and *S. lindsayi* from the late Pliocene of Texas (Strain 1966; Akersten 1970; Martin and Prince 1989).

Inglis 1A and Inglis 1C (29° 00' 43" N, 82° 40' 05" W; Citrus County, Florida; Figure 1) are sand-filled sinkhole deposits in the Eocene Ocala Limestone that were intersected during the now-aborted attempt to cut a canal across peninsular Florida (Ruez 2001). Although each of these deposits originally was assigned to the Irvingtonian land mammal age (Morgan and Hulbert 1995; Ruez 2001), a subsequent revision of land mammal age boundaries in North America (Bell et al. 2004) places Inglis 1A and Inglis 1C within the Blancan. In terms of absolute age, both localities were suggested as being deposited between 2.01 and 1.78 Ma, with Inglis 1C being younger by an unknown amount

(Ruez 2001). These localities are important to the fossil history of Florida because they are the only Blancan localities from the state with diverse and abundant microfaunas; the temporally closest locality comparable in diversity and abundance is the late Irvingtonian Coleman 2A from about 400 ka years ago (Martin 1974; Ruez 2001). Detailed locality data for Inglis 1A and Inglis 1C, including the geology (Emslie 1998; Ruez 2002), excavation history (Emslie 1998; Klein 1971; Ruez 2001), and the mammalian fauna (Morgan and Hulbert 1995; Ruez 2001) are discussed elsewhere.

The more taxonomically diverse of the two localities, Inglis 1A, contains at least 51 species of mammals, including at least 12 rodents (Ruez 2001). Only a portion of the mammalian fossils from this site have been described (e.g., Frazier 1981; Klein 1971; Morgan 1991; White 1991; Wilkins 1984), along with the birds (Carr 1981; Emslie 1996; Steadman 1980) and squamates (Meylan 1982).

Inglis 1C contains 33 species of mammals, including 11 species of rodents (Ruez 2001). Emslie (1998) and Emslie and Czaplewski (1999) evaluated the avian fauna, but the abundant herpetological specimens remain undescribed. The Inglis 1C deposit was shown to be attritional in nature, with the small-mammalian fossils accumulated as the result of predation and fluvial transport (Ruez 2002).

MATERIALS AND METHODS

All fossils examined from Inglis 1A and Inglis 1C are curated in the Division of Vertebrate Paleontology of the Florida Museum of Natural History (UF). Specimens of *Sigmodon hudsphethensis* are from the Madden Arroyo and Red Light faunas of Texas and are housed at the Vertebrate Paleontology Laboratory of the Texas Natural Science Center (TMM). Because the diagnostic characters of fossil *Sigmodon* are primarily on the lower first molar (m1), only isolated m1s and mandibles containing the m1 were included in this study (Appendix 1). Dental terminology follows Martin and Prince (1989).

Measurements of teeth were made through a Wilde monocular microscope with an optical micrometer (Figure 2); all measurements are in millimeters. Because fossil specimens are often fragmentary and may include juveniles that do not have fully formed molar crowns, length and width of the teeth were measured at the occlusal surface. Abbreviations: m1, first lower molar; m2, second lower molar; m3, third lower molar.

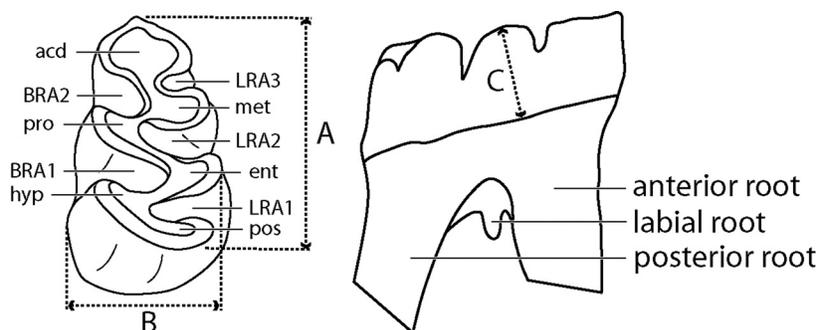


FIGURE 2. Dental terminology and methodology for measuring *Sigmodon* m1. Length (A) and width (B) were measured on the occlusal surface. The enamel height (C) was measured on the lingual side of the tooth from the tip of the metaconid to the lower extent of the enamel, perpendicular to the straight portion of the linea sinuosa below the anteroconid, metaconid, and entoconid. Abbreviations: acd, anteroconid; BRA 1 and BRA2, first and second buccal reentrant angles; LRA1, LRA2, and LRA3, first, second, and third lingual reentrant angles; ent, entoconid; hyp, hypoconid; met, metaconid; pos, posterolophid; pro, protoconid (following Martin and Prince 1979).

RESULTS

Qualitative Variation

Variation in the occlusal pattern of the lower dentition of *Sigmodon curtisi* was examined and a sequence of change noted (Table 1). One specimen (UF 196273) shows little wear on the occlusal surface, and no roots had yet developed on this isolated right m1 (Figure 3.1). Isolated fields of dentine are exposed in the anteroconid and the major folds. Specimens with slight wear, but not yet exhibiting the mature wear pattern, are here called juveniles. However, the correlation between dental pattern and sexual maturity is unknown in *S. curtisi*, so the terms juvenile and mature are used here only for convenience. The mature pattern is considered present once dentine is visible in the connections between the anteroconid, metaconid, protoconid, entoconid, hypoconid, and posterolophid, and the anteroconid is symmetrical.

Qualitative variation in the occlusal pattern through ontogeny is the same for the populations from both Inglis 1A and Inglis 1C, with the exceptions specified below. Few individuals in either population exhibit a juvenile pattern, possibly due, at least in part, to the brachydont nature of the teeth that show change in occlusal morphology with relatively little wear and destruction during predation. The symmetrical shape of the anteroconid is the last feature on the m1 to attain the mature wear pattern. After the mature pattern of the m1 is reached, both the associated m2 and m3 develop an enamel pit from the constriction of the second buccal reentrant angle (BRA2; protoflexid of Peláez-Compomanes and Martin 2005) anterolabially by the anterior cingulum (Figure 3.2). The anterior cingulum is low on the tooth and therefore does not close off the BRA2 in ontogenetically-younger individuals. Among the Inglis 1C specimens, each instance of an m3 with a BRA2 pit occurs with an

TABLE 1. Description of age cohorts from Inglis 1A and Inglis 1C. Cohorts are separated qualitatively. Height is the height of the enamel from the linea sinuosa to the metaconid; the average is given, with the range following parenthetically. Abbreviations: N, number of specimens; BRA, buccal reentrant angle; LRA, lingual reentrant angle; acd, anteroconid complex; met, metaconid.

Cohort	Qualitative description	Inglis 1A		Inglis 1C	
		N	Height	N	Height
I	Completely unworn	0	-	1	1.29
II	Barely any wear visible; juvenile wear pattern	4	1.10 (1.08-1.14)	2	1.09 (1.08-1.09)
III	Mature wear pattern, except on acd; m2-3 BRA2 pits not yet at occlusal surface	15	0.97 (0.79-1.01)	5	0.98 (0.94-1.00)
IV	Mature wear pattern; m2-3 BRA2 pits at occlusal surface	10	0.95 (0.80-0.98)	21	0.84 (0.79-0.91)
V	Constricted opening of LRA1 and LRA3; acd-met dentine tract expanded	5	0.77 (0.65-0.90)	7	0.70 (0.63-0.74)
VI	LRA1 and LRA3 completely eroded away	0	-	3	0.56 (0.54-0.58)

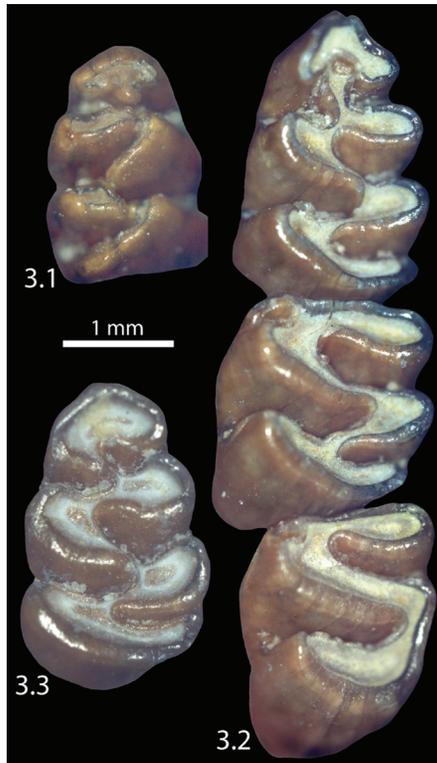


FIGURE 3. *Sigmodon curtisi* from Inglis 1C. 3.1, UF 196273, right m1; 3.2, UF 195133, left m1-3 in mandible; 3.3, UF 196268, left m1.



FIGURE 4. *Sigmodon curtisi* from Inglis 1C. 4.1, UF 195799, right m1-3 in mandible; 4.2, UF 191886, UF 191886, right m1-3 in mandible.

m2 having the same feature. This consistency is not seen in the Inglis 1A collection. In one specimen (UF 22068), the BRA2 is closed in the m3 to form an enamel pit, but the m2 is not sufficiently worn to show the same constriction of this reentrant. In another specimen (UF 22043), the m3 has a BRA2 enamel pit, but the feature is worn away in the m2 such that the anteroconid and protoconid are confluent via a wide band of dentine. In summary, although the formation and disappearance of the enamel pits from the constriction of the BRA2 of both the m2 and m3 is roughly synchronous, there is at least some slight variation in the occurrence of this feature.

With progressive wear all BRA2 enamel pits on the m2 and m3 are worn away, and the lingual openings in all lower molars become tightly constricted (Figures 3.2, 4.1). This constriction is least developed in the second lingual reentrant angle (LRA) of the m1 (because this feature is deeper than other lingual reentrant angles) and the buccal reentrant angles of the m1 (because of asymmetrical wear of the teeth). In the most advanced wear stage observed in *S. curtisi*, the lingual reentrant angles are closed, or nearly so (Figure 4.2); these

individuals still retain the buccal reentrant angles on the m1 and the first buccal reentrant angle on the m2 and m3. The connection between the anteroconid and metaconid is along the labial edge of the tooth. Enamel pits from the constriction of the BRA2 never developed on the m1.

Quantitative Variation

The age cohorts of individuals of *S. curtisi* from Inglis 1A and Inglis 1C correlate closely with the height of the m1 (as measured from the linea sinuosa to the metaconid; Table 1), which is reduced as a result of increased wear in ontogenetically older individuals. Two exceptions are specimens from Inglis 1A: UF 22024 does not yet have the BRA2s constricted into enamel pits (cohort III in Table 1) and has a shorter than expected height of 0.79 mm; and UF 22044 has a taller than expected height of 0.90 mm for an individual with the BRA2 enamel pits already eroded away (cohort V in Table 1).

Plotting the length and width of the m1 against the height of the tooth shows how little these dimensions change with increasing wear (= age) in either sample of *Sigmodon curtisi* (Figure 5). The

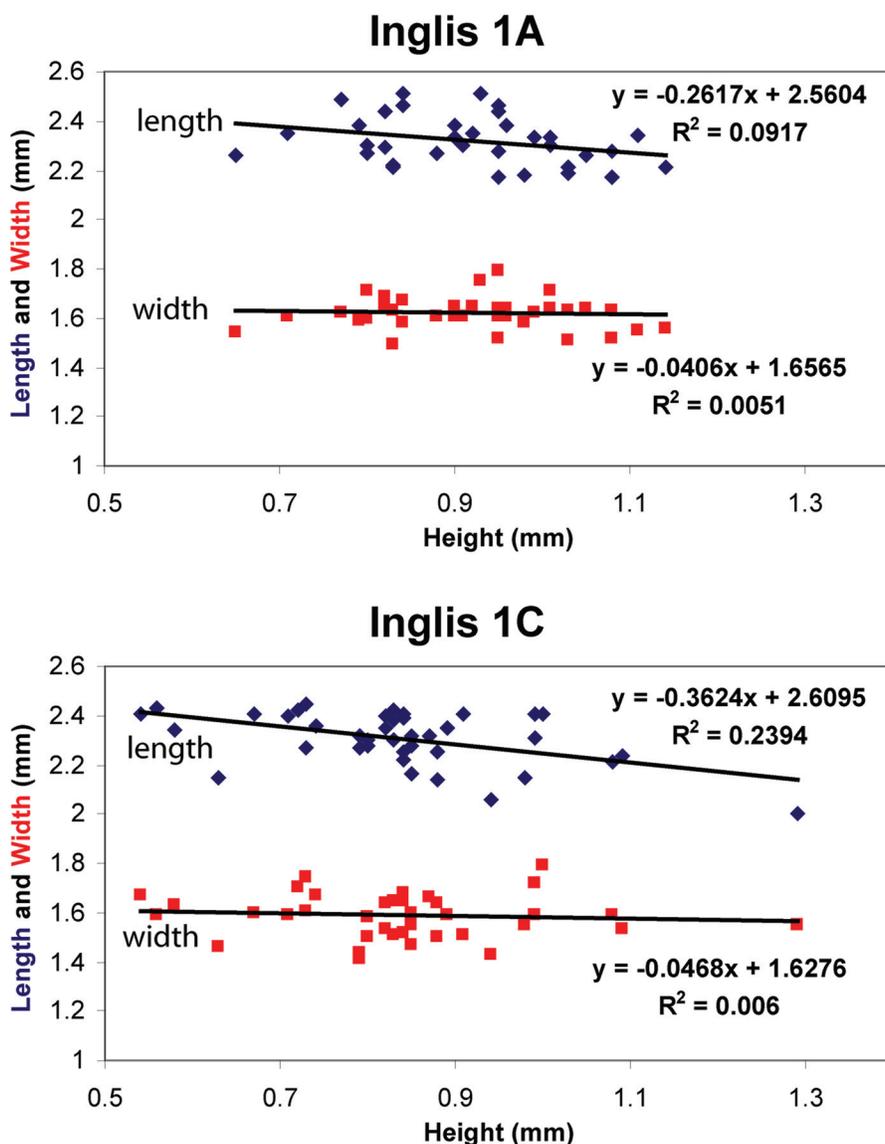


FIGURE 5. Bivariate plot of length and width against height of m1. Lengths are marked as diamonds; squares are widths.

stronger correlation between height and length occurs in the Inglis 1C sample; however, the amount of variation it explains (0.27 mm) is only 12% of the average length (2.31 mm). There is even less correlation between crown height and occlusal width.

The number of roots on the m1 was shown previously to vary within samples of fossil cotton rats, and this variation has been used, in part, for species and species-group identifications (Martin 1979). Previous examination of *S. curtisi* from Inglis 1A documented three roots in 14 of 16 m1s, with the remaining two m1s having four roots (Martin 1979). My study includes specimens not then

known to Martin, plus the larger sample from Inglis 1C. Table 2 shows a higher occurrence of four-rooted m1s in *S. curtisi* than previously recorded; more notable is the rare occurrence (not previously noted in published literature) of specimens with only two roots in both the Inglis 1A and Inglis 1C samples.

I compared the abundance of roots to measurements of the m1. Within each of the Inglis 1A and Inglis 1C samples, there was no significant difference in the length, width, or height when specimens were pooled according to their number of roots (Table 2).

TABLE 2. Comparison of number of roots against height, length, and width. Some specimens are fragmentary, and the number of roots could not be determined for them. This distribution of roots differs slightly from, and supersedes, previous reports on these localities (Martin 1979; Ruez 2001).

Roots	Inglis 1A				Inglis 1C			
	N	length	width	height	N	length	width	height
2	1 (4%)	2.19	1.51	1.03	1 (3%)	2.39	1.68	0.84
3	22 (79%)	2.30	1.62	0.93	21 (68%)	2.31	1.60	0.83
4	5 (18%)	2.34	1.62	0.91	9 (29%)	2.32	1.59	0.83

DISCUSSION

The intraspecific variation documented here for *Sigmodon curtisi* supports the use of some of the criteria commonly used in the identification of extinct cotton rats, but also points out some of the limitations. Hopefully this work will be augmented by similar descriptions of variation through ontogeny in other species of *Sigmodon* in order to better understand these limitations.

The length and width of the occlusal surface of the m1 in *S. curtisi* change little through ontogeny. Therefore dimensions of the tooth are useful in delimiting the species of cotton rats, even in the absence of knowing the age of the individual. All other species of cotton rat, except *S. minor* and *hudspethensis*, are relatively more hypsodont, and would therefore show even less change in occlusal dimensions through ontogeny. Although there is significant overlap in the size of most species of *Sigmodon*, the addition of crown height helps separate the species.

Potential Confusion to Similar Species

Qualitative variation is here examined in light of the occlusal morphology of the other species of *Sigmodon* most similar to *S. curtisi*. This is not meant to be an exhaustive review of the morphology of those other species. Instead, the intent is to illustrate the potential problems with taxonomic identification based on some previously published characters, especially with regard to particular wear stages of *S. curtisi*.

The occlusal pattern of m1 in *S. curtisi* is similar overall to that of the modern *Sigmodon leucotis*, but the former is distinguished by the presence of a deep LRA1 on the m2 and a shallow LRA1 on the m3 (Martin 1979). Although these folds are lacking in *S. leucotis*, as described above, the diagnostic LRA1s will disappear from both the m2 and m3 in *S. curtisi* in advanced stages of wear, resulting in a pattern identical to *S. leucotis*. The m1 of *S. leucotis* is longer and wider than the same tooth in *S. curtisi*, however, the lengths and widths of the m2s

and m3s of the two species are nearly identical (Martin 1979, table 1). Isolated m2s and m3s of *S. curtisi* in advanced wear stages may be confused with teeth of *S. leucotis* in occlusal morphology and size. Crown height is required to identify such specimens; *S. leucotis* is more hypsodont.

Sigmodon hudspethensis is an extinct form known from two Pliocene-age localities in west Texas (Akersten 1970). The species is also morphologically similar to the geologically younger *S. curtisi* in the brachydont nature of the molars and the shared occurrence of LRA1s on the m2 and m3 (Martin 1979; Ruez 2001). The only distinguishing occlusal feature is the wider reentrants in *S. hudspethensis*. In *S. curtisi* reentrants narrow with advancing ontogenetic age. Most of the few specimens referable to *S. hudspethensis* show advanced wear, yet retain the wide reentrants. These two taxa seem to be distinct when examining older wear stages, but ontogenetically young specimens of *S. hudspethensis* and *S. curtisi* might not confidently be distinguished. It should be noted that this author is aware of only six m1s of *S. hudspethensis*. Therefore, the recovery of new material and documentation of the variation in the species is necessary to better elucidate the relationship between the taxon and *S. curtisi*.

A third morphologically similar species of cotton rat, *S. lindsayi*, occurs in the Palm Springs Formation of Anza-Borrego Desert State Park in California (Martin and Prince 1989). Martin referred specimens from this area both to *S. curtisi* (1979:14, 16) and *Sigmodon cf. S. curtisi* (1979:23-24). However, when Martin and Prince (1989) named *S. lindsayi*, they did not include any of the specimens cited in the 1979 study, did not mention whether or not they considered *S. curtisi* or *Sigmodon cf. S. curtisi* to be present in the Palm Springs Formation, and did not make any comparisons of the holotype of *S. lindsayi* (an m1) to *S. curtisi*. (See Murray [2008] for an extensive description of the taxonomic history of these specimens.) This ambiguity is especially problematic because the published description of *S. lindsayi* is

very similar to that of *S. curtisi*. One striking difference is in a few m1s of *S. lindsayi* that exhibit slight wear: two have an enamel atoll in the anteroconid, and one has an anteroconid separated completely from the metaconid. These unique specimens suggest either extreme variation in the m1 of *S. lindsayi* during early ontogeny or the presence of multiple species within the sample identified as *S. lindsayi* (Martin and Prince 1989). Molars of *S. lindsayi* are on average larger and more hypsodont than those of *S. curtisi*, but there is extensive overlap in molar size between these two species (Martin 1979; Martin and Prince 1989). In the absence of the anomalous slightly worn m1s mentioned above, it is difficult to distinguish small individuals of *S. lindsayi* from large individuals of *S. curtisi* (which explains the above-mentioned allocation of the Palm Springs Formation specimens to *S. curtisi*). Detailed description of the ontogenetic variation in the occlusal morphology of molars of *S. lindsayi* may provide possible characters that can differentiate individuals of these species that overlap in size.

The number of roots on m1s of *Sigmodon curtisi* from Inglis 1A and Inglis 1C did not vary with either ontogenetic age or body size. This invariance suggests that the use of the number of roots on the m1 may be a reliable character upon which to identify species of cotton rats and establish phylogenetic scenarios by grouping species as done previously (Martin 1979). Similar study of other large samples of cotton rats known to vary in root-count is needed to make more definite statements about this character.

The presence of two-rooted m1s of *Sigmodon curtisi* is not entirely unexpected; *S. minor* overlaps in geological distribution with *S. curtisi* and typically has two-rooted m1s, which could indicate that the origin of *S. curtisi* is earlier than previously suggested based on currently known stratigraphic placement (Martin 1979; Peláez-Campomanes and Martin 2005). Additionally, the higher occurrence of four-rooted m1s in *S. curtisi* than previously documented makes the tentatively proposed evolutionary transition into *Sigmodon libitinus* (Martin 1979) less likely.

CONCLUSIONS

The intraspecific variation documented here for *Sigmodon curtisi* has important implications for the taxonomic identification of fossil cotton rats. Multiple characters previously considered diagnostic are here shown to vary during the age of the individual. None of the observations presented

here call into question the validity of any species of *Sigmodon*, but do suggest a couple categories of individuals that may be difficult to identify taxonomically to species based on published descriptions:

- mature individuals of *S. curtisi* and small individuals of *S. leucotis*,
- young individuals of
- *S. curtisi* and young individuals of *S. hudsphethensis*, and
- mature individuals of
- *S. curtisi* and mature individuals of *S. lindsayi*.

Hopefully this study soon will be supplemented by similar work documenting the ontogenetic variation in other fossil cotton rats. Such studies could provide details to reject my concerns, or could help establish limits to our ability to identify species of various dental wear stages.

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APPENDIX

SPECIMENS EXAMINED

Sigmodon curtisi

- Inglis 1A, Citrus County, Florida: UF
15155, 16195, 22020, 22023, 22024,
22031, 22034, 22038, 22039, 22041,
22042, 22043, 22044, 22045, 22046,
22047, 22050, 22066, 22067, 22068,
22069, 22070, 22071, 198775, 198776,
198777, 198778, 198779, 198780,
198781, 198782, 198783, 198784,
198785, 198786, 198787.
- Inglis 1C, Citrus County, Florida: UF
186071, 186072, 186073, 186074,
191886, 195133, 195134, 195137,
195138, 195799, 195800, 195805,

195806, 195810, 195811, 196260, 196261,
196262, 196264, 196265, 196266,
196268, 196269, 196270, 196271,
196273, 196274, 196275, 196276,
196277, 196712, 196713, 196716,
197876, 197878, 197880, 197881,
198463, 198467.

Sigmodon hudspethensis

- Madden Arroyo, Hudspeth County, Texas:
TMM 40240-2, 40240-40, 40240-43,
40240-44.
- Red Light, Hudspeth County, Texas: TMM
40857-10, 40857-11.